Evolutionary and ontogenetic patterns of diet and support for tropical niche conservatism in the origins of the latitudinal diversity gradient in clupeiforms (anchovies, herrings, and relatives)

A DISSERTATION
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

Joshua Patrick Egan

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Andrew M. Simons

August 2019

Acknowledgements

This research was made possible by a huge amount of help and support from my advisor, Andrew Simons. I also received invaluable assistance from my committee Sharon Jansa, Keith Barker, and David Fox. I am very grateful for my fabulous partner, Kaila Akina, who supported me during my time as a student. Thanks to the friends who assisted with my dissertation research and I thank the following people in particular: Peter Hundt, Uik-Sen Chew, Chien-Hsien Kuo, Nong Kaeoprakan, Michael Bradley, Christina Buelow, Michael Hammer, Prasert Tongnunui, Marcus Sheaves, the 2013 Summer Institute in Taiwan staff, Gao Zheng Aquaculture, and the students at National Chiayi University (Taiwan), James Cook University (Australia), Rajamangala Institute of Technology (Thailand), and University of Southern Alabama (USA) who helped with fieldwork. Thanks to A. Buchheister for providing advice on statistical analysis of diet data. I thank the following people and institutions for tissue samples: Dr. Melanie Stiassny and Dr. Barbara Brown (American Museum of Natural History), Victoria Magath (University of Hamburg Zoological Museum), Dr. Kwang-Tsao Shao (Academia Sinica Biodiversity Research Museum), Dr. Larry Page (Florida Museum of Natural History), and Mark Adams (South Australian Museum). This work was funded in part by the Lerner-Gray Memorial Fund for Marine Research (American Museum of Natural History), Dayton Research Fund (Bell Museum of Natural History, University of Minnesota), the Minnesota Agricultural Experiment Station, and the East Asia and Pacific Summer Institutes Program from the National Science Council of Taiwan and the National Science Foundation, U.S.A. (1316912). During my doctoral research I received financial support from a National Science Foundation Graduate Research Fellowship (00039202).

DEDICATION

This dissertation is dedicated to my family.

Abstract

The increase in species richness from the poles to the equator is one of the most pervasive and enigmatic spatial patterns of biodiversity. This latitudinal diversity gradient has been intensively studied since it was first described in 1807 and yet there is still no accepted explanation for its existence. My dissertation tested hypotheses about the origins of the latitudinal diversity gradient in the ecologically and economically important clupeiform fishes (anchovies, sardines, and relatives) with a focus on the hypothesized role of niche breadth evolution in the formation of the diversity gradient. My first chapter described the diets of near-shore, marine clupeiforms from Taiwan and compared their diets to co-occurring fish species. My second dissertation chapter identified increasing ranges of prey-size consumption through ontogeny in twelve species of Indo-Pacific clupeiforms. For my third dissertation chapter, I inferred a time-calibrated clupeiform phylogeny and patterns of diet evolution, which revealed a latitudinal herbivory gradient in clupeiforms. My fourth dissertation chapter found support for climate niche conservatism in the origins of the latitudinal diversity gradient in clupeiforms using diet data from chapter one, two, and three and the phylogeny from chapter three. My dissertation research contributes to the development of biological theory and efforts to sustainably manage fisheries.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Diets and trophic guilds of small fishes from coastal marine habitats in western Taiwan

1. Introduction

Food web structure in shallow, coastal, marine ecosystems is variable over space and time (Deegan and Garritt 1997; Wilson and Sheaves 2001; Vander Zanden and Fetzer 2007; Bergamino et al. 2011). In these ecosystems, assemblages of small-sized fishes comprise a significant proportion of consumer biomass. Small-sized fishes play diverse roles in food webs, consuming a variety of prey types ranging from detritus to fishes and transferring energy and nutrients within and between food webs (Hajisamae et al. 2003; Baker and Sheaves 2005; Inoue et al. 2005; Nelson et al. 2013). The diets of many small, coastal fishes are poorly studied, especially in tropical and subtropical environments. This limits the resolution and accuracy of food web models and antagonizes attempts to describe and understand spatial and temporal variation in food web structure (Kitching 1987; Winemiller 1990; Montoya and Solé 2003).

Trophic guilds are groups of species eating similar prey (Root 1967; Simberloff and Dayan 1991; Garrison and Link 2000). Assigning fishes to trophic guilds facilitates comparisons of food web structure by synthesizing and reducing the complexity of diet data (Simberloff and Dayan 1991; Garrison and Link 2000; Elliot et al. 2007; Simon et al. 2013). Preliminary research shows that tropical and subtropical fish assemblages in shallow, marine environments typically contain five to eight of the following trophic guilds when analyses are based upon prey types consumed: herbivores, omnivores, insectivores, piscivores, detritivores, crustacivores (sometimes multiple guilds), annelidivores, and molluskivores (Hajisamae et al. 2003; Nakamura et al. 2003; Kanou et al. 2004; Inoue et al. 2005; Elliot et al. 2007; Nanjo et al. 2008; Nakane et al. 2011; Zagars et al. 2013). Certain guilds such as crustacivores and zooplanktivores are reported by nearly every study, but other guilds such as herbivores and molluscivores appear to be less common. Additional diet studies representing the diversity of habitat types are required to understand drivers of trophic guild representation in coastal ecosystems.

Measuring fish prey size consumption, and how it changes through ontogeny, can provide insight into fish biology, coastal fish community composition, and food web structure that is not gained by only quantifying the types of prey consumed. Biologically meaningful differences in prey size consumption can occur between fishes consuming the same prey types. Datasets that also describe prey size consumption may better identify potential interspecific competition or explain species coexistence and allow predictions of changes in fish populations in response to fluctuations in prey populations (Werner 1977; Paszkowski et al. 1989; Shannon et al. 2004). A coarse understanding of prey size consumption can be gleaned by identifying prey types. For example, zooplankton prey are likely smaller than fish prey. However, because much variation in prey size exists within prey categories, information is lost when prey are not directly measured.

Furthermore, prey size data are needed for the development of models that predict fish prey sizes using fish predator size data, which is useful when modeling food webs and making management decisions when diet data are unavailable (Scharf et al. 2000; Gravel et al. 2013).

The objectives of this study were to: (1) quantify the diets of small, near-shore, marine fishes from four localities along the Western coast of Taiwan (Republic of China), (2) identify trophic guilds in these assemblages, (3) describe ontogenetic shifts in maximum prey size consumption, and (4) determine if fish standard length (SL) predicts maximum prey size consumption at the assemblage level. This study described the diets of 54 fish species and is the first assemblage-level diet study of near-shore fishes in Taiwan. This research provides insight into coastal, marine food web structure and data useful for ecosystem-based fisheries management and comparative evolutionary and ecological research.

2. Materials and methods

2.1 *Fish collecting and identification*

Small fishes (small species and small individuals from larger growing species) were collected from two sandy beaches and two muddy, mangrove-lined estuaries at depths less than 1.5 m in Western Taiwan during the rainy season in 2013 and 2014 (Figure. 1.1): (1) subtropical Chonggang Estuary, Houlong Township, Miaoli County (24.622886

N, 120.754339 E), (2) tropical Haomei Beach, Budai Township, Chiayi County (23.363514 N, 120.129653 E), (3) tropical Haomei Estuary, Budai Township, Chiayi County (23.360451 N, 120.130372 E), and (4) tropical Shuang Chun Beach, Beimen District, Tainan City (23.305965 N, 120.108181 E). A beach seine (8·7 m x 1·9 m x 0·5 cm mesh) was used to capture fish. This study did not quantify prey availability in the environment. After capture, fish were euthanized with tricaine methanesulfonate then placed on ice to prevent degradation of specimens during transport. Whole specimens were fixed in a 10% formaldehyde solution, transferred to 70% ethanol for long-term storage, and deposited in the fish collection at the University of Minnesota James Ford Bell Museum of Natural History (JFBM), Minnesota, U.S.A. Museum catalog numbers associated with specimens are in Table 1.1. Fishes were identified with the help of dichotomous keys (Carpenter and Niem 1999; Chakrabarty et al. 2010).

2.2 Diet quantification

The SL of each specimen was measured using digital calipers following Hubbs and Lagler (1941), except for Hemiramphidae species, for which SL was measured to the tip of the upper jaw (Shakman and Kinzelbach 2006). Digestive tract contents were then dissected onto microscope slides, taking care to avoid contaminating samples with fragments of fish tissue, which can be confused with detritus. Fishes digest different prey types at different rates, which can bias diet quantification if digestive tract contents are heavily digested (Gannon 1976). Therefore, only relatively undigested prey in the anterior portion of the digestive tract were examined (Hundt et al. 2014; Costalago et al.

2015). Prey were identified to the lowest practical taxonomic level using dissecting and binocular microscopes. Rocks and sand were not counted as prey items. The largest representative of every prey type from each fish was photographed with a microscope-mounted Spot Insight™ digital camera (Model 14.2 Color Mosaic; www.spotimaging.com) and its maximum width measured using ImageJ software (Schneider et al. 2012; imagej.nih.gov/ij/). An index of gut fullness was not quantified because this measurement is time-consuming, difficult to estimate accurately for small specimens, and there is no consensus that these indices are important for simple descriptions of fish diets (Hyslop 1980). The diet of each species was expressed as frequency of occurrence, which is calculated by dividing the number of fish a particular type of prey was positively identified in by the total number of fish (for the species in question) with prey in their digestive tracts (Baker et al. 2014). Alternative diet quantification approaches exist. Because this study examined the diets of many individuals, the frequency of occurrence method was selected. This method has been demonstrated to be faster than many approaches while still yielding comparable results (Baker et al. 2014). Only fish species represented by at least five individuals were included in statistical analyses unless noted otherwise, following Nakamura et al. (2003). Three barracuda species *Sphyraena* spp. were combined into a single group for analysis because sample sizes were small and all individuals ate the same prey. Sixteen prey categories were used for trophic guild analyses (Table 1.4). Prey categories were not strictly taxonomic and included prey that were morphologically or functionally similar (e.g. Collembola is placed in the Crustacea prey category because of some similarities aquatic members of this taxon share with other members of the Crustacea prey category).

An unpaired t-test was used to test for differences in mean fish SL between beach and estuary habitats. A P-value of < 0·05 was the threshold for statistical significance for all comparisons unless noted otherwise and all statistical analyses were implemented in program R v. 3.3.1 (R Development Core Team 2016).

2.3 Trophic guild analyses

Many fishes undergo ontogenetic diet shifts. In these cases it is appropriate to separate species into length groups prior to trophic guild analyses (Scharf et al. 2000; Specziár and Rezsu 2009). Consequently, all species with sample sizes of at least 10 individuals were tested for ontogenetic shifts in prey types consumed. Data from all sites were pooled and species were divided into 5 mm SL bins. When necessary, adjacent bins were collapsed until each bin contained at least five individuals. The dissimilarity in prey type consumption between SL groups was estimated using Czekanowski Dissimilarity index matrices (Czekanowski 1909) using the program R “vegan” package (Oksanen et al. 2016). Plant material and detritus were not included in analysis if there was strong evidence that they were incidentally ingested (Table 1.3).

Two approaches were used to determine if diet differences between SL groups were statistically significant. First, a bootstrap randomization approach was employed. Resampling with replacement for 1,000 iterations was conducted according to the “RA4” algorithm (Lawlor 1980). This method is commonly used in diet studies (Jaksić and Medel 1990; Specziár and Rezsu 2009; Buchheister and Latour 2015). Additionally, the

Similarity Profile (Simprof) permutation method was implemented (Clarke et al. 2008). One thousand permutations were specified and a P-value of < 0·01 was used to determine statistical significance following Clarke et al. (2008). The Simprof analyses used the Simprof function in the program R "clustsig" package (Whitaker and Christman 2015). After testing for ontogenetic diet shifts and dividing species into multiple groups for analysis if needed, trophic guilds were identified via hierarchical agglomerative clustering using Czekanowski Dissimilarities with group-average linkage with data from all localities pooled. Clusters were considered to be trophic guilds if bootstrapping and Simprof analyses (following conditions described above) identified them as significantly dissimilar from other clusters.

2.4 *Prey size consumption*

Patterns of maximum prey width consumption were examined by pooling prey width data from all sites. It was not feasible to measure detrital particle widths directly. These were assigned a width of one *u*m based upon observations of detritus from several specimens with a binocular microscope. Simple linear regression was used to test for correlation between maximum prey width and SL for individual species and at the assemblage level. For the assemblage level analysis all diet data were included, even for species excluded from other analyses because fewer than five individuals were sampled.

3. Results

3.1 Fish collecting and identification

Fifty-four fish species were collected from the four sampling sites (Table 1.4). Fifty-two species occurred in estuaries and 18 along sandy beaches. Eighteen species were collected at multiple sites and 16 in both estuary and sandy beach habitats. Two to three species, all collected in Haomei Estuary (Figure. 1.1), have not been previously reported to occur Taiwan: barcheek amoya *Acentrogobius moloanus* (Herre 1927), goby *Aulopareia unicolor* (Valenciennes 1837), and possibly bluemarked drombus *Drombus ocyurus*, for which identification is preliminary. Fishes ranged in size from 11·74 - 97·11 (mean: 36·75) and 14·70 - 151·2 (mean: 35·80) mm SL in beach and estuary habitats, respectively. Mean fish SL was not significantly different between beach and estuary habitats (unpaired *t*-test, $t = 0·50$, d.f. = 169, $P > 0·05$).

3.*2 Diet quantification*

Of the fishes examined, 599 contained identifiable prey, 468 from estuaries and 131 from sandy beaches. Prey that occurred in the greatest number of individuals were copepods, eggs, detritus, pennate diatoms, Cirripedia cypris, and algae. Zooplankton was the most frequently occurring prey category in 20 of the 31 species subjected to cluster analysis (Figure. 1.2). Eggs were found in 25 of 31 species, but they were never the most common prey item. Fish were found in five of 31 species and were the most frequently occurring prey in *Sphyraena* spp. Detritus was the most commonly occurring prey in largescale mullet *Chelon macrolepis* (Smith 1846), longarm mullet *Moolgarda cunnesius*

(Valenciennes 1836), and Istern Pacific gizzard shad *Nematalosa come* (Richardson 1846). Detritus and phytoplankton were found in 25 and 22 of 31 species, respectively, but in most cases they occurred in small quantities and were likely incidentally ingested.

3.3 Trophic guilds

No ontogenetic shifts in prey type consumption were discovered. The Simprof analysis identified six statistically significant clusters corresponding to the following trophic guilds: (1) piscivores, (2) crustacivores, (3) detritivores, (4) omnivores, (5) zooplanktivores, and (6) terrestrial invertivores (Figure. 1.2 and Table 1.5). All trophic guilds occurred in estuaries. The piscivore, terrestrial invertivore, and omnivore guilds did not occur along sandy beaches. Bootstrap resampling identified a critical dissimilarity value of 0·67 as the threshold for statistical significance. This yielded three statistically significant clusters corresponding to the piscivore and crustacivore trophic guilds and a combined cluster of the detritivore, omnivore, zooplanktivore, and terrestrial invertivore guilds (Figure. 1.2).

3.4 Prey size consumption

Eight species of fish exhibited statistically significant ontogenetic shifts in maximum prey width consumption. Maximum prey width and SL were positively correlated in seven species and negatively correlated in the detritivorous *C. macrolepis* (Table 1.6, Figure 1.3a). A statistically significant positive correlation was found between SL and maximum prey width at the assemblage level. This relationship is stronger with detritivores excluded from the analysis (Table 1.6 and Figure 1.3b).

4. Discussion

Diet studies of fishes are needed to improve my understanding of coastal marine food webs. This study describes the diets, trophic guilds, and size relationships between fish predators and their prey in near-shore, marine and estuarine habitats in Western Taiwan. Copepods were identified as key prey in the investigated fish communities. The trophic guild scheme proposed by this study is largely consistent with similar fish assemblages. Eight species of fishes were found to exhibit ontogenetic shifts in maximum prey width consumption and fish SL was predictive of maximum prey width consumption in this assemblage. This study provides information that can inform comparative evolutionary and ecological research and ecosystem-based fisheries management in coastal tropical and subtropical ecosystems.

4.1 Fish diets

The first objective of this study was to describe the diets of small, near-shore, marine and estuarine fishes in Taiwan. The diets of 54 species were described, including three species for which no diet data were previously available and 52 species that have never been subjected to gut content analysis in Taiwan (Lin et al. 2007; Table 1.7). The diets described herein are largely congruent with previous research (Table 1.7); however, consumption of terrestrial insects by the Sumatran silverside *Hypoatherina valenciennei* (Bleeker 1854) has not been previously reported and scale eating by doublespotted queenfish *Scomberoides lysan* (Forsskål 1775), reported by Major (1973), was not observed.

Most fishes sampled were zooplanktivores (Figure. 1.2) and the most common prey were copepods, followed by eggs, detritus, and pennate diatoms. Many similar studies of coastal fish assemblages also report that copepods are one of the most frequently consumed prey types (Kanou et al. 2004; Inoue et al. 2005; Nanjo et al. 2008; Nakane et al. 2011). This demonstrates their importance in tropical and subtropical near-shore food webs and suggests copepods may be key regulators of predator population sizes via bottom-up effects, a role they play in some temperate marine ecosystems (Frederiksen et al. 2006). Phytoplankton was more frequently consumed and fishes and crustaceans less frequently consumed in this study than several other studies (Kanou et al. 2004; Inoue et al. 2005; Nanjo et al. 2008; Nakane et al. 2011). It is unclear why phytoplankton was more prevalent in the present study, but this could be a result of methodology. In many species phytoplankton was present in very small quantities and likely incidentally ingested. These small quantities were often detected when viewing prey through a binocular microscope prior to photography for prey size measurements. This, in combination with the frequency of occurrence method of diet quantification, may have artificially inflated the importance of phytoplankton in the diets of some fishes. The present study was restricted to smaller sizes of fish than many similar studies, which may partially explain why fishes and crustaceans were consumed relatively infrequently (detailed inter-study comparisons of the fish sizes examined are not possible because individual-level data are typically not reported). Environmental factors such as habitat or prey availability also may have contributed to this result. Nakane et al. (2011) sampled a similar size-range of fishes (9 to 285 mm SL) and report that Mysidacea and Amphipoda were the most important prey in 26 and 20 species of marine sandy beach fishes, respectively. Baker and Sheaves (2005) report many piscivores in shallow coastal habitats in Australia within the SL range sampled by the present study, which also contrasts with several previous studies (Inoue et al. 2005; Nanjo et al. 2008; Nakane et al. 2011).

4.2 Trophic guilds

The second objective of this study was to identify trophic guilds. The Simprof analysis identified six trophic guilds and bootstrapping identified three (Table 1.5 and Figure. 1.2). The six-guild scheme is most similar to previous studies and the trophic guild classification for estuaries outlined by Elliot et al. (2007). Bootstrapping identified a dissimilarity value of 0·67 as the cut-off for statistical significance. This is very similar to the critical dissimilarity value of 0·69 identified via bootstrapping in a study of trophic guilds in a temperate fish assemblage (Buchhiester and Latour 2015) and only slightly more stringent than the arbitrary dissimilarity threshold of 0·60 used by many previous studies (Nakamura et al. 2003; Inoue et al. 2005; Nanjo et al. 2008). All guilds identified by this study, except the omnivore guild, are frequently represented in similar assemblages (Kanou et al. 2004; Inoue et al. 2005; Nanjo et al. 2008; Nakane et al. 2011).

This indicates there is considerable consistency in food web structure among coastal fish assemblages. The omnivore cluster was often present in comparable studies, but not significantly different from either the zooplanktivore or detritivore guilds (e.g. Nakamura et al. 2003; Nanjo et al. 2008). This study did not identify herbivore, annelidivore, or molluscivore trophic guilds, although fish did consume these prey types. Fish size does not explain these results because these guilds frequently contain fishes within the SL range examined (Kanou et al. 2004; Inoue et al. 2005; Nanjo et al. 2008; Nakane et al. 2011). The absence of herbivores and molluscivores is not surprising because these guilds are less common, indicating their representation may be relatively more dependent on environmental factors than common guilds such as zooplanktivore. Limited annelid consumption is more surprising because this guild is common in soft-bottomed coastal marine and estuarine environments (Hajisamae et al. 2003; Kanou et al. 2004; Inoue et al. 2005; Nanjo et al. 2008) where polychaetes are abundant (Sarkar et al. 2005; Froján et al. 2006). This study did not quantify prey availability in the environment. A survey of the macroinvertebrate communities in the areas this study sampled may help determine if limited polychaete availability contributed to this result.

4.3 Prey size consumption

A positive correlation between SL and maximum prey width consumption was identified in seven species and a negative correlation in a single detritivorous species (Table 1.6 and Figure. 1.3a). This finding is consistent with previous research reporting ontogenetic shifts in prey size consumption, even in the absence of shifts in prey type consumption

(Scharf et al. 2000; Jensen et al. 2008; Specziár and Rezsu 2009). It is likely that additional ontogenetic shifts in prey size consumption as well as ontogenetic shifts in prey type consumption would be identified with examination of a wider range of fish SLs and larger sample sizes.

Fish SL was correlated with maximum prey width consumption at the assemblage level (Figure. 1.3b). This is consistent with previous studies finding that the maximum prey sizes consumed is typically positively correlated with SL in fish assemblages (Scharf et al. 2000). The detritivores *C. macrolepis*, *M. cunnesius*, and *N. come*, which ate very small prey even at long SLs, were an exception to this pattern. When these species were excluded from the analysis, linear regression better accounted for variation in maximum prey width consumption (Table 1.6 and Figure. 1.3a). Consequently, predictions of prey size consumption based upon SL may be undermined if detritivory is unaccounted for, even at short SLs. In near-shore fish assemblages in Taiwan detritivores likely provide a unique direct trophic link between detritus and piscivores (Wilson et al. 2003; Hundt et al. 2014).

4.4 Implications and conclusions

This study described the diets, trophic guilds, and size relationships between fish predators and their prey in near-shore marine fish assemblages in Taiwan. The findings of this study are congruent with previous research and add to a growing body of work showing consistent representation of some trophic guilds in marine fish assemblages (e.g.

zooplanktivores and crustacivores), but variable representation of others (e.g. herbivores and terrestrial invertivores). This suggests that certain trophic guilds may exhibit particularly tight links with environmental attributes. Additional diet studies of marine fishes, especially those with accompanying descriptions of the habitats sampled, adjacent habitat types, and prey availability, are needed to identify the factors governing spatial variation in trophic guild representation. The trophic guilds identified by this study are consistent with the estuarine trophic guilds of Elliot et al. (2007), which supports the use of this framework in ecosystem-based fisheries management. The diet data and trophic guild scheme produced by this study contribute to my understanding of the biology of marine fishes and food web structure and ecosystem-based fisheries management.

Table 1.1. Individual-level diet data with locality collected, standard length (SL), and James Ford Bell Museum catalog number (JFBM). Gastropoda and Bivalva refer to planktonic stages unless noted otherwise.

Species	Locality	SL (mm)	Diet	JFBM
Acanthopagrus sp.	Haomei estuary	30.48	Gammaridea, shrimp, eggs	47999
Acentrogobius moloanus	Haomei estuary	23.08	Copepoda, egg	47503
Acentrogobius moloanus	Haomei estuary	23.95	Copepoda, pennate diatom, Merismopedia, macrophyte fragments, detritus	47587
Acentrogobius moloanus	Haomei estuary	24.61	Copepoda, Merismopedia, filimentous algae, detritus	47503
Acentrogobius moloanus	Haomei estuary	25.94	Bivalve veliger, eggs	47650
Acentrogobius moloanus	Haomei estuary	28.38	Nematoda, Merismopedia, copepoda, chain cyanobacteria, detritus	47650
Acentrogobius moloanus	Haomei estuary	28.90	Copepoda, detritus	47596
Acentrogobius moloanus	Haomei estuary	30.84	Filamentous algae, Merismopedia, pennate diatoms, copepoda, detritus, cyanobacteria	47650
Acentrogobius moloanus	Haomei estuary	51.63	Detritus, copepoda, plant leaf, dinoflagellata	47587
Acentrogobius moloanus	Haomei estuary	61.37	Merismopedia, detritus, plant leaf, pennate diatoms, copepoda, other algae	47587
Acentrogobius nebulosus	Haomei estuary	24.73	Copepoda, filamentous algae, plant leaf, pennate diatom, Polychaeta, Nematoda, detritus	47503
Acentrogobius nebulosus	Haomei estuary	36.01	Copepoda, gammaridea, eggs, leaf	47995
Acentrogobius nebulosus	Haomei estuary	40.42	Filamentous algae, plant leaf	47503
Acentrogobius nebulosus	Haomei estuary	42.84	Copepoda, Merismopedia, leaves	47596
Acentrogobius nebulosus	Haomei estuary	47.29	Detritus, filamentous algae, other algae, Polychaeta, copepoda, gammeridea	48338
Acentrogobius nebulosus	Haomei estuary		Other algae, plant fragments, copepoda, detritus	47596
Acentrogobius cf *plaufamii*	Haomei estuary	25.62	Copepoda, eggs, pennate diatom, nematode, Merismopedia, detritus	47650
Acentrogobius cf *plaufamii*	Haomei estuary	26.34	Copepoda, Crustacean nauplii	47650
Acentrogobius cf *plaufamii*	Haomei estuary	28.32	Filamentous algae, detritus	47596

Acentrogobius cf *plaufamii*	Haomei estuary	30.56	Copepoda, Merismopedia, Nematoda, pennate diatoms, detritus	47650
Acentrogobius cf *plaufamii*	Haomei estuary	30.76	Gammeridea, copepoda, filamentous algae, egg	47997
Acentrogobius cf *plaufamii*	Haomei estuary	32.31	Amphipoda, filamentous algae	47997
Albula vulpes	Chonggang estuary	77.99	Fish, gammaridea	47956
Alepes djedaba	Shuang Chun beach	18.94	Gammeridea, filamentous algae	48026
Alepes djedaba	Chonggang estuary	26.44	Copepoda	48008
Alepes djedaba	Chonggang estuary	27.83	Filamentous algae, copepoda, pennate diatom	48008
Alepes djedaba	Haomei estuary	28.34	Copepoda	48002
Alepes djedaba	Chonggang estuary	28.94	Pennate diatom, copepoda	48008
Alepes djedaba	Haomei beach	33.18	Copepoda	48031
Alepes djedaba	Haomei estuary	36.63	Copepoda	48002
Alepes djedaba	Shuang Chun beach	41.15	Detritus, copepoda, pennate diatoms, Tintinnida	48026
Alepes djedaba	Haomei estuary	42.16	Copepoda, detritus, filamentous algae	48021
Alepes djedaba	Haomei estuary	43.96	Copepoda	48021
Alepes djedaba	Haomei estuary	44.57	Filamentous algae, copepoda, fish, unidentifiable Crustacea	48021
Alepes djedaba	Haomei estuary	48.24	Filamentous algae, copepoda	48021
Alepes djedaba	Haomei estuary	50.80	Copepoda, fish	48021
Alepes djedaba	Haomei beach	78.98	Shrimp, fish	47628
Alepes djedaba	Haomei beach	83.95	Shrimp	47628
Alepes djedaba	Haomei beach	84.09	Shrimp, filamentous algae	47628
Alepes djedaba	Haomei beach	86.64	Thryssa setirostris, shrimp	47628
Alepes djedaba	Haomei beach	88.20	Shrimp, fish, filamentous algae	47628
Alepes djedaba	Haomei beach	88.43	Filamentous algae, shrimp, egg, Tintinnida, detritus	47628
Alepes djedaba	Haomei beach	88.94	Shrimp, fish	47628
Ambassis cf. *gymnocephalus*	Haomei beach	18.74	Cirripedia cypris, copepoda	47989
Ambassis cf. *gymnocephalus*	Haomei beach	20.47	Cirripedia cypris, copepoda	47989
Ambassis cf. *gymnocephalus*	Haomei beach	20.91	Cirripedia cypris, copepoda	47989
Ambassis cf. *gymnocephalus*	Haomei beach	21.10	Cirripedia cypris, copepoda, amphipoda	47989
Ambassis cf. *gymnocephalus*	Haomei beach	23.29	Cirripedia cypris, copepoda, decapoda megalopa, eggs	47989
Ambassis cf. *gymnocephalus*	Haomei estuary	25.41	Copepoda	48005
Ambassis cf. *gymnocephalus*	Haomei beach	28.29	Copepoda, Cirripedia cypris	47590
Ambassis cf. *gymnocephalus*	Houmeili estuary	28.32	Copepoda, eggs, centric diatom	47885

Ambassis cf. *gymnocephalus*	Houmeili estuary	28.42	Copepoda, filamentous algae, eggs	47885
Ambassis cf. *gymnocephalus*	Haomei beach	29.68	Copepoda	47590
Ambassis cf. *gymnocephalus*	Houmeili estuary	29.82	Copepoda, Crustacea nauplii, eggs	47885
Ambassis cf. *gymnocephalus*	Houmeili estuary	30.68	Copepoda, eggs	47885
Ambassis cf. *gymnocephalus*	Haomei beach	31.44	Copepoda	47590
Ambassis cf. *gymnocephalus*	Houmeili estuary	33.90	Copepoda, Crustacea nauplii, eggs	47885
Ambassis cf. *gymnocephalus*	Haomei beach	34.10	Copepoda	47590
Ambassis cf. *gymnocephalus*	Houmeili estuary	34.27	Copepoda, decapod zoea, eggs	47885
Ambassis cf. *gymnocephalus*	Houmeili estuary	35.27	Copepoda	47885
Ambassis cf. *gymnocephalus*	Houmeili estuary	35.43	Copepoda, decapod zoea, eggs	47885
Ambassis cf. *gymnocephalus*	Houmeili estuary	38.74	Copepoda, eggs	47885
Ambassis cf. *gymnocephalus*	Haomei beach	40.46	Copepoda, Cirripedia cypris, filamentous algae, decapoda, eggs	47989
Ambassis cf. *gymnocephalus*	Houmeili estuary	41.21	Copepoda, decapoda zoea, Crustacea nauplii	47885
Ambassis miops	Houmeili estuary	25.55	Gastropoda	47502
Ambassis miops	Haomei estuary	25.85	Tintinnida, copepoda	48025
Ambassis miops	Houmeili estuary	26.58	Copepoda, eggs, Tintinnida	47502
Aulopareia unicolor	Haomei estuary	39.75	Copepoda, egg	47997
Bathygobius sp.	Chonggang estuary	27.33	Copepoda, Cirripedia cypris, bivalve veliger	47550
Boleophthalmus pectinirostris	Haomei estuary	109.29	Pennate diatom, detritus, Crustacea, terrestrial plant fragment, Merismopedia	47646
Bothidae sp.	Haomei estuary	69.36	Shrimp, fish	47998
Callionymus sagitta	Chonggang estuary	28.00	Detritus, copepoda	47969
Callionymus sagitta	Chonggang estuary	41.10	Copepoda, unidentifiable Crustacea, Cirripedia cypris, centric diatom, Bivalva	47517
Carangidae sp.	Chonggang estuary	15.78	Amphipoda, unidentifiable Crustacea	47967
Carangoides sp.	Haomei estuary	26.10	Copepoda, trematoda	47887
Caranx sexfasciatus	Shuang Chun beach	39.68	Fish	48677
Chanos chanos	Haomei estuary	79.93	Formicidae, detritus, filamentous algae	48150
Chanos chanos	Haomei estuary	87.85	Detritus	48150
Chanos chanos	Haomei estuary	96.63	Centric diatoms, other algae, detritus	48150
Chelon macrolepis	Haomei	22.60	Centric diatom, filamentous algae, dinoflagellata, detritus	47990

Chelon macrolepis	Haomei beach	23.75	Centric and pennate diatoms, copepoda, egg, detritus	47990
Chelon macrolepis	Shuang Chun beach	24.26	Detritus	47976
Chelon macrolepis	Shuang Chun beach	24.44	Detritus, Cirripedia cypris	47976
Chelon macrolepis	Haomei beach	24.47	Detritus, copepoda, Cirripedia cypris, centric and pennate diatoms, bivalve larvae, dinoflagellata	47990
Chelon macrolepis	Haomei estuary	24.78	Detritus, pennate diatoms	48024
Chelon macrolepis	Shuang Chun beach	25.89	Detritus, copepoda, Bivalva, shrimp	47976
Chelon macrolepis	Shuang Chun beach	27.03	Detritus	47976
Chelon macrolepis	Shuang Chun beach	27.51	Unidentifiable Crustacea, detritus, filamentous algae	47976
Chelon macrolepis	Haomei beach	27.86	Pennate diatoms, dinoflagellata, detritus	47990
Chelon macrolepis	Haomei beach	27.86	Detritus, Gastropoda, dinoflagellata, egg, pennate diatoms	47990
Chelon macrolepis	Haomei beach	28.13	Pennate and centric diatom, filamentous algae, copepoda cypris, Cirripedia, dinoflagellata, Polychaeta, detritus	47990
Chelon macrolepis	Shuang Chun beach	28.26	Detritus	47976
Chelon macrolepis	Shuang Chun beach	28.26	Gastrapoda, copepoda	47976
Chelon macrolepis	Haomei beach	28.93	Detritus, egg, copepoda, Cirripedia cypris, pennate diatoms, Nematoda	47990
Chelon macrolepis	Haomei beach	31.54	Centric and pennate diatoms, dinoflagellata, filamentous algae, egg, Gastropoda, detritus	47990
Chelon macrolepis	Shuang Chun beach	32.90	Detritus	47976
Chelon macrolepis	Haomei estuary	32.94	Centric, pennate, and colonial diatoms, filamentous algae, eggs, Gastropoda, Crustacea nauplii, detritus	48024
Chelon macrolepis	Haomei estuary	33.13	Centric and pennate diatoms, filamentous algae, eggs, detritus, Merismopedia	48024
Chelon macrolepis	Haomei estuary	33.44	Cyanobacteria, centric and pennate diatoms, other	47583

			algae, detritus	
Chelon macrolepis	Shuang Chun beach	35.51	Detritus, egg	47976
Chelon macrolepis	Haomei beach	39.18	Eggs, dinoflagellata, centric and pennate diatoms, Crustacea nauplii, copepoda, detritus	47990
Chelon macrolepis	Haomei estuary	39.27	Detritus, centric and pennate diatoms, eggs, Merismopedia, copepoda, macrophyte, other algae	47583
Chelon macrolepis	Haomei estuary	40.04	Detritus, eggs, other algae, Merismopedia	47583
Chelon macrolepis	Haomei estuary	41.32	Detritus, pennate diatoms, eggs, Gastropoda, Merismopedia, cyanobacteria	47649
Chelon macrolepis	Haomei beach	41.39	Dinoflagellata, centric and pennate diatoms, copepoda, detritus	47990
Chelon macrolepis	Haomei estuary	43.84	Detritus, centric and pennate diatoms, eggs, Crustacea nauplii, Gastropoda	48024
Chelon macrolepis	Haomei estuary	47.62	Detritus, eggs, cyanobacteria, Merismopedia, pennate diatoms	47649
Chelon macrolepis	Haomei estuary	48.88	Detritus, centric diatom, egg	47883
Chelon macrolepis	Haomei estuary	49.21	Detritus, pennate diatoms, egg, Merismopedia	47649
Chelon macrolepis	Haomei estuary	52.44	Detritus, filamentous algae, pennate diatoms, Tintinnida, eggs, copepoda, hydrozoa	47501
Chelon macrolepis	Haomei beach	66.08	Detritus	47595
Chelon macrolepis	Haomei beach	76.69	Mud, unidentifiable Crustacea	47595
Chelon macrolepis	Shuang Chun beach	92.62	Detritus	47976
Chelon macrolepis	Shuang Chun beach	97.11	Detritus	47976
Chelon subviridis	Haomei estuary	62.73	Detritus, pennate diatoms, Foraminifera, egg	48672
Crenimugil crenilabis	Haomei estuary	67.10	Detritus, cyanobacteria, Merismopedia, egg, pennate diatoms	48674
Cryptocentrus yatsui	Haomei estuary	24.24	Copepoda, filamentos algae	47996
Cryptocentrus yatsui	Haomei estuary	28.92	Copepoda	47996
Cryptocentrus yatsui	Haomei estuary	36.20	Copepoda	47996
Cryptocentrus yatsui	Haomei estuary	38.03	Merismopedia, macrophyte fragment, Foraminifera, detritus, copepoda	47587

Cryptocentrus yatsui	Haomei estuary	38.63	Copepoda	47650
Drombus cf. *ocyurus*	Haomei estuary	19.07	Merismopedia, copepoda, amphipoda	47650
Drombus cf. *ocyurus*	Haomei estuary	21.55	Copepoda, filamentous algae, eggs	47997
Drombus cf. *ocyurus*	Haomei estuary	22.96	Filamentous algae, ostracoda, copepoda, Merismopedia, pennate diatoms	47997
Drombus cf. *ocyurus*	Haomei estuary	23.07	Copepoda	47997
Drombus cf. *ocyurus*	Haomei estuary	24.15	Copepoda	47650
Drombus cf. *ocyurus*	Haomei estuary	24.16	Filamentous algae, copepoda, amphipoda, eggs	47997
Drombus cf. *ocyurus*	Haomei estuary	24.50	Filamentous algae, copepoda, pennate diatoms, cyanobacteria	47997
Drombus cf. *ocyurus*	Haomei estuary	25.04	Copepoda, Merismopedia, Nematoda, detritus, pennate diatom	47650
Drombus cf. *ocyurus*	Haomei estuary	26.15	Copepoda, gammeridea	47997
Drombus cf. *ocyurus*	Haomei estuary	27.03	Copepoda, gammeridea, filamentous algae, pennate diatom	47997
Dussumieria elopsoides	Chonggang estuary	40.25	Unidentifiable Crustacea	47516
Dussumieria elopsoides	Chonggang estuary	41.52	Copepoda, unidentifiable Crustacea	47516
Dussumieria elopsoides	Chonggang estuary	42.94	Unidentifiable Crustacea	47516
Dussumieria elopsoides	Chonggang estuary	43.55	Fish, unidentifiable Crustacea	47516
Dussumieria elopsoides	Chonggang estuary	44.11	Shrimp	47516
Dussumieria elopsoides	Chonggang estuary	44.16	Decapoda, fish	47516
Dussumieria elopsoides	Chonggang estuary	45.70	Fish, unidentifiable Crustacea	47516
Encrasicholina heteroloba	Chonggang estuary	26.14	Crustacea nauplii, Cirripedia cypris	48013
Encrasicholina heteroloba	Chonggang estuary	27.67	Copepoda	48013
Encrasicholina heteroloba	Chonggang estuary	27.96	Cirripedia	48013
Encrasicholina heteroloba	Chonggang estuary	28.47	Cirripedia cypris, copepoda	48013
Encrasicholina heteroloba	Chonggang estuary	28.62	Nauplii	48013
Encrasicholina heteroloba	Chonggang estuary	28.73	Copepoda	48013
Encrasicholina heteroloba	Chonggang estuary	28.73	Cirripedia cypris	48013
Encrasicholina heteroloba	Chonggang estuary	28.89	Copepoda	48013

Encrasicholina heteroloba	Chonggang estuary	29.73	Copepoda	48013
Encrasicholina heteroloba	Chonggang estuary	29.84	Cirripedia cypris, copepoda	48013
Encrasicholina heteroloba	Haomei beach	47.52	Copepoda, bivalve larvae, decapoda zoea, Cirripedia cypris, egg, detritus	47978
Eubleekeria splendens	Qigu estuary	33.26	Copepoda, cyanobacteria, macrophyte, Nematoda, Gastropoda, detritus, pennate diatom	48046
Eubleekeria splendens	Haomei beach	37.42	Copepoda, eggs, amphipoda	47881
Eubleekeria splendens	Haomei beach	46.19	Copepoda, eggs, Nematoda, pennate diatoms, Foraminifera, benthic Gastropoda, plant, detritus	48594
Eubleekeria splendens	Qigu estuary	47.01	Copepoda, detritus, Bivalva larvae	48046
Eubleekeria splendens	Shuang Chun beach	56.97	Copepoda, detritus, Polychaeta, gammeridea, hydrozoa, shrimp	48027
Eublekeeria splendens	Chonggang estuary	14.70	Copepoda, Cirripedia cypris, centric diatoms	48009
Eublekeeria splendens	Chonggang estuary	14.96	Copepoda, Cirripedia cypris, eggs, Bivalva larvae	48009
Eublekeeria splendens	Chonggang estuary	15.15	Copepoda, Cirripedia cypris, eggs	48009
Eublekeeria splendens	Chonggang estuary	16.67	Copepoda, bivalve larvae, Cirripedia cypris, Crustacea nauplii, eggs	48009
Eublekeeria splendens	Chonggang estuary	17.36	Copepoda, Cirripedia cypris, centric diatoms	47968
Eublekeeria splendens	Chonggang estuary	17.40	Copepoda, Cirripedia cypris, Bivalva	48009
Eublekeeria splendens	Chonggang estuary	18.00	Copepoda, Gastropoda	47968
Eublekeeria splendens	Chonggang estuary	19.28	Unidentifiable Crustacea	47968
Eublekeeria splendens	Chonggang estuary	19.63	Copepoda, Cirripedia nauplii and cypris, appendicularia, cladocera	48009
Eublekeeria splendens	Chonggang estuary	19.68	Copepoda, pennate diatom	47968
Eublekeeria splendens	Chonggang estuary	19.69	Copepoda, Cirripedia nauplii, eggs	48009
Eublekeeria splendens	Chonggang estuary	20.31	Copepoda	47968
Eublekeeria splendens	Chonggang estuary	20.40	Copepoda, Cirripedia nauplii, Nematoda	48009
Eublekeeria splendens	Chonggang estuary	20.42	Copepoda, Cirripedia cypris, Bivalva, centric diatoms	47968
Eublekeeria splendens	Chonggang estuary	21.99	Copepoda, Cirripedia nauplii and cypris,	48009

			appendicularia	
Eublekeeria splendens	Chonggang estuary	23.16	Copepoda, Cirripedia cypris and exopod	47968
Eublekeeria splendens	Chonggang estuary	23.30	Copepoda, centric and pennate diatoms, eggs, sillicoflagellata, cyanobacteria, Foraminifera, Bivalva	47968
Eublekeeria splendens	Chonggang estuary	25.07	Copepoda, Bivalva, Cirripedia nauplii and cypris, Polychaeta, Tintinnida	48009
Eublekeeria splendens	Chonggang estuary	25.43	Copepoda, ostracoda, Cirripedia cypris, pennate diatom, cyanobacteria	47968
Eublekeeria splendens	Chonggang estuary	26.00	Copepoda, other algae, pennate diatoms, unidentifiable Crustacea, sipuncula, eggs, Bivalva	47968
Gazza minuta	Chonggang estuary	28.36	Shrimp	48012
Gerres limbatus	Haomei estuary	20.08	Copepoda, eggs	48595
Gerres limbatus	Haomei estuary	37.61	Copepoda, eggs, Nematoda	47655
Hypoatherina valenciennei	Haomei estuary	28.04	Copepoda, Crustacea naulpii	47994
Hypoatherina valenciennei	Haomei beach	30.65	Cirripedia cypris, copepoda, Bivalva veliger, Crustacea nauplii	47983
Hypoatherina valenciennei	Haomei beach	31.50	Cirripedia cypris, copepoda, Bivalva veliger, gammeridea	47983
Hypoatherina valenciennei	Haomei beach	34.16	Cirripedia cypris, copepoda, planktonic hydrozoan, Bivalva veliger	47983
Hypoatherina valenciennei	Haomei estuary	43.24	Copepods	47465
Hypoatherina valenciennei	Haomei estuary	45.10	Hymenoptera, detritus	47465
Hypoatherina valenciennei	Haomei estuary	46.70	Hymenoptera	47465
Hypoatherina valenciennei	Haomei estuary	48.19	Copepods	47465
*Hyporhamphus s*p.	Haomei estuary	53.63	Terrestrial insects, copepoda	47586
Hyporhamphus sp.	Haomei estuary	67.77	Copepoda, terrestrial insect, plant leaf	47586
Hyporhamphus sp.	Haomei estuary	73.40	Copepoda, plant leaves, eggs, filamentous algae, pennate diatoms, terrestrial insect	47586
Hyporhamphus sp.	Haomei beach	77.50	Copepoda, terrestrial insect, filamentous algae, eggs	47647
Hyporhamphus sp.	Haomei estuary	86.23	Filamentous algae, copepoda, plant leaves, Merismopedia, decapod	47586

			zoea, eggs, terrestrial insects, pennate diatoms	
Lutjanus argentimaculatus	Haomei estuary	126.50	Filamentous algae, dinoflagellata, fish, eggs, detritus	48221
Moolgarda cunnesius	Haomei beach	20.20	Detritus, egg, centric and pennate diatoms, copepoda	48673
Moolgarda cunnesius	Haomei beach	25.88	Copepoda, pennate diatoms, filamentous algae, Bivalva larvae, Merismopedia, detritus	48673
Moolgarda cunnesius	Haomei beach	26.00	Filamentous algae, eggs, copepoda	48673
Moolgarda cunnesius	Chonggang estuary	27.65	Detritus, pennate diatoms, dinoflagellata, unidentifiable Crustacea, copepoda, Crustacea nauplii	47958
Moolgarda cunnesius	Chonggang estuary	27.69	Centric and pennate diatoms, eggs, plant, detritus, filamentous algae	47958
Moolgarda cunnesius	Haomei beach	28.19	Detritus	48675
Moolgarda cunnesius	Haomei beach	28.35	Centric and pennate diatoms, filamentous algae, egg, Merismopedia, detritus	48673
Moolgarda cunnesius	Haomei beach	28.45	Detritus, centric and pennate diatoms, cyanobacteria	48673
Moolgarda cunnesius	Haomei beach	28.49	Centric diatoms, cyanobacteria, detritus	48673
Moolgarda cunnesius	Haomei beach	30.01	Detritus, filamentous and other algae, Merismopedia, centric and pennate diatoms, eggs	48673
Moolgarda cunnesius	Chonggang estuary	30.45	Detritus	47958
Moolgarda cunnesius	Chonggang estuary	31.82	Centric and pennate diatom, detritus	47958
Moolgarda cunnesius	Chonggang estuary	32.55	Centric and pennate diatoms, detritus	47958
Moolgarda cunnesius	Haomei beach	32.81	Detritus, filamentous algae, eggs, pennate diatoms, Bivalva	47981
Moolgarda cunnesius	Haomei beach	33.66	Filamentous algae, detritus, pennate diatom	48675
Moolgarda cunnesius	Haomei beach	34.00	Detritus, egg	48675
Moolgarda cunnesius	Chonggang estuary	34.60	Eggs, pennate diatoms, dinoflagellata, detritus	47958
Moolgarda cunnesius	Haomei beach	34.66	Pennate diatom, detritus	48675
Moolgarda cunnesius	Chonggang estuary	35.31	Pennate diatoms, detritus	47958
Moolgarda cunnesius	Haomei beach	35.33	Filamentous algae, other algae, eggs, detritus, dinoflagellata	48673

Moolgarda cunnesius	Haomei estuary	35.47	Detritus, Cirripedia cypris, Crustacea nauplii, filamentous algae, Gastropoda, dinoflagellata, centric, pennate, and colonial diatoms, eggs	48003
Moolgarda cunnesius	Chonggang estuary	36.95	Pennate diatoms, eggs, dinoflagellata, detritus	47958
Moolgarda cunnesius	Chonggang estuary	37.21	Pennate diatoms, detritus	47958
Moolgarda cunnesius	Chonggang estuary	37.76	Eggs, centric diatom, pennate diatom, Foraminifera, Nematoda, detritus	47958
Moolgarda cunnesius	Haomei estuary	38.63	Detritus, eggs, dinoflagellata, filamentous algae, centric diatoms	48003
Moolgarda cunnesius	Chonggang estuary	38.85	Eggs, detritus	47958
Moolgarda cunnesius	Chonggang estuary	43.55	Pennate diatoms, filamentous algae, eggs, detritus	47958
Moolgarda cunnesius	Haomei beach	65.76	Pennate diatoms, Crustacea nauplii, dinoflagellata, formanifera, Tintinnida, egg, detritus	47626
Nematalosa come	Chonggang estuary	28.18	Detritus, Cirripedia cypris, egg, ostracoda, centric diatom, copepoda	47960
Nematalosa come	Chonggang estuary	31.25	Detritus, copepoda, Cirripedia cypris, centric diatom	47960
Nematalosa come	Chonggang estuary	32.08	Detritus, macrophyte, other algae, phytoflagellata	47960
Nematalosa come	Haomei estuary	33.20	Copepoda, Crustacea nauplii, centric diatom	48018
Nematalosa come	Chonggang estuary	33.33	Detritus, dinoflagellete, centric diatom, egg	47960
Nematalosa come	Haomei beach	33.56	Copepoda, detritus, Cirripedia cypris, decapod zoea	47984
Nematalosa come	Chonggang estuary	33.64	Detritus, pennate diatom	47960
Nematalosa come	Haomei estuary	34.64	Detritus	48018
Nematalosa come	Haomei estuary	35.33	Copepoda, detritus, Crustacea nauplii, egg	48018
Nematalosa come	Chonggang estuary	36.44	Detritus, filamentous and other algae, egg	47960
Nematalosa come	Chonggang estuary	36.82	Detritus, filamentous algae, macrophyte, pennate diatom	47960
Nematalosa come	Chonggang estuary	38.30	Filamentous algae, detritus, pennate diatom	47960

Nematalosa come	Chonggang estuary	39.17	Deritus, dinoflatelleta, filamentous and other algae, macrophyte	47960
Nematalosa come	Haomei estuary	42.74	Detritus, pennate diatom, Crustacea nauplii, copepoda, planktonic Gastropoda, egg	48151
Nematalosa come	Haomei estuary	43.79	Pennate and centric diatoms, unidentifiable Crustacea, dinoflagellata, detritus	48151
Nematalosa come	Haomei estuary	44.95	Detritus, pennate diatom, unidentifiable Crustacea, egg	48151
Nematalosa come	Chonggang estuary	45.97	Detritus, cyanobacteria, centric diatom, limpet, egg	47960
Nematalosa come	Haomei estuary	54.53	Detritus, pennate diatom	48151
Nematalosa come	Haomei estuary	59.59	Cyanobacteria, filamentous algae, Crustacea nauplii, pennate diatom, detritus	48151
Nematalosa come	Haomei estuary	60.48	Detritus, pennate diatom, filamentous algae	48151
Nematalosa come	Haomei estuary	60.51	Pennate diatoms, detritus, eggs, Merismopedia	48151
Nematalosa come	Haomei estuary	61.08	Detritus, cyanobacteria, pennate diatom	48151
Nematalosa come	Haomei estuary	64.14	Algae, pennate diatom, detritus	48151
Nematalosa come	Haomei estuary	66.78	Pennate and centric diatoms, detritus	48151
Nematalosa come	Haomei estuary	73.88	Merismopedia, other algae, detritus	47648
Nematalosa come	Haomei estuary	74.13	Other algae, pennate diatom, detritus, Merismopedia, Bivalva	47648
Nematalosa come	Haomei estuary	76.27	Cyanobacteria, pennate diatom, detritus, Merismopedia	47582
Nematalosa come	Chonggang estuary	151.12	Copepoda, detritus	47620
Netuma thalassina	Chonggang estuary	49.10	Centric diatom, Gastropoda, pennate diatom, unidentified benthic Crustacea, Cirripedia cypris, eggs, copepoda, detritus	47514
Netuma thalassina	Chonggang estuary	51.28	Cirripedia cypris, Polychaeta, copepoda, eggs, centric diatom, dinoflagellate, unidentifiable Crustacea, detritus	47514
Netuma thalassina	Chonggang estuary	51.30	Copepoda, eggs, decapoda, centric diatoms, pennate diatoms, hydrozoa,	47514

			dinoflagellata, detritus, Cirripedia cypris	
Netuma thalassina	Chonggang estuary	51.75	Cirripedia cypris, filamentous algae, centric diatoms, eggs, copepoda, detritus	47514
Netuma thalassina	Chonggang estuary	52.73	Cirripedia cypris, Gastropoda, copepoda, eggs, centric diatom, detritus, bivalve larvae, pennate diatom, unidentifiable Crustacea	47514
Netuma thalassina	Chonggang estuary	53.02	Copepoda, Cirripedia cypris, Cirripedia exopods, centric diatom, detritus, bivalve larvae	47514
Netuma thalassina	Chonggang estuary	54.23	Copepoda, Cirripedia cypris, macrophyte, bivalve larvae, detritus, eggs	47514
Netuma thalassina	Chonggang estuary	55.48	Filamentous algae, copepoda, eggs, Cirripedia cypris, detritus, large unidentifiable Crustacea	47514
Netuma thalassina	Chonggang estuary	55.74	Eggs, copepoda, Cirripedia cypris, detritus	47514
Netuma thalassina	Chonggang estuary	61.94	Copepoda, Cirripedia cypris, eggs, centric diatom, detritus	47514
Oligolepis acutipennis	Haomei estuary	30.57	Copepoda, cyanobacteria, Crustacea nauplii, pennate diatoms, Nematoda, Merismopedia, detritus	47650
Oligolepis acutipennis	Haomei estuary	34.54	Cyanobacteria, Merismopedia, pennate diatom, copepoda, detritus	47596
Oligolepis acutipennis	Haomei estuary	36.30	Copepoda, centric diatom, Merismopedia, pennate diatom, cyanobacteria, other algae	47650
Paraplagusia bilineata	Chonggang estuary	30.35	Unidentified benthic Crustacea	47549
Paraplagusia bilineata	Chonggang estuary	35.78	Shrimp	48010
Paraplagusia bilineata	Chonggang estuary	36.47	Shrimp, unidentifiable benthic Crustacea	48010
Paraplagusia bilineata	Chonggang estuary	38.89	Copepoda, decapoda	48010
Paraplagusia bilineata	Chonggang estuary	81.47	Detritus, filamentou algae, unidentified benthic Crustacea	47970

Photopectoralis bindus	Haomei beach	11.74	Copepoda, eggs	47992
Photopectoralis bindus	Haomei beach	11.88	Copepoda, eggs	47992
Photopectoralis bindus	Haomei beach	13.98	Copepoda, eggs, gammeridea	47992
Photopectoralis bindus	Haomei beach	14.20	Copepoda, Gastropoda, eggs	47992
Photopectoralis bindus	Haomei beach	15.80	Copepoda	47992
Photopectoralis bindus	Haomei beach	15.87	Copepoda, eggs	47992
Photopectoralis bindus	Haomei beach	17.53	Copepoda	47992
Photopectoralis bindus	Haomei beach	19.56	Copepoda, eggs, gammeridea	47992
Photopectoralis bindus	Haomei beach	21.00	Copepoda, Cirripedia nauplii	47992
Photopectoralis bindus	Haomei beach	21.69	Copepoda, eggs, filamentous algae	47881
Photopectoralis bindus	Haomei beach	22.53	Copepoda, eggs, filamentous algae, Crustacea nauplii	47881
Photopectoralis bindus	Houmeili estuary	22.89	Copepoda, eggs	48000
Photopectoralis bindus	Haomei beach	23.06	Copepoda, amphipoda, pennate diatom	47881
Photopectoralis bindus	Haomei estuary	23.39	Copepoda	48000
Photopectoralis bindus	Haomei estuary	23.54	Copepoda	47584
Photopectoralis bindus	Haomei beach	24.66	Copepoda, eggs	47992
Photopectoralis bindus	Houmeili estuary	26.04	Copepoda, eggs, amphipoda	48000
Photopectoralis bindus	Houmeili estuary	26.30	Copepoda	48000
Photopectoralis bindus	Houmeili estuary	26.43	Copepoda	48000
Photopectoralis bindus	Haomei estuary	26.62	Copepoda	47584
Photopectoralis bindus	Haomei estuary	27.20	Copepoda	48000
Photopectoralis bindus	Haomei estuary	27.71	Copepoda	47654
Photopectoralis bindus	Haomei estuary	27.83	Copepoda, eggs	47654
Photopectoralis bindus	Houmeili estuary	27.91	Copepoda	48000
Photopectoralis bindus	Haomei beach	28.16	Copepoda, filamentous algae, eggs, Merismopedia, Nematoda, amphipoda	47881
Photopectoralis bindus	Haomei estuary	28.55	Copepoda, Cirripedia nauplii, eggs	47584
Photopectoralis bindus	Haomei estuary	29.56	Copepoda, filamentous algae, pennate diatoms, eggs, cyanobacteria	47654
Photopectoralis bindus	Haomei estuary	29.60	Copepoda, eggs, Merismopedia	47654
Photopectoralis bindus	Haomei estuary	29.63	Copepoda	47584
Photopectoralis bindus	Haomei estuary	29.87	Copepoda, eggs	47584

Photopectoralis bindus	Haomei beach	30.32	Copepoda, Nematoda	47881
Photopectoralis bindus	Haomei estuary	30.99	Copepoda, eggs	47584
Photopectoralis bindus	Haomei estuary	31.17	Copepoda, eggs	47584
Photopectoralis bindus	Haomei estuary	32.01	Copepoda, eggs, pennate diatoms, Merismopedia	47654
Photopectoralis bindus	Haomei estuary	32.28	Copepoda, eggs, filamentous algae	47654
Photopectoralis bindus	Haomei estuary	32.46	Copepoda, Polychaeta, detritus	47584
Photopectoralis bindus	Haomei estuary	32.91	Copepoda, eggs	47584
Photopectoralis bindus	Haomei estuary	33.10	Copepoda	47584
Photopectoralis bindus	Haomei estuary	33.28	Copepoda, eggs, Merismopedia	47654
Photopectoralis bindus	Haomei estuary	33.40	Copepoda, eggs, filamentous algae, Merismopedia	47654
Photopectoralis bindus	Haomei estuary	33.54	Copepoda, eggs, filamentous algae, pennate diatoms	47654
Photopectoralis bindus	Houmeili estuary	33.83	Copepoda, eggs, amphipoda	48000
Photopectoralis bindus	Haomei estuary	34.19	Copepoda, eggs, filamentous algae	47654
Photopectoralis bindus	Houmeili estuary	34.21	Copepoda, eggs, amphipoda	48000
Photopectoralis bindus	Haomei beach	34.25	Copepoda, eggs	47881
Photopectoralis bindus	Haomei beach	35.80	Copepoda, eggs	47881
Photopectoralis bindus	Houmeili estuary	36.33	Copepoda, eggs, gammeridea, filamentous algae, detritus	48000
Photopectoralis bindus	Houmeili estuary	36.34	Copepoda, gammeridea, eggs, pennate diatoms, unidentifiable Crustacea	48000
Photopectoralis bindus	Haomei estuary	38.55	Copepoda, Merismopedia, pennate diatoms, eggs	47654
Photopectoralis bindus	Houmeili estuary	60.42	Copepoda, macrophyte, eggs, detritus, unidentifiable Crustacea, gammeridea	48000
Sardinella gibbosa	Chonggang estuary	30.84	Copepoda, centric and colonial diatoms, Cirripedia cypris	47505
Sardinella gibbosa	Chonggang estuary	30.94	Copepoda, Cirripedia cypris, filamentous algae, centric diatoms, eggs, detritus, collembola	47962
Sardinella gibbosa	Chonggang estuary	31.53	Copepoda, Cirripedia cypris, ostracoda, eggs	47962
Sardinella gibbosa	Chonggang estuary	32.01	Chaetognatha, Cirripedia cypris, copepoda, detritus, ostracoda, eggs	47962

Sardinella gibbosa	Chonggang estuary	33.40	Copepoda, Cirripedia cypris and exopods, eggs, pennate diatom	47962
Sardinella gibbosa	Chonggang estuary	35.04	Copepoda, Cirripedia cypris, eggs, centric diatoms	47962
Sardinella gibbosa	Chonggang estuary	35.79	Copepoda, Cirripedia cypris, centric diatom, detritus	47962
Sardinella gibbosa	Chonggang estuary	36.61	Copepoda, dinoflagellata, centric diatom, detritus, trematoda	47962
Sardinella gibbosa	Chonggang estuary	37.18	Copepoda, centric diatom, detritus, bivalve larvae, Cirripedia cypris, Crustacea nauplii, cladocera, eggs	47505
Sardinella gibbosa	Chonggang estuary	42.41	Centric diatoms, copepoda, detritus, eggs, Cirripedia nauplii	47962
Sardinella gibbosa	Chonggang estuary	58.03	Copepoda, centric diatom, detritus, cerrepedia cypris, eggs, bivalve larvae, dinoflagellata, filamentous algae	47505
Sardinella gibbosa	Chonggang estuary	74.35	Copepoda, Crustacea nauplii, Cirripedia cypris, egg, detritus	47621
Sardinella lemuru	Chonggang estuary	48.40	Copepoda, Gastropoda, eggs, pennate diatom, Bivalva veliger, Nematoda, detritus	48015
Sardinella lemuru	Chonggang estuary	53.55	Pennate diatoms, other algae, eggs	47961
Sardinella lemuru	Chonggang estuary	54.24	Copepoda, other algae, centric and pennate diatoms, eggs, macrophyte, Gastropoda, detritus, Foraminifera	47961
Sardinella lemuru	Chonggang estuary	58.21	Centric and pennate diatoms, Cirripedia cypris, filamentous and other algae, copepoda, detritus	47961
Sciaenidae sp.	Chonggang estuary	53.56	Shrimp	47528
Scomberoides lysan	Chonggang estuary	26.28	Shrimp	47966
Scomberoides lysan	Haomei beach	26.66	Copepoda	47588
Scomberoides lysan	Haomei beach	29.62	Copepoda, eggs	47588
Scomberoides lysan	Chonggang estuary	38.54	Unidentifiable Crustacea, filamentous algae	47529
Scomberoides lysan	Chonggang estuary	38.96	Cyanobacteria, shrimp, Nematoda	47966

Scomberoides lysan	Chongqang estuary	39.99	Copepoda	47529
Scomberoides lysan	Haomei beach	42.16	Copepoda, colonial diatom	47588
Scomberoides lysan	Chonggang estuary	43.01	Shrimp	47529
Scomberoides lysan	Chonggang estuary	48.95	Cirripedia cypris, centric diatom, copepoda	47529
Scomberoides lysan	Haomei estuary	53.20	Cirripedia exopods	48022
Scomberoides lysan	Chonggang estuary	61.63	Fish	47622
Scomberoides lysan	Haomei beach	62.93	Shrimp, filamentous algae	47624
Scomberoides lysan	Haomei beach	67.45	Shrimp, fish	47624
Scomberoides lysan	Chonggang estuary	69.70	Decapoda megalopa, fish	47622
Scomberoides lysan	Haomei beach	70.65	Shrimp	47624
Scomberoides lysan	Chonggang estuary	93.58	Fish	47622
Secutor interruptus	Haomei beach	17.61	Copepoda, eggs	47882
Secutor interruptus	Haomei beach	18.16	Copepoda	47882
Secutor interruptus	Shuang Chun beach	22.79	Copepoda	48027
Secutor interruptus	Haomei beach	23.48	Copepoda, eggs	47882
Secutor interruptus	Shuang Chun beach	25.42	Copepoda	48027
Secutor interruptus	Chonggang estuary	26.32	Copepoda	47527
Secutor interruptus	Haomei beach	28.24	Copepoda, eggs, Gastropoda	47882
Secutor interruptus	Chonggang estuary	28.37	Copepoda, Crustacea nauplii	47527
Secutor interruptus	Haomei beach	28.59	Copepoda, eggs	47882
Secutor interruptus	Haomei beach	28.64	Copepoda, eggs	47882
Secutor interruptus	Chonggang estuary	29.03	Copepoda	47527
Secutor interruptus	Chonggang estuary	29.83	Copepoda	47527
Secutor interruptus	Chonggang estuary	30.53	Copepoda	47527
Secutor interruptus	Chonggang estuary	30.72	Copepoda	47527
Secutor interruptus	Chonggang estuary	31.10	Copepoda	47527
Secutor interruptus	Chonggang estuary	31.26	Copepoda	47527
Secutor interruptus	Chonggang estuary	31.58	Copepoda	47527
Secutor interruptus	Chonggang estuary	32.27	Copepoda, Cirripedia nauplii	47527
Sillago asiatica	Haomei estuary	20.85	Copepoda, filamentous algae	47884
Sillago asiatica	Haomei estuary	24.61	Copepoda	47585
Sillago asiatica	Haomei estuary	25.72	Copepoda, eggs	47652
Sillago asiatica	Haomei beach	27.36	Copepoda, Polychaeta, Cirripedia cypris, eggs	47982

Sillago asiatica	Haomei estuary	29.16	Copepoda	47585
Sillago asiatica	Chonggang estuary	35.83	Amphipoda, copepoda, Cirripedia cypris, eggs, dinoflagellata	48016
Sillago asiatica	Haomei beach	40.94	Detritus, eggs, copepoda	47644
Sillago asiatica	Haomei estuary	46.98	Gammeridea, copepoda, eggs	48001
Sillago asiatica	Haomei beach	49.02	Copepoda, detritus	47991
Sillago asiatica	Haomei beach	52.44	Pennate diatoms, amphipoda	47991
Sillago asiatica	Haomei estuary	53.29	Copepoda, gammeridea, Polychaeta	48001
Sillago asiatica	Haomei estuary	54.62	Detritus, copepoda, Polychaeta, gammeridea, eggs	47585
Sillago asiatica	Haomei beach	62.46	Detritus, copepoda, eggs, Polychaeta	47644
Sillago asiatica	Haomei estuary	73.50	Copepoda, eggs, detritus	47585
Sphyraena barracuda	Haomei estuary	133.20	Fish	47597
Sphyraena flavicauda	Chonggang estuary	80.85	Unidentifiable fish	47515
Sphyraena jello	Chonggang estuary	50.58	Fish	48014
Sphyraena jello	Haomei estuary	81.15	Fish, eggs	48676
Sphyraena jello	Chonggang estuary	103.86	Fish (stolephorus)	47963
Stolephorus indicus	Houmeili estuary	20.26	Copepoda	48020
Stolephorus indicus	Houmeili estuary	22.92	Copepoda, eggs, Bivalva larvae, decapod zoea	48020
Stolephorus indicus	Houmeili estuary	23.29	Copepoda, Gastropoda	48020
Stolephorus indicus	Haomei estuary	23.66	Copepoda	48020
Stolephorus indicus	Houmeili estuary	25.13	Copepoda	48020
Stolephorus indicus	Haomei estuary	25.49	Copepoda, Gastropoda	48020
Stolephorus indicus	Haomei estuary	25.99	Copepoda, trematoda	48006
Stolephorus indicus	Houmeili estuary	27.05	Gastropoda, copepoda, trematoda	48020
Stolephorus indicus	Haomei estuary	27.37	Copepoda	48006
Stolephorus indicus	Haomei estuary	27.93	Copepoda, trematoda, Gastropoda	48006
Stolephorus indicus	Haomei estuary	27.97	Copepoda	48006
Stolephorus indicus	Houmeili estuary	28.10	Gastropoda, Bivalva larvae, copepoda, trematoda	48020
Stolephorus indicus	Haomei estuary	28.17	Copepoda, trematoda	48006
Stolephorus indicus	Houmeili estuary	28.37	Gastropoda, copepoda	48020
Stolephorus indicus	Houmeili estuary	28.87	Gastropoda, copepoda	48020
Stolephorus indicus	Houmeili	30.56	Gastropoda, trematoda,	48020

	estuary		copepoda	
Stolephorus indicus	Haomei estuary	31.04	Copepoda, Gastropoda, trematoda, decapoda zoea	48006
Stolephorus indicus	Haomei estuary	31.31	Copepoda, bivalve larvae, Gastropoda	48020
Stolephorus indicus	Haomei estuary	31.38	Copepoda, Gastropoda	48006
Stolephorus indicus	Houmeili estuary	32.80	Gastropoda, trematoda, copepoda	48020
Stolephorus indicus	Haomei estuary	33.40	Copepoda, Gastropoda, trematoda	48006
Stolephorus indicus	Haomei estuary	34.38	Copepoda, Gastropoda, detritus	48020
Stolephorus indicus	Haomei estuary	34.48	Copepoda, Gastropoda	48006
Stolephorus indicus	Houmeili estuary	35.16	Gastropoda, copepoda	48020
Stolephorus indicus	Haomei estuary	36.89	Copepoda	48006
Stolephorus indicus	Haomei estuary	37.05	Copepoda, decapoda zoea	48006
Stolephorus indicus	Haomei estuary	41.00	Decapoda, decapoda zoea, decapoda megalopa, Gastropoda, copepoda	48006
Stolephorus insularis	Chonggang estuary	19.78	Eggs	47504
Stolephorus insularis	Haomei beach	25.00	Copepoda, centric diatom, eggs, Bivalva	47865
Stolephorus insularis	Chonggang estuary	25.19	Copepoda, eggs	47623
Stolephorus insularis	Chonggang estuary	25.19	Bivalve larvae, Cirripedia cypris, eggs, copepoda	47504
Stolephorus insularis	Chonggang estuary	25.64	Copepoda, eggs, Chaetognatha	47623
Stolephorus insularis	Chonggang estuary	26.01	Copepoda	47623
Stolephorus insularis	Chonggang estuary	26.90	Copepoda, Cirripedia cypris, bivalve veliger, decapod zoea, eggs	47623
Stolephorus insularis	Haomei estuary	27.00	Copepoda, decapod zoea, eggs, centric diatoms	47863
Stolephorus insularis	Chonggang estuary	27.14	Cirripedia cypris, copepoda, bivalve	47623
Stolephorus insularis	Haomei beach	27.37	Copepoda, eggs, Cirripedia cypris	47593
Stolephorus insularis	Chonggang estuary	27.69	Copepoda	47623
Stolephorus insularis	Chonggang estuary	27.91	Bivalve larvae, Cirripedia cypris, eggs, copepoda	47504
Stolephorus insularis	Chonggang estuary	28.04	Cirripedia cypris, bivalve larvae, eggs, copepoda	47623
Stolephorus insularis	Chonggang estuary	28.08	Bivalve larvae, Cirripedia cypris, eggs, copepoda	47504
Stolephorus insularis	Chonggang estuary	28.12	Eggs, Cirripedia cypris	47504
Stolephorus insularis	Chonggang estuary	28.21	Bivalve larvae, Cirripedia cypris, eggs, copepoda	47504

Stolephorus insularis	Chonggang estuary	28.67	Bivalve larve, copepoda	47504
Stolephorus insularis	Chonggang estuary	28.75	Eggs, copepoda	47504
Stolephorus insularis	Chonggang estuary	29.64	Copepoda, Cirripedia cypris, eggs, bivalve larvae	47623
Stolephorus insularis	Haomei estuary	30.23	Copepoda	47581
Stolephorus insularis	Haomei estuary	30.79	Copepoda, bivalve larvae	47464
Stolephorus insularis	Chonggang estuary	30.83	Copepoda, bivalve veliger, centric diatoms, filamentous and other algae, decapod zoea	47504
Stolephorus insularis	Chonggang estuary	31.02	Eggs, Cirripedia cypris, bivalve larvae	47504
Stolephorus insularis	Chonggang estuary	31.32	Bivalve larvae, Cirripedia cypris, eggs, copepoda	47504
Stolephorus insularis	Haomei estuary	31.59	Copepoda, Bivalva larvae, unidentifiable Crustacea, decapod zoea	47581
Stolephorus insularis	Chonggang estuary	31.76	Copepoda, bilvalve veliger, filamentous algae, Cirripedia cypris, Gastropoda, eggs	47623
Stolephorus insularis	Chonggang estuary	32.33	Copepoda, bivalve larvae, Cirripedia cypris, eggs, decapoda	47623
Stolephorus insularis	Haomei estuary	32.81	Copepoda, bivalve larvae, egg	47464
Stolephorus insularis	Haomei estuary	33.26	Copepoda, eggs, bivalve veliger, decapoda, decapoda zoa	47863
Stolephorus insularis	Haomei estuary	33.65	Copepoda, bivalve larvae	47464
Stolephorus insularis	Haomei estuary	34.95	Copepoda, bivalve larvae	47464
Stolephorus insularis	Haomei estuary	37.82	Copepoda	47464
Stolephorus insularis	Haomei estuary	39.74	Copepoda, bivalve larvae	47464
Stolephorus insularis	Haomei estuary	40.85	Copepoda, bivalve larvae	47464
Stolephorus insularis	Haomei estuary	42.20	Copepoda, decapod zoea, Cirripedia cypris, bivalve larvae, detritus	47581
Stolephorus insularis	Chonggang estuary	43.17	Cirripedia cypris, copepoda, shrimp, eggs, bivalve larvae	47504
Stolephorus insularis	Chonggang estuary	45.76	Cirripedia cypris, copepoda, shrimp, bivalve larvae	47504
Stolephorus insularis	Chonggang estuary	45.80	Shrimp	47504
Stolephorus insularis	Chonggang estuary	45.83	Bivalve veliger, Cirripedia cypris, mysida	47504
Stolephorus insularis	Chonggang estuary	46.47	Bivalve veliger, Cirripedia cypris	47504
Stolephorus insularis	Chonggang estuary	46.79	Cirripedia cypris, copepoda, shrimp	47504
Stolephorus insularis	Chonggang estuary	47.43	Bivalve veliger, Cirripedia cypris, pennate diatom, Gastropoda	47504

Stolephorus insularis	Chonggang estuary	47.77	Bivalve veliger, shrimp, copepoda, Cirripedia cypris, filamentous algae	47504
Takifugu niphobles	Chonggang estuary	34.66	Detritus, copepoda, decapoda	47518
Takifugu niphobles	Chonggang estuary	38.73	Gastropoda (benthic), Cirripedia cypris, amphipoda	47518
Takifugu niphobles	Chonggang estuary	40.84	Amphipoda	47964
Takifugu niphobles	Chonggang estuary	54.28	Shrimp, detritus	47964
Takifugu niphobles	Chonggang estuary	56.09	Amphipoda, detritus, isopoda	47964
Terapon jarbua	Haomei estuary	22.29	Copepoda, unidentifiable Crustacea, detritus	47642
Terapon jarbua	Haomei estuary	37.38	Fish, isopoda, amphipoda, Polychaeta, decapoda, Bivalva	48004
Terapon jarbua	Haomei estuary	62.09	Macrophyte, trematoda, ostracoda, unidentifiable Crustacea	47627
Thryssa chefuensis	Chonggang estuary	28.34	Copepoda, Cirripedia cypris, decopoda, detritus, Chaetognatha	47959
Thryssa chefuensis	Chonggang estuary	30.06	Chaetognatha, copepoda, detritus	47959
Thryssa chefuensis	Chonggang estuary	31.71	Copepoda	47959
Thryssa chefuensis	Chonggang estuary	32.45	Ostracoda	47959
Thryssa chefuensis	Chonggang estuary	33.11	Macrophyte, copepoda	47959
Thryssa chefuensis	Chonggang estuary	33.18	Cirripedia cypris, copepoda, detritus	47959
Thryssa chefuensis	Chonggang estuary	33.43	Copepoda, Polychaeta, trematoda	47959
Thryssa chefuensis	Chonggang estuary	34.29	Copepoda	47959
Thryssa chefuensis	Chonggang estuary	36.19	Copepoda, Chaetognatha, gammeridea, Crustacea	47959
Thryssa chefuensis	Chonggang estuary	37.30	Copepoda, trematoda	47959
Thryssa chefuensis	Chonggang estuary	41.74	Chaetognatha, copepoda, Cirripedia cypris, egg, unidentifiable benthic Crustacea, Polychaeta, decapod zoea	47959
Thryssa chefuensis	Chonggang estuary	44.26	Copepoda, Chaetognatha, pennate diatom, egg, Crustacea	47959
Thryssa chefuensis	Chonggang estuary	44.44	Copepoda, Crustacea, Chaetognatha	47959
Thryssa chefuensis	Chonggang estuary	46.62	Decapoda megalopa, Chaetognatha, shrimp, copepoda, eggs	47959

Thryssa chefuensis	Chonggang estuary	47.65	Copepoda, Chaetognatha	47959
Thryssa chefuensis	Chonggang estuary	47.93	Copepoda	47959
Thryssa chefuensis	Chonggang estuary	50.43	Decapoda, copepoda	47959
Thryssa chefuensis	Chonggang estuary	50.55	Chaetognatha, copepoda	47959
Thryssa chefuensis	Chonggang estuary	55.52	Chaetognatha, copepoda, Cirripedia cypris, detritus	47959
Thryssa chefuensis	Chonggang estuary	58.14	Filamentous algae, copepods, Chaetognatha	47959
Thryssa hamiltonii	Haomei estuary	19.44	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	19.77	Copepoda	47458
Thryssa hamiltonii	Haomei beach	20.30	Copepoda	47985
Thryssa hamiltonii	Haomei estuary	20.31	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	20.41	Copepoda	47458
Thryssa hamiltonii	Houmeili estuary	20.77	Copepoda, unidentifiable Crustacea	48019
Thryssa hamiltonii	Haomei estuary	20.84	Copepoda	47458
Thryssa hamiltonii	Haomei beach	21.69	Centric diatoms, copepoda	47985
Thryssa hamiltonii	Haomei estuary	21.93	Copepoda	47598
Thryssa hamiltonii	Houmeili estuary	22.00	Copepoda, decapod zoea	48019
Thryssa hamiltonii	Haomei estuary	22.29	Copepoda	48400
Thryssa hamiltonii	Houmeili estuary	22.41	Copepoda	48019
Thryssa hamiltonii	Houmeili estuary	22.47	Copepoda	48019
Thryssa hamiltonii	Houmeili estuary	22.48	Copepoda	48019
Thryssa hamiltonii	Haomei estuary	22.57	Copepoda	47598
Thryssa hamiltonii	Haomei estuary	22.57	Copepoda	48007
Thryssa hamiltonii	Houmeili estuary	22.77	Copepoda	48019
Thryssa hamiltonii	Haomei beach	22.77	Copepoda	47985
Thryssa hamiltonii	Haomei estuary	23.17	Copepoda	48007
Thryssa hamiltonii	Haomei estuary	23.26	Copepoda	47458
Thryssa hamiltonii	Houmeili estuary	23.30	Copepoda, Gastropoda	48019
Thryssa hamiltonii	Haomei estuary	23.41	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	23.50	Copepoda	48007
Thryssa hamiltonii	Haomei estuary	23.67	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	23.69	Copepoda	48007
Thryssa hamiltonii	Houmeili estuary	23.73	Copepoda, centric diatom, Gastropoda, Crustacea nauplii	48019
Thryssa hamiltonii	Houmeili estuary	23.81	Copepoda	48019
Thryssa hamiltonii	Haomei estuary	24.06	Copepoda	47598
Thryssa hamiltonii	Haomei estuary	24.15	Copepoda, bivalve larvae	47598

Thryssa hamiltonii	Haomei estuary	24.36	Copepoda	47862
Thryssa hamiltonii	Haomei estuary	24.40	Copepoda, mystery eggs	48007
Thryssa hamiltonii	Haomei estuary	24.53	Copepoda	48007
Thryssa hamiltonii	Haomei estuary	24.60	Copepoda, Crustacea nauplii	48007
Thryssa hamiltonii	Houmeili estuary	24.62	Copepoda, centric diatom, Gastropoda, trematoda	48019
Thryssa hamiltonii	Haomei estuary	24.63	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	25.23	Copepoda, Crustacea nauplii, eggs	48007
Thryssa hamiltonii	Haomei estuary	25.48	Copepoda	48007
Thryssa hamiltonii	Haomei beach	25.58	Copepoda, ostracoda, egg	47985
Thryssa hamiltonii	Haomei estuary	26.24	Copepoda	47598
Thryssa hamiltonii	Haomei estuary	26.48	Copepoda	47598
Thryssa hamiltonii	Haomei estuary	26.68	Copepoda	47458
Thryssa hamiltonii	Houmeili estuary	26.73	Copepoda, trematoda	48019
Thryssa hamiltonii	Haomei estuary	27.16	Copepoda	48007
Thryssa hamiltonii	Haomei estuary	27.20	Copepoda	47458
Thryssa hamiltonii	Haomei beach	27.69	Copepoda, decapoda megalopa, centric diatom, Chaetognatha, trematoda, eggs	47985
Thryssa hamiltonii	Haomei estuary	28.02	Copepoda	47862
Thryssa hamiltonii	Houmeili estuary	28.11	Copepoda, egg, Bivalva larva	48019
Thryssa hamiltonii	Houmeili estuary	28.49	Copepoda, centric diatom, Gastropoda, Bivalva	48019
Thryssa hamiltonii	Haomei estuary	28.54	Copepoda	47458
Thryssa hamiltonii	Houmeili estuary	29.01	Copepoda, centric diatom, Gastropoda, trematoda	48019
Thryssa hamiltonii	Houmeili estuary	29.33	Copepoda, Gastropoda, centric diatoms, colonial diatoms, decapod zoea	48019
Thryssa hamiltonii	Haomei estuary	29.61	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	30.01	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	30.17	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	30.19	Copepoda, decapoda zoea	47458
Thryssa hamiltonii	Houmeili estuary	30.87	Copepoda, Gastropoda, Cirripedia cypris, centric diatom	48019
Thryssa hamiltonii	Haomei estuary	31.19	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	31.38	Copepoda, eggs, pennate diatom	48007
Thryssa hamiltonii	Haomei beach	31.55	Unidentifiable Crustacea	48030
Thryssa hamiltonii	Haomei estuary	31.63	Copepoda, amphipoda	47458
Thryssa hamiltonii	Haomei estuary	32.28	Copepoda, bivalve veliger, eggs	47862
Thryssa hamiltonii	Haomei estuary	32.35	Copepoda	47458
Thryssa hamiltonii	Haomei estuary	32.89	Copepoda	47862
Thryssa hamiltonii	Haomei estuary	33.70	Copepoda, eggs	47862

Thryssa hamiltonii	Haomei estuary	33.88	Copepoda	47458
Thryssa hamiltonii	Haomei beach	34.09	Copepoda, Cirripedia cypris	47591
Thryssa hamiltonii	Haomei estuary	35.48	Copepoda	47862
Thryssa hamiltonii	Haomei estuary	35.55	Copepoda	47862
Thryssa hamiltonii	Haomei estuary	36.78	Copepoda	47862
Thryssa hamiltonii	Haomei estuary	39.34	Copepoda, shrimp	47862
Thryssa hamiltonii	Haomei estuary	41.88	Copepoda, eggs	47862
Thryssa hamiltonii	Houmeili estuary	50.68	Bivalva, copepoda, fish, Polychaeta, Cirripedia exopods	48019
Thryssa setirostris	Haomei beach	20.79	Eggs	47864
Thryssa setirostris	Haomei beach	22.33	Copepoda, eggs	47864
Thryssa setirostris	Haomei estuary	22.40	Copepoda	47463
Thryssa setirostris	Haomei beach	22.65	Copepoda	47977
Thryssa setirostris	Haomei beach	23.03	Copepods, eggs	47864
Thryssa setirostris	Haomei beach	23.14	Copepods, eggs	47864
Thryssa setirostris	Haomei beach	23.26	Eggs, copepoda	47864
Thryssa setirostris	Haomei beach	23.33	Trematoda	47977
Thryssa setirostris	Haomei beach	23.63	Copepods, eggs, Foraminifera, macrophyte	47864
Thryssa setirostris	Haomei beach	24.35	Gammeridia	47645
Thryssa setirostris	Haomei beach	24.37	Copepoda	47645
Thryssa setirostris	Haomei estuary	25.23	Calanoid copepoda, Crustacea nauplii	47463
Thryssa setirostris	Haomei beach	25.38	Copepoda	47645
Thryssa setirostris	Haomei estuary	25.46	Copepoda, decapoda, detritus	47463
Thryssa setirostris	Haomei beach	25.75	Trematoda	47645
Thryssa setirostris	Haomei estuary	25.88	Copepoda	47463
Thryssa setirostris	Haomei beach	25.95	Copepoda, gammeridea, Crustacea nauplii	47986
Thryssa setirostris	Haomei beach	26.66	Copepoda	47645
Thryssa setirostris	Haomei estuary	26.87	Gastropoda, copepoda, filamentous algae, dinoflagellata, Crustacea nauplii	47463
Thryssa setirostris	Haomei estuary	27.55	Copepoda, decapoda	47463
Thryssa setirostris	Haomei estuary	27.56	Copepoda, bivalve veliger, Gastropoda, decapoda megalopa	47463
Thryssa setirostris	Haomei estuary	27.72	Copepoda	47463
Thryssa setirostris	Haomei estuary	28.39	Copepoda, bivalve veliger, eggs	47463
Thryssa setirostris	Haomei estuary	28.48	Copepoda, gastrapoda, eggs	47463
Thryssa setirostris	Haomei beach	29.43	Copepoda	47645
Trachinotus blochii	Shuang Chun beach	41.69	Polychaete	47975

Trachinotus blochii	Shuang Chun beach	44.20	Shrimp	47975
Trachinotus blochii	Haomei beach	60.13	Copepoda	47625
Trachinotus blochii	Haomei beach	60.72	Bivalva, copepoda, hydrozoa, Cirripedia exopods, caprellidae	47589
Trachinotus blochii	Haomei beach	61.03	Copepoda	47625
Trachinotus blochii	Haomei beach	61.64	Bivalva, copepoda, eggs, centric diatoms, pennate diatoms, hydrozoa, Cirripedia exopods, echinodermata larvae, collembola, caprellidae, other algae, detritus	47589
Trachinotus blochii	Haomei beach	62.96	Bivalva, eggs, copepoda, Crustacea, centric diatoms, hydrozoa, Cirripedia exopods, detritus, collembola, gastrapoda	47589
Trachinotus blochii	Haomei beach	66.25	Bivalva, copepoda, eggs, centric diatoms	47589
Trachinotus blochii	Haomei beach	66.82	Bivalva, eggs, copepoda, centric diatoms, Nematoda, detritus	47589
Trachinotus blochii	Haomei beach	72.77	Detritus, copepoda, Polychaeta	47625
Zenarchopterus sp.	Haomei estuary	25.54	Terrestrial insects, Gastropoda, filamentous algae, copepoda	47993
Zenarchopterus sp.	Haomei estuary	32.33	Gastropoda, Crustacea nauplii, colonial diatom	48023
Zenarchopterus sp.	Haomei estuary	33.16	Terrestrial insects, Gastropoda, copepod	47993
Zenarchopterus sp.	Haomei estuary	33.53	Terrestrial insects, Gastropoda	48023
Zenarchopterus sp.	Haomei estuary	38.13	Copepoda, terrestrial insects, Gastropoda	48023
Zenarchopterus sp.	Haomei estuary	38.17	Terrestrial insect, Gastropoda	48023
Zenarchopterus sp.	Houmeili estuary	39.82	Terrestrial insects, Gastropoda, Araneae	47993
Zenarchopterus sp.	Houmeili estuary	40.64	Terrestrial insects, Gastropoda, filamentous algae, copepoda	48023
Zenarchopterus sp.	Houmeili estuary	45.42	Plants, terrestrial insects	47993
Zenarchopterus sp.	Houmeili estuary	52.72	Terrestrial insects, Gastropoda	48023

Zenarchopterus sp.	Houmeili estuary	52.78	Plants, terrestrial insects	47993

Table 1.2 Prey types comprising each prey category used for statistical analysis of fish diets. Prey categories are not strictly taxonomic.

Prey category	Prey category composition
Detritus (Det)	Detritus
Zooplankton (Zoo)	Copepoda, Bivalva and Gastropoda veligers, Ostracoda, Cirrepedia cypris and exopods, Crustacea nauplii, Decapoda zoea, Echinodermata larvae, Cladocera, Appendicularia, planktonic Hydrozoa, Trematoda
Benthic mollusca (Mol)	Gastropoda, Bivalva
Eggs (Egg)	Vertebrate and invertebrate eggs
Plants (Pla)	Aquatic and terrestrial macrophytes
Algae (Alg)	Algae, cyanobacteria
Phytoplankton (Phy)	Centric and pennate diatoms, Dinoflagellata, Silicoflagellata, Tintinnida, Phytoflagellata
Crustacea (Cru)	Decapoda adults and megalopa, shrimp, Amphipoda, Isopoda, Collembola
Foraminifera (For)	Foraminifera
Nematoda (Nem)	Nematoda
Polychaeta (Pol)	Polychaeta
Fish (Fis)	Actinopterygii
Terrestrial invertebrata (Ter)	Insecta, Araneae
Hydrozoa (Hyd)	Sessile Hydrozoa
Sipuncula (Sip)	Sipuncula
Chaetognatha (Cha)	Chaetognatha

Table 1.3. Observed percent frequency of plants and detritus (A), corrected % frequencies used in statistical analyses (B), and justification for considering plants and/or detritus as incidentally ingested material. Morphological evidence consisted of observations of trophic structures such as jaws, teeth, and the gastrointestinal tract.

Species	Detritus		Plants		Justification	References
	A	B	A	B		
Acentrogobius nebulosus	83	0			Morphology, small quantities of detritus in guts, and previous study of this species	Heithaus et al. 2011; Zagars et al. 2013
Alepes djedaba	70	0			Morphology, small quantities of detritus in guts, and previous study of this species	Sivakami 1990; Raje 1993; Deshmukh 2007
Encrasicholina heteroloba	9	0			Morphology, small quantities of detritus in guts, and previous study of this species	Rao 1967; Milton et al. 1990
Hypoatherina valenciennei	13	0			Morphology, small quantities of detritus in guts, and previous study of this species	Nakane et al. 2011
Eubleekeria splendens	10	0			Morphology, small quantities of detritus in guts, and diet data from closely related species	Hajisamae et al. 2003; 2004; Hajisamae and Ibrahim 2008; Seah et al. 2009
Netuma thalassina	100	0	10	0	Morphology, small quantities of detritus in guts, benthic feeding, and previous study of this species	Rainboth 1996
Paraplagusia bilineata	20	0			Morphology, small quantities of detritus in guts, benthic feeding, and diet data from closely related species	Lakshmi 2010
Photopectoralis bindus	6	0	2	0	Morphology, small quantities of detritus in guts, and diet data from closely related species	Hajisamae et al. 2003; 2004; Hajisamae and Ibrahim 2008; Seah et al. 2009
Secutor interruptus	6	0			Morphology, small quantities of detritus in guts, and diet data from closely related species	Hajisamae et al. 2003; 2004; Hajisamae and Ibrahim 2008; Seah et al. 2009
Sillago asiatica	43	0			Morphology, small quantities of detritus in guts, benthic feeding, and diet data from closely related species	Hajisamae et al. 2003; 2004; Hajisamae and Ibrahim 2008; Krück et al. 2009
Stolephorus indicus	4	0			Morphology, small quantities of detritus in guts, and previous study of this species	Chacko 1948; De Troch et al. 1998; Hajisamae et al. 2003; Hajisamae and Ibrahim 2008; Horinouchi et al. 2012

Stolephorus insularis	2	0			Morphology, small quantities of detritus in guts, and previous study of this species	Rao 1967
Takifugu niphobles	60	0			Morphology, small quantities of detritus in guts, and previous study of this species	Yamahira et al. 1996; Nakane et al. 2011
Thryssa chefuensis	20	0	5	0	Morphology, small quantities of detritus in guts, and diet data from closely related species	Hajisamae et al. 2003; Baker and Sheaves 2005
Thryssa setirostris	4	0	4	0	Morphology, small quantities of detritus in guts, and previous study of this species	Hajisamae et al. 2003
Trachinotus blochii	70	0			Morphology, small quantities of detritus in guts, and previous study of this species	Nakane et al. 2011

Table 1.4. Species of fish collected in Taiwan, number of individuals collected in estuary (Individuals estuaries) and beach (Individuals beaches) habitats, range of standard lengths (SL) sampled, and trophic guild (abbreviations defined in Table 1.3) if estimated.

Species	Individuals estuaries	Individuals beaches	Trophic guild	SL range (mm)
Acanthopagrus sp.	1			30.48
Acentrogobius moloanus	9		Omni	23.08-61.37
Acentrogobius nebulosus	6		Omni	24.73-47.29
Acentrogobius cf plaufamii	6		Omni	25.62-32.31
Albula vulpes	1			77.99
Alepes djedaba	10	10	Crus	18.94-88.94
Ambassis cf gymnoephalus	11	10	Zoop	18.74-41.21
Ambassis miops	3			25.55-26.58
Aulopareia unicolor	1			39.75
Bathygobius sp.	1			27.33
Boleophthalmus pectinirostris	1			109.29
Bothidae sp.	1			69.36
Callionymus sagitta	2			28.00-41.10
Carangidae sp.	1			15.78
Carangoides sp.	1			26.10
Caranx sexfasciatus		1		39.68
Chanos chanos	3			79.93-96.63
Chelon macrolepis	12	23	Detr	22.60-97.11
Chelon subviridis	1			62.73
Crenimugil crenilabis	1			67.10
Cryptocentrus yatsui	5		Zoop	24.24-38.63

Drombus cf ocyurus	10		Omni	19.07-27.03
Dussumieria elopsoides	7		Crus	40.25-45.70
Encrasicholina heteroloba	10	1	Zoop	26.14-47.52
Eubleekeria splendens	20	2	Zoop	14.70-56.97
Gazza minuta	1			28.36
Gerres limbatus	2			20.08-37.61
Hypoatherina valenciennei	5	3	Zoop	28.04-48.19
Hyporhamphus sp.	5		Terr	47.45-65.36
Lutjanus argentimaculatus	1			126.50
Moolgarda cunnesius	21	7	Detr	20.20-65.76
Nematalosa come	27	1	Detr	28.18-151.12
Netuma thalassina	10		Zoop	49.10-61.94
Oligolepis acutipennis	3			30.57-36.30
Paraplagusia bilineata	5		Crus	30.35-81.47
Photopectoralis bindus	33	18	Zoop	11.74-60.42
Sardinella gibbosa	12		Zoop	30.84-74.35
Sardinella lemuru	4			48.40-58.21
Sciaenidae sp.	1			53.56
Scomberoides lysan	10	6	Crus	26.28-93.58
Secutor interruptus	10	8	Zoop	17.61-32.27
Sillago asiatica	9	5	Zoop	20.85-73.5
Sphyraena barracuda	1		Pisc	133.20
Sphyraena flavicauda	1		Pisc	80.85
Sphyraena jello	3		Pisc	50.58-103.86
Stolephorus indicus	27		Zoop	20.26-41.00
Stolephorus insularis	41	2	Zoop	19.78-47.77
Takifugu niphobles	5		Crus	34.66-56.09
Terapon jarbua	1	2		22.29-62.09

Thryssa chefuensis	20		Zoop	28.34-58.14
Thryssa hamiltonii	65	7	Zoop	19.44-50.68
Thryssa setirostris	10	15	Zoop	20.79-29.43
Trachinotus blochii		10	Zoop	41.69-66.82
Zenarchopterus sp.	11		Terr	25.54-52.78
Total:	468	131		

Table 1.5. Five most important prey types, listed in order of importance, of each trophic guild identified in this study.

Guild	Important prey
Crustacivores (Crus)	Crustacea nekton, zooplankton, fish, algae, phytoplankton
Detritivores (Detr)	Detritus, phytoplankton, eggs, algae, zooplankton
Omnivores (Omni)	Zooplankton, algae, detritus, phytoplankton, plant matter
Piscivores (Pisc)	Fish, eggs
Terrestrial invertivores (Terr)	Terrestrial invertebrates, zooplankton, plant matter, eggs, phytoplankton
Zooplanktivores (Zoop)	Zooplankton, eggs, phytoplankton, crustacea nekton, algae

Table 1.6. Parameters estimated by simple linear regressions of fish standard length vs. maximum prey width for individual species with a statistically significant correlation between standard length and prey width and analyses including all species and all species except detritivores.

Species	**Slope**	**Intercept**	**r^2**	**p-value**
Alepes djedeba (Adje)	42.41	-1201.82	0.75	<0.0001
Chelon macrolepis (Cmac)	-2.41	242.38	0.10	0.0336
Photopectoralis bindus (Pbin)	2.11	237.84	0.07	0.0369
Scomberoides lysan (Slys)	39.23	-336.89	0.34	0.0165
Stolephorus indicus (Sind)	26.43	-434.31	0.41	0.0002
Stolephorus insularis (Sins)	21.86	-304.07	0.39	<0.0001
Thryssa hamiltonii (Tham)	20.10	-181.33	0.28	<0.0001
Thryssa setirostris (Tset)	32.88	-524.51	0.16	0.0290
All species	18.07	-196.26	0.22	<0.0001
All species except detritivores	24.50	-352.92	0.35	<0.0001

Table 1.7. Review of previous diet studies on species investigated in the present study (when identified to the species-level) with remarks on congruence between studies. For references it is indicated if gut content analysis (GCA) or stable isotope analysis (SI) was used to describe diets and, when available, the range or mean of fish lengths examined in mm total length (TL), fork length (FL), or standard length (SL).

Species	SL (mm)	Congruence	References (diet quantification method; sizes examined)
Acentrogobius moloanus	23.08-61.37	Yes	Zagars et al. 2013 (SI & GCA; 25-60 SL)
Acentrogobius nebulosus	24.73-47.29	Detritus, plant material, and phytopankton found in this study likely incidentally consumed	Heithaus et al. 2011 (SI, 52.6 mean TL); Zagars et al. 2013 (SI & GCA, 20-30 SL),
Albula vulpes	77.99	Yes	Colton and Alevizon 1983 (256-630 SL); Crabtree et al. 1998 (228-702 FL); Iinberger and Posada 2005 (336-644 FL)
Alepes djedaba	18.94-88.94	Detritus found in this study likely incidentally consumed	Sivakami 1990 (150-319 TL); Raje 1993 (151-336 TL); Deshmukh 2007
Ambassis cf. *gymnoephalus*	18.74-41.21	Yes	Venkataraman 1963 (GCA; 45-91 TL); Martin and Blaber 1983 (GCA; <30 & >30 SL groups)
Ambassis miops	25.55-26.58	Yes	Nanjo et al. 2008 (GCA; 20-46 SL)
Aulopareia unicolor	39.75	No data available	
Boleophthalmus pectinirostris	109.29	In contrast to Yang, this study found crustacea	Yang et al. 2003 (GCA; 19-110 SL)
Callionymus sagitta	28.00-41.10	No data available	
Caranx sexfasciatus	39.68	Yes	Blaber and Cyrus 1983 (GCA; 35-500 SL); Bachok et al. 2004 (GCA; 370-700 SL); Baker and Sheaves 2005 (GCA; 28-265 FL)
Chanos chanos	79.93-96.63	Yes	Chacko 1949 (120-1200 TL); Tampi 1958 (GCA; 282-1003 SL); Nakane et al. 2011 (29-39 SL)
Chelon macrolepis	22.60-97.11	Yes	Blaber and Whitfield 1977 (GCA; 10-59 SL); Lin et al. 2007 (SI & GCA); Nanjo et al. 2008 (GCA; 44-202 SL)
Chelon subviridis	62.73	Yes	Fatema et al. 2015 (GCA)
Crenimugil crenilabis	67.10	Yes	Blaber and Whitfield 1977 (GCA; 10-59 SL)
Cryptocentrus yatsui	24.24-38.63	No data available	

Drombus cf. *ocyurus*	19.07-27.03	No data available	
Dussumieria elopsoides	40.25-45.70	Yes	Chacko 1949 (GCA; 90-200 SL); Rao 1967 (GCA; 48-125 SL)
Encrasicholina heteroloba	26.14-47.52	Yes, detritus found in this study likely incidentally consumed	Rao 1967 (GCA; 55-68 TL); Milton et al. 1990 (GCA; 34-68 SL)
Eubleekeria splendens	14.70-56.97	Yes, detritus found in this study likely incidentally consumed	Chew et al. 2012 (SI & GCA)
Gazza minuta	28.36	Yes	Seah et al. 2009 (GCA); Seah et al. 2011 (GCA)
Gerres limbatus	20.08-37.61	Yes	Prabhakara Rao 1968 (GCA)
Hypoatherina valenciennei	28.04-48.19	This is the first study to report terrestrial insects, detritus found in this study likely incidentally consumed	Kanou et al. 2004 (GCA; 11-15 SL); Inoue et al. 2005 (GCA; 64-83 SL); Nakane et al. 2011 (GCA; 18-64 SL)
Lutjanus argentimaculatus	126.50	Zooplankton and crustacea	De Troch et al. 1998 (GCA; 20-120 SL)
Moolgarda cunnesius	20.20-65.76	Yes	Blaber and Whitfield 1977 (SI & GCA; 19-59 SL); Lin et al. 2007 (SI)
Nematalosa come	28.18-151.12	Yes	Nanjo et al. 2008 (GCA; 37-257 SL)
Netuma thalassina	49.10-61.94	Yes, detritus and plant material found in this study likely incidentally consumed	Rainboth 1996 (GCA)
Oligolepis acutipennis	30.57-36.30	Yes	Nanjo et al. 2008 (GCA; 42 SL)
Paraplagusia bilineata	30.35-81.47	Yes	Lakshmi 2010 (GCA)
Photopectoralis bindus	11.74-60.42	Yes	Seah et al. 2009 (GCA); Seah et al. 2011 (GCA); Rao et al. 2015 (GCA; 35-127 TL)
Sardinella gibbosa	30.84-74.35	Yes	Chacko 1949 (GCA); Nyunja et al. 2002 (GCA); Mavuti et al. 2004 (GCA; 57-94 SL); Shahraki et al. 2014 (SI)
Sardinella lemuru	48.40-58.21	Yes	Horinouchi et al. 2012 (GCA; 32.9-40.8 TL)
Scomberoides lysan	26.28-93.58	This study did not observe scale eating reported by Major et al., 1973	Blaber and Cyrus 1983 (GCA; 20-60 SL), Major 1973 (GCA; 21.8-127 SL)
Secutor interruptus	17.61-32.27	No data available	
Sillago asiatica	20.85-73.5	No data available	
Sphyraena barracuda	133.20	Yes	De Troch et al. 1998 (GCA; 90-350 SL)
Sphyraena flavicauda	80.85	Yes	Nakamura et al. 2003 (GCA; 87-133 SL)

Sphyraena jello	50.58-103.86	Yes	Hajisamae et al. 2003 (GCA; 91 mean TL); Bachok et al. 2004 (GCA; 550-1000 SL)
Stolephorus indicus	20.26-41.00	Yes	Chacko 1949 (GCA; 40-140 TL); De Troch et al. 1998 (GCA; 40-75 SL); Hajisamae et al. 2003 (GCA; 60 mean TL); Hajisamae and Ibrahim 2008 (GCA; 66 mean SL); Horinouchi et al. 2012 (GCA; 42-70.1 TL)
Stolephorus insularis	19.78-47.77	Yes	Rao 1967 (GCA; 40-75 SL)
Takifugu niphobles	34.66-56.09	Detritus found in this study likely incidentally consumed	Yamahira et al. 1996 (GCA); Nakane et al. 2011 (GCA; 15-118 SL)
Terapon jarbua	22.29-62.09	Yes	Nanjo et al. 2008 (GCA; 31-173 SL); Nakane et al. 2011 (GCA; 73-86 SL)
Thryssa chefuensis	28.34-58.14	No data available	
Thryssa hamiltonii	19.44-50.68	Yes	Bapat and Bal 1950 (GCA; 22-93 TL); Rao 1967 (GCA; 165 SL); Brewer et al. 1995 (GCA; 115-200 SL); Salini et al. 1998 (GCA; 74-270 SL); Hajisamae et al. 2003 (GCA; 40 mean TL); Baker and Sheaves 2005 (GCA; 66-207 FL); Hajisamae and Ibrahim 2008 (GCA; 79 mean TL); Taher 2010 (GCA; 81-215 TL); Zagars et al. 2013 (SI & GCA; 57-101 SL);
Thryssa setirostris	20.79-29.43	Yes	Hajisamae et al. 2003 (GCA; 55 mean TL)
Trachinotus blochii	41.69-66.82	Yes	Nakane et al. 2011 (GCA; 85-98 SL)

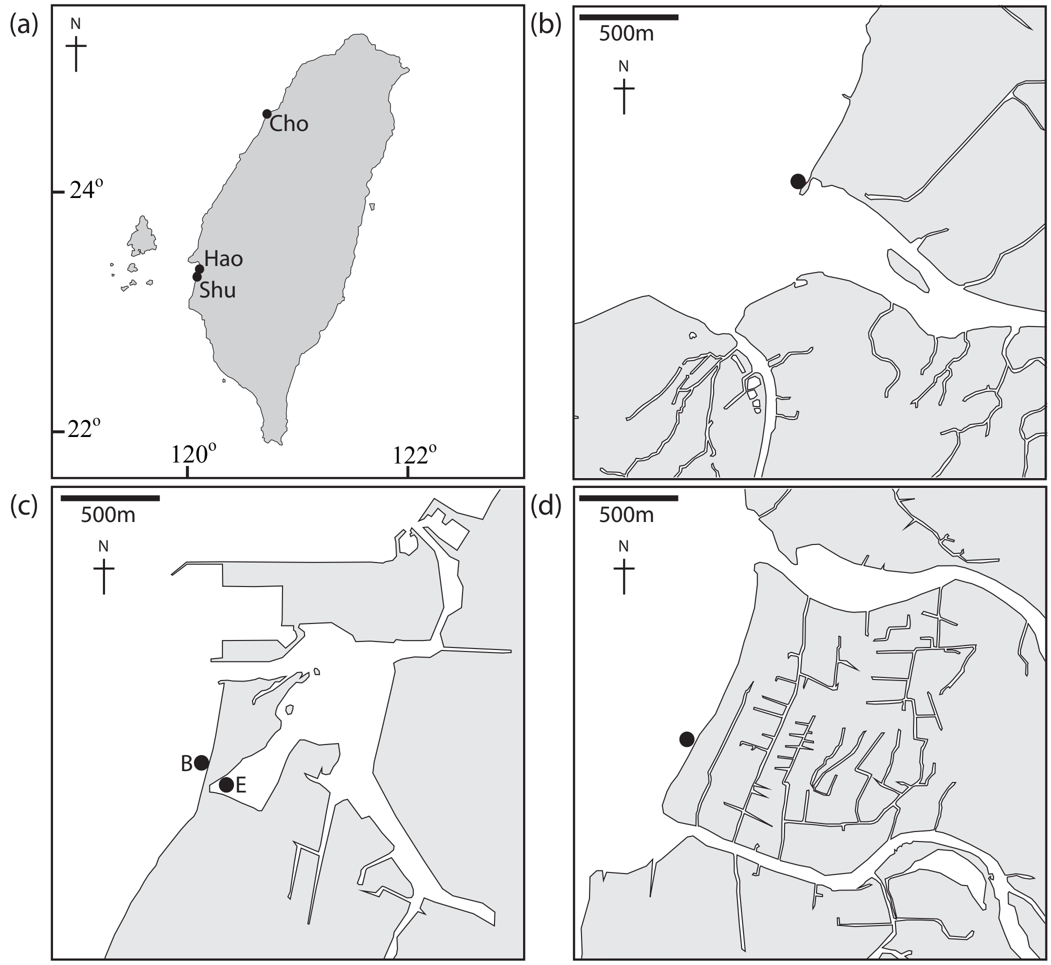
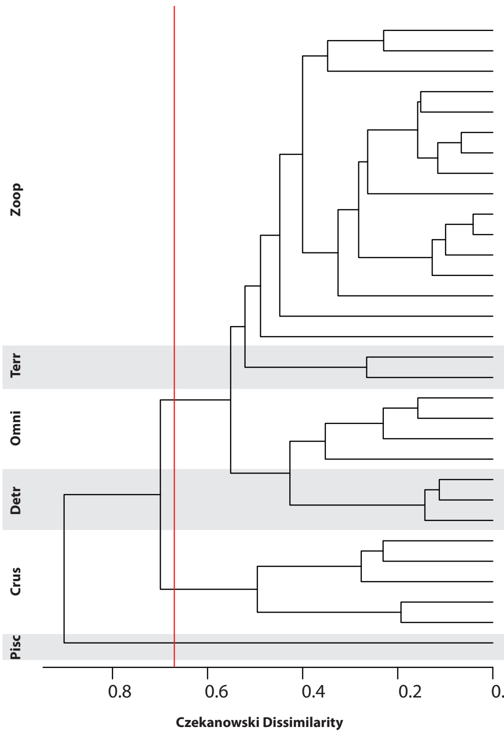


Figure 1.1. (a) Locations of sampling sites in Taiwan (Chonggang Estuary (Cho), Haomei Estuary and Beach (Hao), and Shuang Chun Beach (Shu). Large-scale maps of each site with points denoting location sampled: (b) Chonggang Estuary, (c) Haomei beach (B) and estuary (E), and (d) Shuang Chun Beach.



	Det	Zop	Mol	Egg	Pla	Alg	Phy	Cru	For	Nem	Pol	Fis	Ter	Hyd	Sip	Cha
Sardinella gibbosa	75	100		75		17	75	8								8
Netuma thalassina		100		70		20	70	50			10			10		
Trachinotus blochii		90	50	40		20	40	40		10	20			30		
Sillago asiatica		93		57		7	14	36			14					
Photopectoralis bindus		100		69		25	12	22		4	2					
Stolephorus insularis		95		51		7	9	21								2
Ambassis cf. *gymnocephalus*		100		48		10	5	14								
Thryssa setirostris		92		32		4	4	20	4							
Eublekeeria splendens		96		29		17	42	13	8	13	8			4	4	
Stolephorus indicus		100		4				4								
Encrasicholina heteroloba		100		9												
Secutor interruptus		100		28												
Thryssa hamiltonii		99	1	13			13	7			1	1				
Thryssa chefuensis		100		15		5	5	35			10					55
Hypoatherina valenciennei		75						13					25			
Cryptocentrus yatsui	20	83			17	33			17							
Zenarchopterus sp.		82			18		9						100			
Hyporhamphus sp.		100		60	60		40						100			
Drombus cf. *oxyurus*	50	100		20		70	40	50		10						
Acentrogobius cf. *plaufamii*	50	67		33		83	33	33		33						
Acentrogobius moloanus	67	100		22	33	56	44			11						
Acentrogobius nebulosus		83		17	83	83	17	33		17	33					
Nematalosa come	96	32		29	11	50	75	7								
Moolgarda cunnesius	96	25		57	4	43	82	4	7	4						
Chelon macrolepis	91	46		46	3	34	60	9		3	3			3		
Takifugu niphobles		20	20					80								
Paraplagusia bilineata		20				20		100								
Dussumieria elopsoides		14						100				43				
Scomberoides lysan		38		6		19	13	50		6		25				
Alepes djedeba		60		5		40	15	40				30				
Sphyraena spp.				20								100				

Figure 1.2. Dendrogram depicting results of cluster analysis based on Czekanowski Dissimilarity showing diet relationships of near-shore marine and estuarine fishes in Taiwan. The red line marks dissimilarity of 0·67, the critical dissimilarity value indicating statistically significant clusters obtained by bootstrapping. Trophic guilds identified by similarity profile analysis are labeled using abbreviations defined in Table 1.3. The percent frequency the 16 prey groups occurred within each species is shown. Prey groups are labeled with three-letter abbreviations described in Table 1.2.

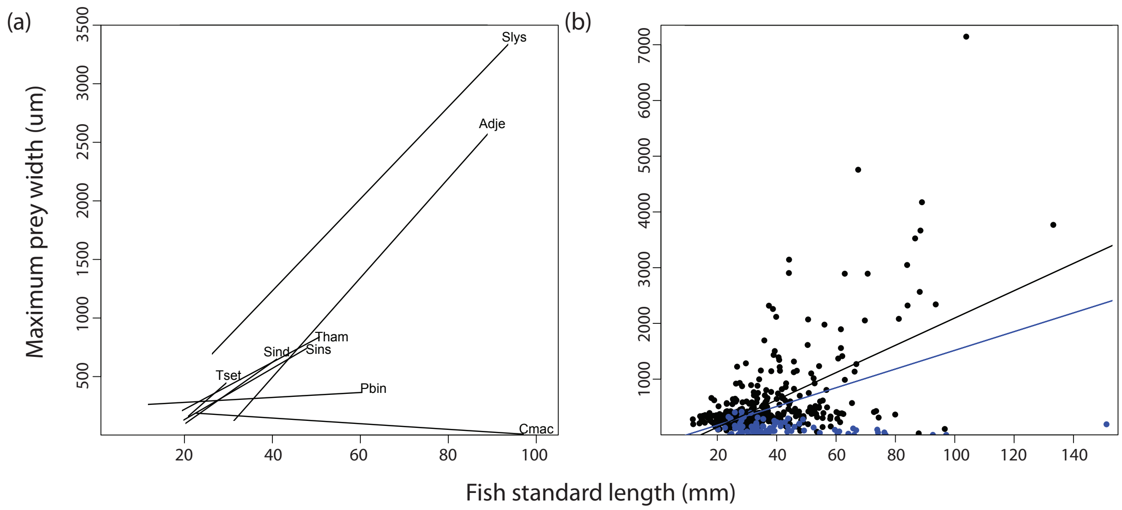


Figure 1.3. (a) Regression lines of maximum prey width consumed versus standard length for species with a statistically significant correlation between these variables. (b) Scatter plot with regression lines of maximum prey width consumed versus standard length of fish for near-shore marine and estuarine fishes in Taiwan. Blue points represent detritivores. The blue and black regression lines are estimated when detritivores are included and excluded from analysis, respectively. Species abbreviations and regression parameters are in Table 1.6.

CHAPTER 2

Trophic niches through ontogeny in twelve species of Indo-Pacific marine Clupeoidei (herrings, sardines, and anchovies)

1. Introduction

My understanding of processes in ecology and evolutionary biology is often hampered by the absence of fundamental knowledge of the biology of species. The trophic niche is an aspect of species biology that is foundational to understanding many biological processes, including interspecific and intraspecific interactions within biotic communities, morphological evolution, and spatial patterns of species richness and community structure (MacArthur and Levins 1967; Gaines and Lubchenco 1982; Floeter et al. 2005; Olden et al. 2006; Crowder and Snyder 2010; Day et al. 2011; Egan et al. 2018a, Ch3). In many species the trophic niche is poorly described, lacking quantitative estimates of the prey sizes and types consumed. Furthermore, diet studies often do not consider ontogeny, creating the assumption that diet is constant throughout an individual's existence. Herein I quantify the trophic niches of twelve ecologically and economically important Indo-Pacific marine clupeoids (herrings, sardines, and anchovies; Whitehead et al. 1988; Cury et al. 2000; Majluf et al. 2017).

In many coastal marine ecosystems small schooling fishes have a large influence on food web dynamics and structure (Cury et al. 2000; Daskalov et al. 2007; Casini et al. 2009; Nelson et al. 2013; Sheaves et al. 2016). These fishes generally feed at low trophic levels, consuming prey items such as zooplankton, small nekton, phytoplankton, macroalgae, and detritus (Espinoza and Bertrand 2008; Costalago and Palomera 2014; Hundt et al. 2014; Buchheister and Latour 2015; Egan et al. 2017, Ch1; Egan et al. 2018, Ch3). Many small coastal fishes attain very large population sizes, transfer substantial amounts of energy between lower and higher trophic levels within and between food webs (Nelson et al. 2013; Sheaves et al. 2016), exert top-down control on populations of plankton and small nekton (Daskalov et al. 2007; Casini et al. 2009), and exert bottom-up control on predator populations (Cury et al. 2000). Despite their importance in marine ecosystems, the diets of many small coastal fishes are either completely unknown or only preliminarily described.

Most fish diet studies quantify the types of prey consumed and frequently use these data to assign predators to trophic guilds, which are groups of species that eat similar prey (Root 1967; Garrison and Link 2000). Assigning predators to trophic guilds is useful because it reduces the complexity of diet data, making it easier to include in statistical analyses (Garrison and Link 2000; Egan et al. 2018a, Ch3). Prey size is also a highly informative aspect of diet because different prey sizes are associated with distinct functional requirements for predators (Pearre 1986; Scharf et al. 2000; Krebs and Turingan 2003; Mihalitsis and Bellwood 2017). For example, gape plays a major role in limiting the maximum size of prey a predator can consume (Pearre 1986; Sabatés and Saiz 2000; Krebs and Turingan 2003; Mihalitsis and Bellwood 2017). Measurements of prey size consumption by small fishes have revealed variation in diet not captured by prey type data. For example, variation in prey size consumption exists between and within zooplanktivorous species largely overlapping in prey type consumption (Pepin and Penney 1997; Ayón et al. 2011; Costalago et al. 2015; Brosset et al. 2016). Subtle differences in prey size consumption have been linked to distinct, large fluctuations in population sizes driven by changes in zooplankton size availability in the Peruvian Humboldt Current (Ayón et al. 2011) and Mediterranean Sea (Brosset et al. 2016). This demonstrates that incorporating prey size data in future ecological and evolutionary research and fisheries population modeling will likely be informative.

Accounting for ontogeny is important when considering the ecological and evolutionary implications of diet because many fishes exhibit ontogenetic diet shifts. Consequently, at different points in ontogeny species may perform very different ecosystem functions (Polis 1984; Linzmaier et al. 2018). Fishes most often consume increasingly larger and more evasive prey as they grow. However, some species exhibit diet shifts from mostly zooplankton to large quantities of sessile and sometimes very small materials such as plants, algae, or detritus (Pepin and Penney 1997; Sabatés and Saiz 2000; Scharf et al. 2000; Scharf and Schlight 2000; Horinouchi et al. 2012; Costalago and Palomera 2014; Henrique et al. 2014; Egan et al. 2017, Ch1; Linzmaier et al. 2018). The rate and extent of ontogenetic diet changes are variable between species and can be difficult to predict using simple measures of morphology such as predator length or gape (Scharf et al. 2000; Gravel et al. 2013; Egan et al. 2017, Ch1).

This study quantifies the trophic niches of twelve species of Indo-Pacific clupeoids (Table 2.1). I adhered to the resource-utilization formulation of the realized ecological niche concept, which defines the ecological niche as a multidimensional volume with each niche axis describing the use of a particular resource. Niche breadth describes the range of resource use along a single niche axis. I used the resource-utilization formulation of the niche concept because there are well-defined rules for its measurement and it focuses on organismal resource use, which facilitates inter- and intraspecific comparisons of organismal biology (MacArthur and Levins 1967; Schoener 2009; Devictor et al. 2010). I used my diet data to address four objectives: (1) assign species to trophic guilds based upon prey type and size consumption, (2) identify ontogenetic shifts in prey type and size consumption, (3) test the hypotheses that niche breadth, measured as the range of prey sizes consumed, and relative niche breadth (ratio of niche breadth to predator size) are positively correlated with predator size, and (4) test the hypotheses that maximum prey size consumption and relative maximum prey size consumption (ratio of maximum prey size to predator size) are positively correlated with predator size. This research provides detailed information on trophic ecology that will be useful for future ecological and evolutionary research and inform ecosystem-based fisheries management.

2. Materials and Methods

2.1 Fish collecting and identification

I collected ten clupeoid species in Australia, Taiwan, and Thailand by gill netting, cast netting, and beach seining (Table 2.1). Because the goal of this study was to characterize realized trophic niches at the species level, I attempted to collect my target species at multiple times and locations to capture spatial and temporal diet variation, which is known to occur in clupeoid fishes (Costalago and Palomera 2014). To maximize my chances of obtaining fish specimens containing relatively undigested prey, I set gill nets set for a maximum of 20 minutes. I collected nine clupeoids in nearshore areas with sandy and muddy substrate at depths <10 m, often near creek and river mouths: shorthead anchovy (*Encrasicholina heteroloba*), China anchovy (*Stolephorus chinensis*), Indian anchovy (*Stolephorus indicus*), Hardenberg's anchovy (*Stolephorus insularis*), Chefoo thryssa (*Thryssa chefuensis*), goldstripe sardinella (*Sardinella gibbosa*), Hamilton's thryssa (*Thryssa hamiltonii*), broadhead anchovy (*Stolephorus brachycephalus*), and longjaw thryssa (*Thryssa setirostris*). I collected Castelnau's herring (*Herklotsichthys castelnaui*) in mangrove-lined creeks and estuaries with muddy substrate at depths <3m. Following capture, I euthanized fishes with MS-222 and placed them on ice to maintain the integrity of gut contents during transport.

I also obtained specimens from fish markets (Table 2.1). I only collected fresh fish that were immediately frozen or placed on ice by fishers following capture. From markets I obtained Dussumier's thryssa (*Thryssa dussumieri*), additional *T. hamiltonii* and *S. gibbosa* specimens, and two epipelagic species that, although still considered coastal, typically occur further offshore than the other species in my dataset (JPE personal observation; Whitehead et al. 1988): *E. heteroloba* and the buccaneer anchovy (*Encrasicholina punctifer*).

I fixed whole specimens in a 10% formalin solution, transferred specimens to 70% ethanol for long-term storage, and deposited them in the fish collection at the University of Minnesota James Ford Bell Museum of Natural History (JFBM), Minnesota, U.S.A. Catalog numbers associated with specimens are in Table 2.2. I identified specimens using dichotomous keys (Munroe and Nizinski 1999a; Munroe et al. 1999) and in a previous study (Egan et al. 2018a, Ch3) verified my identifications using nuclear and mitochondrial gene sequences. I borrowed additional preserved fish specimens for gut content analysis from the American Museum of Natural History (AMNH) and the Museum and Art Gallery of the Northern Territory (MAGNT).

2.2 Diet quantification

I measured the standard length (SL) of each fish (Hubbs and Lagler 1941) using digital calipers, then dissected gut contents onto a microscope slide with a 1 x 1 mm grid. I only examined prey in the anterior portion of digestive tracts because some prey types digest more readily than others, which can bias diet descriptions if heavily digested gut contents are considered (Gannon 1976; Hyslop 1980). I quantified prey in the first ¼ of digestive tracts in species with no stomachs and prey in the digestive tract up to the posterior end of stomach in species with stomachs. I excluded predators with empty digestive tracts and predators with primarily highly degraded prey in the anterior portion of their digestive tracts from my study. I identified prey to the lowest practical taxonomic level (Table 2.3), photographed prey using a microscope-mounted Spot Insight digital camera (Model 14.2 Color Mosaic; www.spotimagin.com), and measured the maximum width, maximum length, and area to the nearest 0.001 mm if prey were in adequate condition using ImageJ software (www.imagej.nih.gov/ij). I excluded fins from measurements of fishes and appendages and the urosome from crustacean measurements. Using my prey measurements and cylinder (for filamentous algae and pennate diatoms) and ellipsoid (for other prey types) equations I estimated the volumes of individual prey following Alcaraz et al. (2003) and Espinoza and Bertrand (2008). In cases when I was only able to measure the width of a prey item, I used simple linear regression to make width-based estimates of prey volume. To maximize the number of prey size measurements included in my dataset I also measured previously unmeasured prey from fish included in a diet study that only considered the types and maximum sizes of prey consumed (Egan et al. 2017, Ch1) and included prey measurements previously reported in Egan et al. (2018a, Ch3). The predator specimens and prey measurements included in previous studies are identified in Table 2.2. I expressed fish diets as percent volume (volume of prey type divided by the total volume of prey). I did not incorporate a measure of gut fullness to weight the contribution of individual fish to diet descriptions because diets were described from pooled individual prey items. However, the prey volume and number of prey items contributed by each fish to diet descriptions is reported in Table 2.2.

2.3 Statistical analyses

I conducted all statistical analyses in program R 3.3.1 (www.r-project.org) and used a p value of $<0{\cdot}05$ as the threshold for statistical significance for all comparisons. For cluster analyses grouping predators based upon dietary similarity I reduced the resolution of my prey type and size data. I condensed the 37 total types of prey identified into nine prey categories based upon the morphological and functional similarity of the prey, rather than taxonomy (Table 2.3). These categories are similar to prey categories used in previous diet studies (Nakamura et al. 2003; Hundt et al. 2014; Egan et al. 2017, Ch1). The prey type categories likely exhibited differences in the sizes of prey they contained, but I did not use prey size as a criterion when defining prey type categories. I condensed individual prey width measurements into bins and expressed prey size consumption as the proportion of total prey volume consumed within each width bin. The narrowest bin contained prey widths from 0 to 100 um and each subsequent bin doubled in size (e.g. 100 um < 300 um, 300 um < 600 um, etc.). This study focused on prey width because prey width is considered to be highly informative for inter- and intraspecific comparisons of diet because this dimension often sets a limit on the maximum size of prey a predator can consume (Pearre 1986; Krebs and Turingan 2003; Mihalitsis and Bellwood 2017). In statistical analyses and niche breadth estimates I did not include prey type categories or prey width bins comprising less than 1% of the diet by volume.

I identified ontogenetic shifts in prey type and prey size consumption using hierarchical agglomerative cluster and regression analyses. First, I divided each fish species into SL groups spanning 10 mm. To ensure small sample sizes did not unduly impact my findings, I excluded predator SL groups containing feIr than 5 individuals in prey type analyses following Nakamura et al. (2003) and Hundt et al. (2014) and predator SL groups containing feIr than 10 individuals from prey size analyses. Using the prey size and prey type datasets separately, I calculated diet dissimilarity (Bray-Curtis dissimilarity indices; Bray and Curtis 1957; Somerfield 2008) between SL groups, then grouped predators via the complete linkage hierarchical agglomerative clustering method

(Legendre and Legendre 2012) with the vegan R package (Oksanen et al. 2016). I identified statistically significant intraspecific predator groups using a bootstrap randomization approach commonly used in diet studies (Lawlor 1980; Jaksić and Medel 1990; Buchheister and Latour 2015; Egan et al. 2017, Ch1). For all cluster analyses I performed 1000 bootstrap iterations, sampling with replacement according to the RA4 algorithm (Lawlor 1980). Multiple statistically significant predator groups within a species indicated ontogenetic differences in prey type and prey size consumption. Additionally, for species with at least 20 individuals sampled, I used quantile regression with the quantreg R package (Koenker et al. 2018) to test for correlations between minimum (0.01 quantile), median (0.5), and maximum (0.99 quantile) prey widths and relative prey widths (prey width/predator SL) and SL following Scharf et al. (1998). I used quantile regression because Breusch-Pagen Tests conducted with the lmtest R package (Hothorn et al. 2017) revealed heteroscedastic variance distributions in most of my prey width/predator SL datasets. The pattern of increasing variance of minimum, mean, and maximum prey width with increasing predator SL observed in my study is common in prey size/predator size datasets (Scharf et al. 1998; Scharf et al. 2000).

Prey size was the focal resource axis of this study. Therefore, I estimated niche breadth as the range of prey widths consumed and did not combine any SL groups because the range of predator sizes included in estimates can impact niche breadth (JPE personal observation). I tested for correlations between niche breadth and SL (lower SL limit of predator size bin), relative niche breadth (niche breadth/lower SL limit of predator size bin) and SL, maximum prey size consumed and SL, and relative maximum prey size (maximum prey size/lower SL limit of predator size bin) and SL using simple linear regression. I used linear regression rather than quantile regression because these datasets did not have heteroscedastic variance distributions.

I delimited trophic guilds based upon prey type and prey size consumption separately using the hierarchical agglomerative clustering and bootstrap randomization approaches described above. For trophic guild analysis I maintained statistically significant intraspecific SL groups and combined intraspecific SL groups that were not significantly dissimilar. I considered clusters of predators that were significantly dissimilar to be trophic guilds.

I examined diet variation between fish sampling events using hierarchical agglomerative clustering and bootstrap randomization. I formed 10 mm SL groups for all species within each sampling event and quantified prey type consumption for all SL groups. If species did not have multiple groups within the same SL range containing at least five individuals, I excluded them from the analysis.

3. Results

My diet dataset included volume estimates for 12,401 prey items, 10,559 (85%) of which were generated by this study and 1,842 (15%) were previously reported in Egan et al. (2018a, Ch3), but not used to examine ontogenetic diet changes or calculate niche breadth, from 619 individual fish predators containing identifiable prey (Table 2.1; Table 2.2). Zooplankton and crustacean nekton were the most pervasive prey types in my dataset (Figure. 1). Fish were found in the diets of five anchovy species: *E. punctifer, S. chinensis, T. chefuensis*, *T. hamiltonii*, and *T. setirostris*. The algae, Annelida, egg, Enteropneusta, phytoplankton, and plant categories were not prevalent in any predator species.

Agglomerative clustering and bootstrap randomization identified statistically significant ontogenetic shifts in both prey type and width consumption in *S. brachycephalus*, *S. indicus*, *S. insularis*, and *T. hamiltonii*, prey type shifts in *E. heteroloba, E. punctifer*, and *S. gibbosa*, a prey width shift in *T. chefuensis*, and no diet shifts in *H. castelnaui* and *T. setirostris*. I was unable to collect enough *S. chinensis* and *T. dussumieri* samples to include these species in ontogenetic diet analyses. Based upon the findings of my intraspecific cluster analyses, the 42 initial prey type predator SL groups were collapsed into 19 SL groups and the 32 prey width predator SL groups were collapsed into 18 SL groups for subsequent trophic guild analyses (Figure 2.1; Figure 2.2).

Quantile regression identified ontogenetic shifts in prey width consumption in all nine species analyzed. Eight, eight, and six species exhibited changes in maximum, median, and minimum prey width consumption, respectively (Figure 2.3; Table 2.4). Quantile regression identified small, but statistically significant ontogenetic shifts in relative prey width consumption in eight of the nine species analyzed. Six, eight, and five species exhibited changes in maximum, median, and minimum relative prey width consumption, respectively (Figure 2.4; Table 2.5). Combined regression of all predator species found statistically significant positive correlations between niche breadth and predator SL ($p <$

0.001; $r^2 = 0.75$; Figure 2.5a), maximum prey width and predator SL ($p < 0.001$; $r^2 = 0.80$; Figure 2.5c), and relative maximum prey width and predator SL ($p = 0.03$; $r^2 = 0.14$; Figure 2.5d), but didn't find a statistically significant correlation between relative niche breadth and predator SL ($p = 0.13$; $r^2 = 0.04$; Figure 2.5b).

Agglomerative clustering and bootstrap randomization identified three prey type and five prey width trophic guilds (Figure 2.1; Figure 2.2). The zooplanktivore prey type guild contained seven SL groups from seven species. Fishes in this guild were generally small (19.77-77.39 mm SL) and all had diets containing between 84% and 100% zooplankton, a prey category dominated by copepods. The piscivore guild contained a single SL group: *E. punctifer* (64.31-69.15 mm). This *E. punctifer* SL group had a diet comprised of 50% small fishes, 6% crustacean nekton, and 44% zooplankton. The crustacivore prey type guild contained eleven predator groups from eleven species. Fishes in this guild were generally larger than fishes in the zooplanktivore guild (20.79-165.25 mm SL) and had diets containing between 36% and 100% nektonic Crustacea. Some species assigned to the crustacivore guild also ate large quantities of zooplankton and four species consumed fish. There was overlap in predator SL between many of the prey width guilds, but generally larger predators were associated with larger prey (Figure 2.2). The two prey width guilds containing predators that mainly ingested prey <600 um wide corresponded to the zooplanktivore prey type guild and the three prey width guilds containing predators that mainly ingested prey >600 um wide corresponded to the piscivore and crustacivore prey type guilds.

Eleven predator SL bins belonging to six species contained sufficient sample sizes to examine intraspecific differences in prey type consumption between sampling events. Fifteen of the 24 total intraspecific comparisons were <5% different and 23 of 24 comparisons were <50% different. *Thryssa hamiltonii* 30.01-39.34 mm varied up to 56% between sampling events in the relative proportions of crustacean nekton versus zooplankton consumed. The critical dissimilarity threshold of 54% identified this as the only case of statistically significant intraspecific variation in prey type consumption between sampling events. Prey types that comprised substantial proportions of the diets of SL groups were present in diets from every sampling event, except in *S. brachycephalus* 40.68-49.63 mm. In this case crustacean nekton were important in the diet, but were not identified in fish collected during one sampling event.

4. Discussion

The trophic niche is an aspect of species biology that is foundational to understanding many biological processes. This study described the prey size and type consumption of twelve species of Indo-Pacific clupeoids through ontogeny. Cluster analysis and quantile regression found significant changes in diet through ontogeny in eight species and cluster analysis identified three prey type and five prey size trophic guilds. I identified positive relationships between niche breadth and predator SL, maximum prey width and predator SL, and relative maximum prey width and predator SL. I found no statistically significant correlation between relative niche breadth and predator SL. My data illustrate that measuring prey size in addition to prey type offers insight into fish trophic ecology by finding substantial inter- and intraspecific variation in diet not revealed by prey type data.

My diet descriptions are generally congruent with previous diet studies regarding prey type consumption, but comparable prey size data were not available for any of my study species: *E. heteroloba* (Milton et al. 1990; Nair 1998; Abrantes and Sheaves 2009), *E. punctifer* (Nair 1998; Salarpmy et al. 2008), *H. castelnaui* (Abrantes 2009), *S. gibbosa* (Mavuti et al. 2004; Abrantes et al. 2009), *S. indicus* (Hajisamae and Ibrahim 2008; Horinouchi et al. 2012), *S. insularis* (Hayase et al. 1999), *T. dussumieri* (Chacko 1949), and *T. hamiltonii* (Baker and Sheaves 2005; Taher 2010). No previous diet data were available for *S. brachycephalus*, *S. chinensis*, *T. chefuensis*, or *T. setirostris*.

My diet dataset revealed ontogenetic changes in both prey width and type consumption in Indo-Pacific clupeoids. Statistically significant changes in prey width were detected in more species than changes in prey type and changes in prey width typically occurred within narrower predator SL ranges than changes in prey type (Table 2.4; Figure 2.1; Figure 2.2; Figure 2.3). For each of the three predator species that did not exhibit ontogenetic prey type changes I only examined a relatively narrow range of SLs and small numbers of individuals (Table 2.1; Table 2.2). Analysis of additional specimens with different SLs might reveal ontogenetic prey type changes in these species. Nearly all changes in prey type were from zooplankton to crustacean nekton, a shift previously documented in many species of small fishes (Pepin and Penney 1997; Nakamura et al. 2003; Horinouchi et al. 2012; Egan et al. 2017, Ch1). The change in prey type detected in

E. punctifer resulted from differences in the quantity of small fishes versus crustacean nekton consumed (Figure 2.1). This difference may reflect prey availability rather than a meaningful ontogenetic diet shift because the prey size data show that the small fishes and crustacean nekton consumed by *E. punctifer* were similar in size.

All species that exhibited ontogenetic changes in prey type also exhibited changes in prey width consumption, which is not surprising given that my prey type categories likely exhibit size differences, and two species exhibited changes in prey width without changes in type. Congruent with previous research (Pepin and Penney 1997; Conway et al. 1998; Krebs and Turingan 2003), changes in prey width consumption were detected within very narrow SL ranges in some species (e.g. *T. setirostris* 20.79-29.43 mm SL and *S. insularis* 19.78-47.77 mm SL). This shows that changes in prey size can occur without major changes in the type of prey consumed and that prey size data allow diets to be described at a higher resolution than prey type data when prey are grouped into coarse prey categories such those used in the present and numerous previous studies (Nakamura et al. 2003; Hundt et al. 2014; Buchheister and Latour 2015; Egan et al. 2017, Ch1). Changes in prey size may be more closely linked to changes in predator standard length than changes in prey type because it is a more direct measure of a prey attribute with functional relevance to the predator (Pearre 1986; Krebs and Turingan 2003; Mihalitsis and Bellwood 2017). The most dramatic prey size changes were in the maximum widths of prey consumed followed by median and finally minimum prey widths. A pattern of greater changes in maximum than mean/median or minimum prey widths through ontogeny appears to be common in fishes (Pepin and Penney 1997; Scharf et al. 2000;

Scharf and Schlight 2000; Jensen et al. 2008). Many of the clupeoids consumed substantial numbers of small prey through ontogeny, but at bigger predator sizes small prey items contributed minimally to the total volume of prey consumed. For example, in three SL groups belonging to three different species prey less than 300 um wide comprised 48%, 50%, and 68% of the diet by number, but only comprised <0.01%, 6%, and 10% of the diet by volume, respectively. This suggests that large, infrequently captured prey may be a crucial component of the energetic intake of some species of clupeoids and may have a substantial impact on the evolution of feeding morphology and behavior. Future research could further examine the contributions of different prey sizes to fish diets by estimating the energetic costs of capturing different sizes and types of prey.

Regression analyses simultaneously incorporating data from all twelve clupeoids supported the hypotheses that niche breadth and maximum prey width are positively correlated with predator SL (Figure 2.5a,c), as has been previously reported (Pepin and Penney 1997; Scharf et al. 2000; Scharf and Schlight 2000; Costalago and Palomera 2014; Henrique et al. 2014). There was substantial interspecific variation in niche breadth within predator size bins and prey type trophic guilds, which indicates that additional research on morphological correlates of niche breadth and spatial and temporal variation in niche breadth are warranted. All predators in my study appear to exclusively feed by selectively consuming whole, individual prey. Predators that suspension feed or bite pieces from larger prey are not expected to necessarily exhibit the same positive relationships between niche breadth and maximum prey size consumption and predator

SL (Horinouchi et al. 2012; Henrique et al. 2014; Egan et al. 2017, Ch1; Linzmaier et al. 2018). The positive relationship between niche breadth and predator SL and ontogenetic changes in prey type and width consumption show that niche breadth estimates are sensitive to the predator sizes and range of predator sizes considered. Furthermore, my study shows that large, infrequently consumed prey can have a big impact on estimates of niche breadth for some species. Consequently, studies measuring niche breadth should include narrow ranges of predator sizes in breadth estimates, report the size ranges of predators examined, sample a sufficient number of predators, and ideally, use mass- or volume-based methods to describe diets.

In the clupeoid species examined, relative mean, median, and maximum prey width consumption changed very little through ontogeny, although several of the changes were statistically significant (Figure 2.4; Table 2.5). Minimum and median relative prey width often decreased slightly through ontogeny and relative maximum prey width exhibited modest increases in some species. The analysis simultaneously incorporating data from all twelve clupeoids supported the hypothesized positive relationship between relative maximum prey width and predator SL (Figure 2.5d), but didn’t find a statistically significant correlation between relative niche breadth and predator SL (Figure 2.5b). Previous studies have also reported largely constant relative prey size consumption through ontogeny, but unlike my study did not find a statistically significant positive relationship between maximum prey size consumption and SL (Pearre 1996; Munk 1997; Scharf et al. 2000). Congruent with my study, previous studies found no correlations between relative niche breadth and predator SL (Pearre 1996; Scharf et al. 2000). Few studies have examined relationships between relative prey size and predator size and have primarily focused on fishes that selectively consume individual prey (Pearre 1996; Munk 1997; Scharf et al. 2000). More research is needed to examine additional fish trophic diversity, such as herbivores, which may exhibit different relationships between relative prey size and predator size.

Cluster analyses revealed three prey type and five prey width trophic guilds in the clupeoids examined by my study. This adds to a growing body of work showing that there is substantial variation in the diets of small, coastal fishes and cautions against considering these species as functionally equivalent when modeling food webs, making inferences about species interactions and the evolution of diet, or making natural resources management decisions. My identification of more prey size than prey type trophic guilds further highlights the usefulness of prey size data. These seemingly small differences in prey size consumption likely have meaningful ecological and evolutionary implications. Small differences in prey size consumption similar to those reported herein have already been linked to distinct population dynamics in clupeoid fishes (Ayón et al. 2011; Brosset et al. 2016). My data support the hypothesis that interspecific differences in prey size consumption might be a form of resource partitioning that limits competition and facilitates the coexistence of many species of small fishes in coastal, marine ecosystems (Macpherson 1981), an idea that should be explored further by future research. The prey type trophic guild analysis emphasizes the importance of zooplankton, especially Copepoda, and small crustacean nekton, especially shrimps, in the diets of small coastal fishes.

My preliminary analysis revealed modest intraspecific differences in prey type consumption between sampling events, with only one instance of statistically significant variation. Important prey types were identified in nearly every sampling event a species was collected. Previous studies have also documented moderate spatial and temporal intraspecific diet variation (Scharf and Schlight 2000; Jensen et al. 2008; Costalago and Palomera 2014). Therefore, when describing realized trophic niches at the species level it is important to sample target species multiple times from multiple places if possible. Trophic niche descriptions based upon predators collected during a single event will likely underrepresent the range of prey types and sizes consumed by a species and thus, should be considered with due caution.

4.1 Conclusions

This study described the trophic niches of twelve species of Indo-Pacific clupeoids, assigned clupeoid predators to trophic guilds based upon prey types and sizes, identified ontogenetic changes in diet, and identified positive correlations between niche breadth, maximum prey width, and relative maximum prey width and predator size. I documented substantial dietary variation within a group of fishes often viewed as homogenous. My regression and agglomerative cluster analyses showed that measuring prey size in addition to prey type offers additional, higher-resolution information about fish trophic ecology. The data produced by this study will be useful for future ecological and evolutionary research and fisheries management.

Table 2.1 Clupeoid predator species included in study (Species)**,** number of individual predators sampled (n), standard length range of predators sampled (SL), number of prey measured (n Prey), and collection locations (Locations).

Species	n	SL (mm)	n Prey	Locations
Encrasicholina heteroloba	46	26.14-79.38	990	Taiwan
Encrasicholina punctifer	17	64.31-79.71	416	Taiwan, Thailand
Herklotsichthys castelnaui	50	50.18-77.39	1389	Australia
Sardinella gibbosa	21	30.84-125.46	937	Taiwan
Stolephorus brachycephalus	114	26.12-81.23	1556	Australia
Stolephorus chinensis	16	59.69-70.46	380	Thailand
Stolephorus indicus	60	22.93-109.17	1473	Australia, Taiwan, Thailand
Stolephorus insularis	43	19.78-47.77	1560	Taiwan
Thryssa chefuensis	55	26.96-96.70	273	Taiwan
Thryssa dussumieri	16	94.81-120.51	199	Taiwan
Thryssa hamiltonii	145	19.44-188.16	2740	Australia, Taiwan, Thailand
Thryssa setirostris	36	20.79-138.81	488	Australia, Taiwan
Total	619		12401	

Table 2.2 Information associated with each collecting event made by the authors of this study: the museum (Museum), catalog number (Catalog), and dates (Date: day/month/year) associated with each collecting event. Collections from fish markets and those not made by the authors of this study are not included in this table.

Species	Museum	Catalog	Date	Latitude	Longitud e	Locality
Encrasicholina heteroloba	JFBM	48013	30/Apr/14	24.62^0 N	120.750 E	Chonggang Estuary, Houlong Township, Miaoli County, Taiwan
Herklotsichthys castelnaui	JFBM	48059	1/Jul/14	18.52^0 S	146.270 E	Mouth of Herbert River, Queensland, Australia
Herklotsichthys castelnaui	JFBM	48082	3/Jul/14	18.42^0 S	146.210 E	Hinchinbrook Island across crom Fischer's Creek, Queensland, Australia
Herklotsichthys castelnaui	JFBM	48110	26/Nov/14	18.45^0 S	146.150 E	Small side channel near Fisher's Creek, Queensland, Australia
Sardinella gibbosa	JFBM	47505	1/Aug/13	24.62^0 N	120.750 E	Chonggang Estuary, Houlong Township, Miaoli County, Taiwan
Sardinella gibbosa	JFBM	47621	12/Aug/13	24.62^0 N	120.750 E	Chonggang Estuary, Houlong Township, Miaoli County, Taiwan
Sardinella gibbosa	JFBM	47962	12/Jun/14	24.62^0 N	120.750 E	Chonggang Estuary, Houlong Township, Miaoli County, Taiwan
Stolephorus brachycephalus	JFBM	48223	18/Jul/14	19.22^0 S	146.780 E	RoIs Bay, Townsville, Queensland, Australia
Stolephorus brachycephalus	JFBM	48146	21/Jul/14	19.22^0 S	146.780 E	RoIs Bay, Townsville, Queensland, Australia
Stolephorus brachycephalus	JFBM	48116	27/Jul/14	19.22^0 S	146.780 E	RoIs Bay, Townsville, Queensland, Australia
Stolephorus chinensis	JFBM	48797	2/Dec/15	7.22^0 N	99.540 E	Estuary off Samran Beach, Trang Province, Thailand
Stolephorus chinensis	JFBM	48793	3/Dec/15	7.22^0 N	99.540 E	Estuary off Samran Beach, Trang Province, Thailand
Stolephorus chinensis	JFBM	48917	5/Dec/15	7.19^0 N	100.580 E	South end of Songkhla Lake near Songkhla City, Songkhla Province, Thailand
Stolephorus chinensis	JFBM	48888	6/Dec/15	7.35^0 N	100.310 E	Songkhla Lake, Pak Phayun District, Phatthalung, Thailand
Stolephorus indicus	JFBM	47978	27/May/14	23.36^0 N	120.120 E	Haomei Beach, Budai Township, Chiayi County
Stolephorus indicus	JFBM	48020	15/Jun/14	23.36^0 N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Stolephorus indicus	JFBM	48645	19/Nov/15	7.54^0 N	99.310 E	Sandy Rajamangala Beach near mangrove creeks, Trang Province, Thailand
Stolephorus indicus	JFBM	48655	30/Nov/15	7.54^0 N	99.310 E	Sandy Rajamangala Beach near mangrove creeks, Trang Province, Thailand

Stolephorus insularis	JFBM	47504	1/Aug/13	24.62⁰ N	120.750 E	Chonggang Estuary, Houlong Township, Miaoli County, Taiwan
Stolephorus insularis	JFBM	47581	4/Aug/13	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Stolephorus insularis	JFBM	47593	4/Aug/13	23.36⁰ N	120.120 E	Haomei Beach, Budai Township, Chiayi County, Taiwan
Stolephorus insularis	JFBM	47623	12/Aug/13	24.62⁰ N	120.750 E	Chonggang Estuary, Houlong Township, Miaoli County, Taiwan
Stolephorus insularis	JFBM	47464	14/Aug/13	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Stolephorus insularis	JFBM	47863	28/Jul/14	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Stolephorus insularis	JFBM	47865	28/Jul/14	23.36⁰ N	120.120 E	Haomei Beach, Budai Township, Chiayi County
Thryssa chefuensis	JFBM	47959	12/Jun/14	24.62⁰ N	120.750 E	Chonggang Estuary, Houlong Township, Miaoli County, Taiwan
Thryssa chefuensis	JFBM	48945	6/May/16	24.62⁰ N	120.750 E	Chonggang Estuary, Houlong Township, Miaoli County, Taiwan
Thryssa hamiltonii	JFBM	47598	4/Aug/13	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Thryssa hamiltonii	JFBM	47458	14/Aug/13	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Thryssa hamiltonii	JFBM	48799	3/Dec/13	7.15⁰ N	99.620 E	Palian Estuary, Trang Province, Thailand
Thryssa hamiltonii	JFBM	47985	14/Jun/14	23.36⁰ N	120.120 E	Haomei Beach, Budai Township, Chiayi County
Thryssa hamiltonii	JFBM	48007	14/Jun/14	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Thryssa hamiltonii	JFBM	48019	15/Jun/14	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Thryssa hamiltonii	JFBM	48062	27/Jul/14	19.22⁰ S	146.780 E	RoIs Bay, Townsville, Queensland, Australia
Thryssa hamiltonii	JFBM	48117	27/Jul/14	19.22⁰ S	146.780 E	RoIs Bay, Townsville, Queensland, Australia
Thryssa hamiltonii	JFBM	47862	28/Jul/14	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Thryssa hamiltonii	JFBM	48748	30/Nov/15	7.46⁰ N	99.350 E	Mangrove creek near south end of Pak Meng Beach, Trang Province, Thailand
Thryssa hamiltonii	JFBM	48871	4/Dec/15	7.46⁰ N	99.350 E	Mangrove creek near south end of Pak Meng Beach, Trang Province, Thailand
Thryssa hamiltonii	JFBM	48884	4/Dec/15	7.46⁰ N	99.300 E	Andaman Sea Bay off coast of Pak Meng Beach, Trang Province, Thailand
Thryssa hamiltonii	JFBM	48895	6/Dec/15	7.46⁰ N	99.350 E	Mangrove creek near south end of Pak Meng Beach, Trang Province, Thailand
Thryssa setirostris	JFBM	47463	14/Aug/13	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Thryssa setirostris	JFBM	47645	14/Aug/13	23.36⁰ N	120.120 E	Haomei Beach, Budai Township, Chiayi County
Thryssa setirostris	JFBM	47977	27/May/14	23.36⁰ N	120.120 E	Haomei Beach, Budai Township, Chiayi County
Thryssa setirostris	JFBM	47986	14/Jun/14	23.36⁰ N	120.120 E	Haomei Beach, Budai Township, Chiayi County
Thryssa setirostris	JFBM	48006	14/Jun/14	23.36⁰ N	120.130 E	Haomei Estuary, Budai Township, Chiayi County, Taiwan
Thryssa setirostris	JFBM	47864	28/Jul/14	23.36⁰ N	120.120 E	Haomei Beach, Budai Township, Chiayi County

Table 2.3. Prey types in each prey category (not taxonomic) used for agglomerative cluster analyses of clupeoid diets.

Prey category	Prey category composition
Algae	Filamentous algae
Annelida	Nematoda, Polychaeta, unidentified Annelida
Crustacea	Amphipoda, Arthropoda, Brachyura, Collembola, Cumacea, Decapoda, Decapoda megalopa, Gammeridea, Isopoda, Lucifer, shrimp, unidentified crustacea nekton
Egg	Invertebrate eggs, fish eggs
Fish	Fish
Enteropneusta	Enteropneusta
Mollusca	Non-planktonic mollusck stages
Phytoplankton	Centric diatom, Dinoflagellata, pennate diatom, single-celled algae
Plant	Aquatic and terrestrial macrophytes
Zooplankton	Bivalva veliger, Chaetognatha, Cirripedia cypris, Cladocera, Copepoda, Crustacea nauplii, Decapoda zoea, Gastropoda veliger, Larvacea, Ostracoa, Trematoda

Table 2.4. Quantile regression equations (equation) and p values (p value) resulting from quantile regressions of predator standard length (SL) in mm versus maximum (0.99 quantile), median (0.50 quantile), and minimum (0.01 quantile) prey width (PW) in um. Regression lines are plotted in Figure 2.3.

Species	Quantile 0.99		Quantile 0.50		Quantile 0.01	
	Equation	p value	Equation	p value	Equation	p value
E. heteroloba	PW = 7.2SL+187.1	0.051	PW = 2.4SL+105.8	< 0.001	PW = -1.4SL+141.2	0.084
H. castelnaui	PW = 11.2SL-145.4	< 0.001	PW = 1.3SL+129.9	0.016	PW = -2.4SL+185.4	0.001
S. gibbosa	PW = 8.0SL+180.98	< 0.001	PW = 1.6SL+140.3	< 0.001	PW = 1.2SL-12.9	< 0.001
S. brachycephalus	PW = 68.2SL-1457.8	< 0.001	PW = 5.2SL+77.9	< 0.001	PW = -0.9SL+111.7	0.008
S. indicus	PW = 27.7SL-381.4	< 0.001	PW = 2.8SL+111.4	< 0.001	PW = -0.3SL+109.2	0.320
S. insularis	PW = 34.2SL-552.9	< 0.001	PW = 4.3SL+42.2	< 0.001	PW = 4.0SL-64.5	0.010
T. chefuensis	PW = 42.2SL-323.2	< 0.001	PW = 7.5SL-85.9	0.049	PW = -0.5SL+100.6	< 0.001
T. hamiltonii	PW = 45.5SL-713.6	< 0.001	PW = 15.1SL-243.0	< 0.001	PW = 1.6SL-52.3	0.082
T. setirostris	PW = 54.3SL-849.8	< 0.001	PW = 21.4SL-398.5	< 0.001	PW = 10.6SL-220.2	< 0.001

Table 2.5 Quantile regression equations (equation) and p values (p value) resulting from quantile regressions of predator standard length (SL) in mm versus maximum (0.99 quantile), median (0.50 quantile), and minimum (0.01 quantile) relative prey width (RPW) in um. Regression lines are plotted in Figure 2.4.

Species	Quantile 0.99		Quantile 0.50		Quantile 0.01	
	Equation	p value	Equation	p value	Equation	p value
E. heteroloba	$RPW = -9.6x10^{-5}SL+1.6x10^{-2}$	0.265	$RPW = -2.8x10^{-5}SL+5.9x10^{-3}$	<0.001	$RPW = -7.3x10^{-5}SL+5.4x10^{-3}$	<0.001
H. castelnaui	$RPW = 4.4x10^{-5}SL+6.1x10^{-3}$	0.372	$RPW = -3.7x10^{-5}SL+5.7x10^{-3}$	<0.001	$RPW = -4.8x10^{-5}SL+3.6x10^{-3}$	0.005
S. gibbosa	$RPW = -5.8x10^{-5}SL+1.6x10^{-2}$	0.004	$RPW = -3.7x10^{-5}SL+6.9x10^{-3}$	<0.001	$RPW = -3.8x10^{-6}SL+6.6x10^{-4}$	0.073
S. brachycephalus	$RPW = 7.0x10^{-4}SL-2.8x10^{-3}$	<0.001	$RPW = -4.3x10^{-5}SL+8.9x10^{-3}$	0.017	$RPW = -4.5x10^{-5}SL+3.7x10^{-3}$	<0.001
S. indicus	$RPW = 1.8x10^{-4}SL+7.8x10^{-3}$	<0.001	$RPW = -5.0x10^{-5}SL+8.0x10^{-3}$	<0.001	$RPW = -8.6x10^{-5}SL+6.1x10^{-3}$	<0.001
S. insularis	$RPW = 6.0x10^{-4}SL-3.0x10^{-3}$	<0.001	$RPW = -3.7x10^{-5}SL+6.9x10^{-3}$	0.004	$RPW = 7.0x10^{-5}SL-2.8x10^{-4}$	0.090
T. chefuensis	$RPW = 1.3x10^{-4}SL+2.7x10^{-2}$	0.285	$RPW = 4.5x10^{-5}SL+3.5x10^{-3}$	0.471	$RPW = -5.0x10^{-5}SL+4.0x10^{-3}$	0.562
T. hamiltonii	$RPW = 2.8x10^{-4}SL+6.1x10^{-3}$	<0.001	$RPW = 6.3x10^{-5}SL+4.7x10^{-3}$	<0.001	$RPW = -1.6x10^{-5}SL+3.8x10^{-3}$	0.207
T. setirostris	$RPW = 2.7x10^{-4}SL+1.3x10^{-2}$	0.001	$RPW = 1.2Sx10^{-4}SL+2.9x10^{-3}$	<0.001	$RPW = 6.5x10^{-5}+8.6x10^{-3}$	<0.001

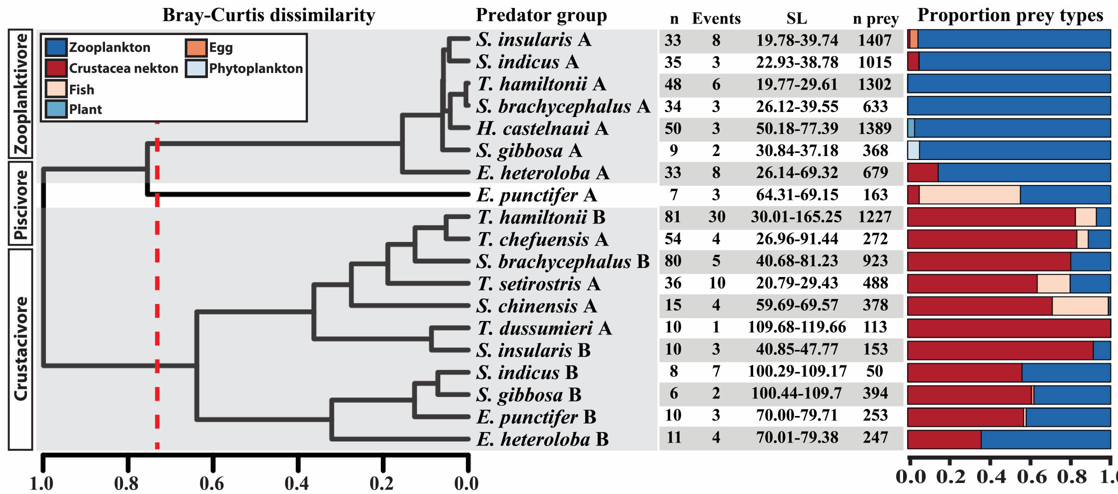


Fig. 2.1. Dendrogram resulting from hierarchical agglomerative clustering based upon Bray-Curtis dissimilarity of prey types consumed by 19 predator groups representing twelve Indo-Pacific clupeoid species. I calculated Bray-Curtis dissimilarity using non-taxonomic prey categories (Table 2.2). For this analysis I combined intraspecific SL groups that did not exhibit statistically significant differences in prey type consumption. Letters following dendrogram species labels distinguish among predator groups belonging to species with multiple intraspecific SL groups. The dashed red line indicates the critical dissimilarity value (0.73) identified by bootstrapping that indicates statistically significant ($P<0.05$) clusters (trophic guilds). The number (n) and standard length range (SL) of predators, number of separate sampling events (Events), and number of prey (n prey) measured are shown for each predator group to the right of dendrogram tip labels. Bars show the proportions of prey types consumed by predator groups.

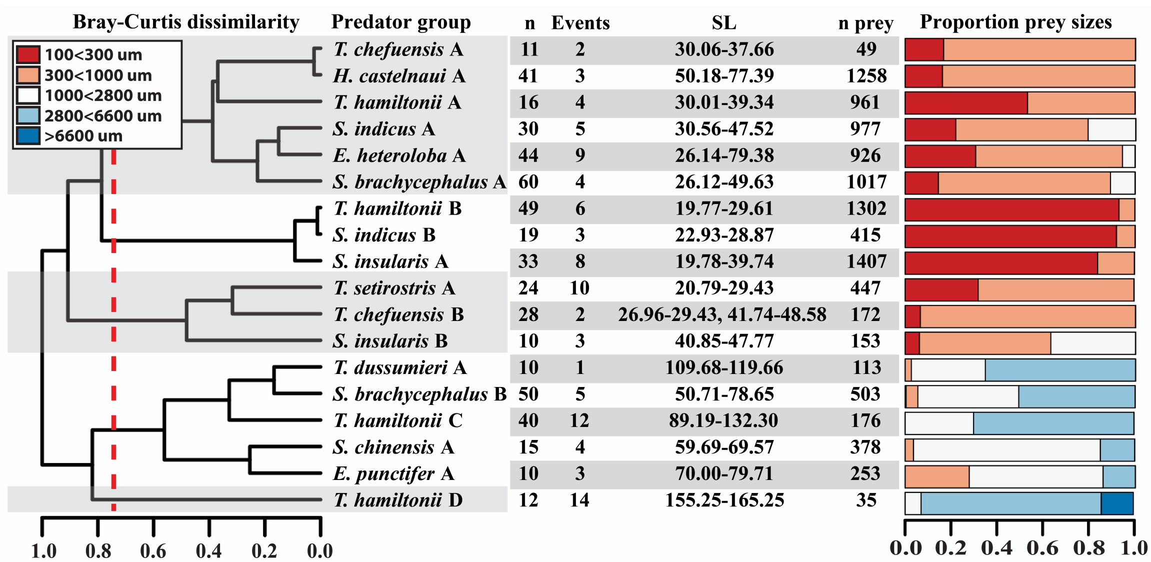


Figure 2.2. Dendrogram resulting from hierarchical agglomerative clustering based upon Bray-Curtis dissimilarity of prey sizes consumed by 18 predator groups representing twelve Indo-Pacific clupeoid species. Letters following dendrogram species labels distinguish among predator groups belonging to species with multiple intraspecific SL groups. The dashed red line indicates the critical dissimilarity value (0.75) identified by bootstrapping that indicates statistically significant ($P<0.05$) clusters. The number (n) and standard length range (SL) of predators, number of separate sampling events (Events), and number of prey (n prey) measured are shown for each predator group right of dendrogram tip labels. Bars show the proportions of prey widths consumed by predator groups.

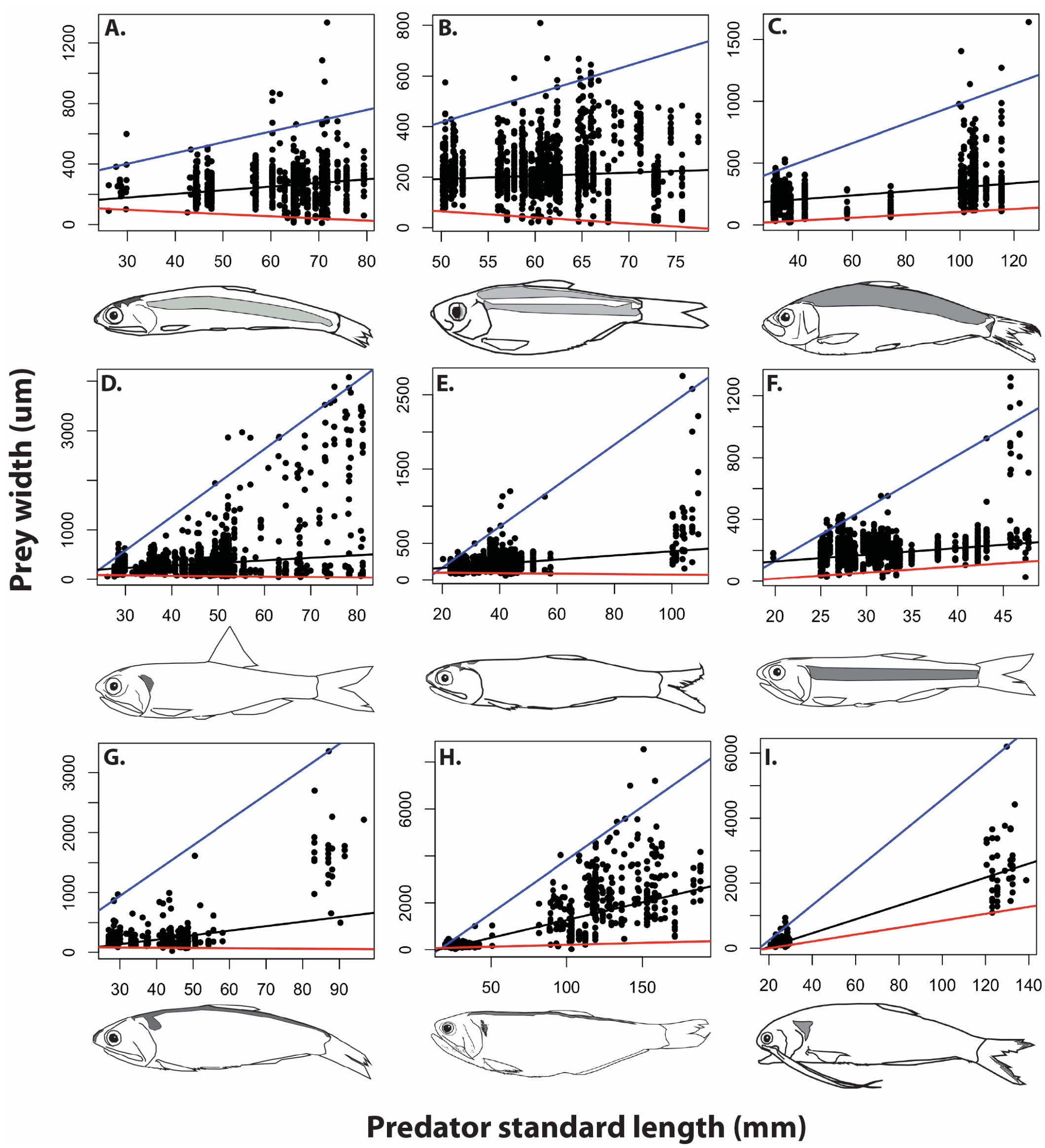


Fig. 2.3 Scatter plots of prey width (y-axis) versus predator SL (x-axis) with quantile regression lines of maximum prey width (blue), median prey width (black), and minimum prey width (red) versus predator SL. Below each scatterplot is a line drawing for the corresponding species: (A) *E. heteroloba*, (B) *H. castelnaui*, (C) *S. gibbosa*, (D) *S. brachycephalus*, (E) *S. indicus*, (F) *S. insularis*, (G) *T. chefuensis*, (H) *T. hamiltonii*, and (I) *T. setirostris*. Predator and prey sample sizes and predator SL ranges are in Table 2.1 and regression equations and p-values are in Table 2.3.

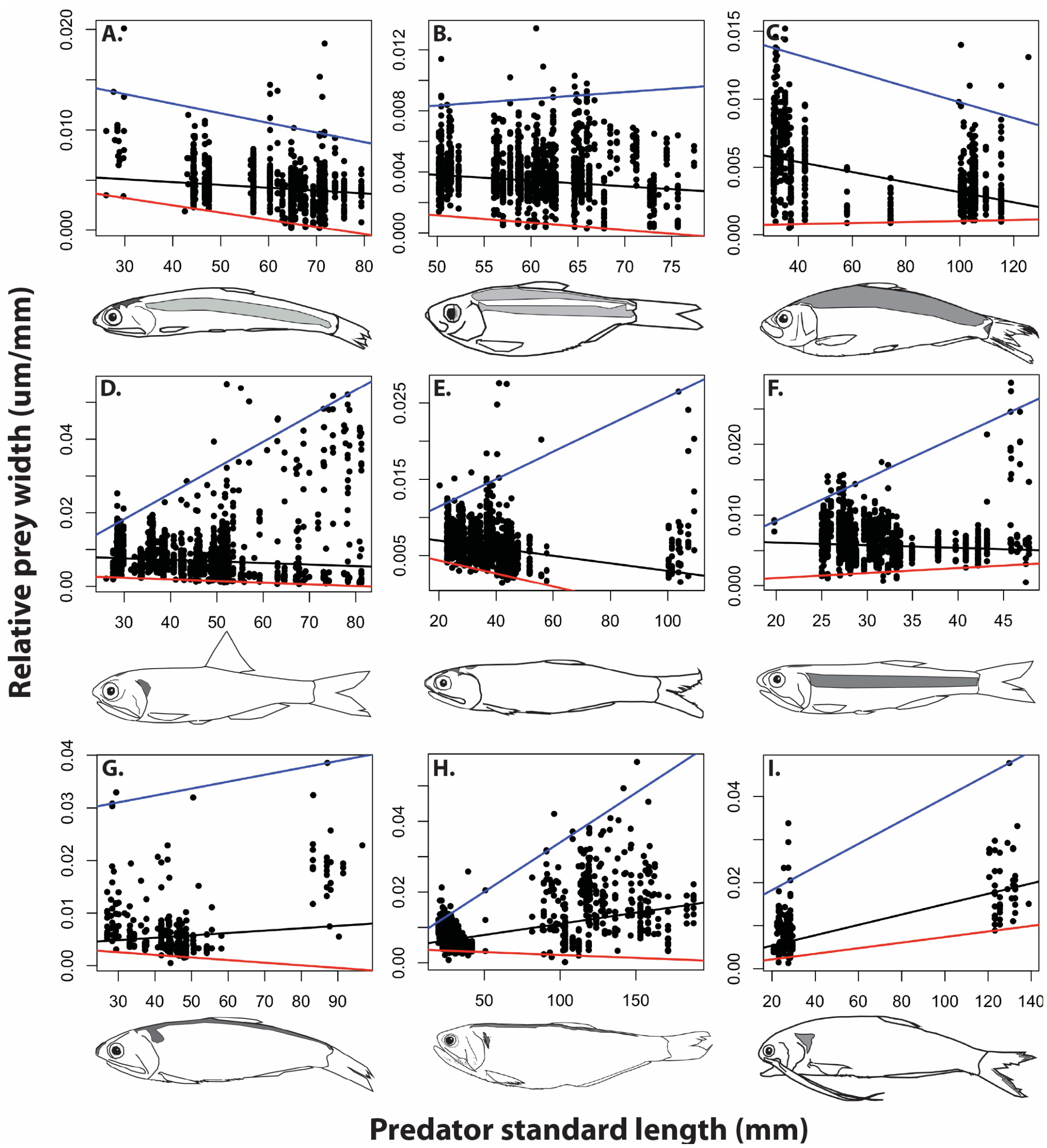


Figure 2.4. Scatter plots of relative prey width (y-axis) versus predator SL (x-axis) with quantile regression lines of maximum prey width (blue), median prey width (black), and minimum prey width (red) versus predator SL. Below each scatterplot is a line drawing for the corresponding species: (A) *E. heteroloba*, (B) *H. castelnaui*, (C) *S. gibbosa*, (D) *S. brachycephalus*, (E) *S. indicus*, (F) *S. insularis*, (G) *T. chefuensis*, (H) *T. hamiltonii*, and (I) *T. setirostris*. Predator and prey sample sizes and predator SL ranges are in Table 2.1 and regression equations and p-values are in Table 2.3.

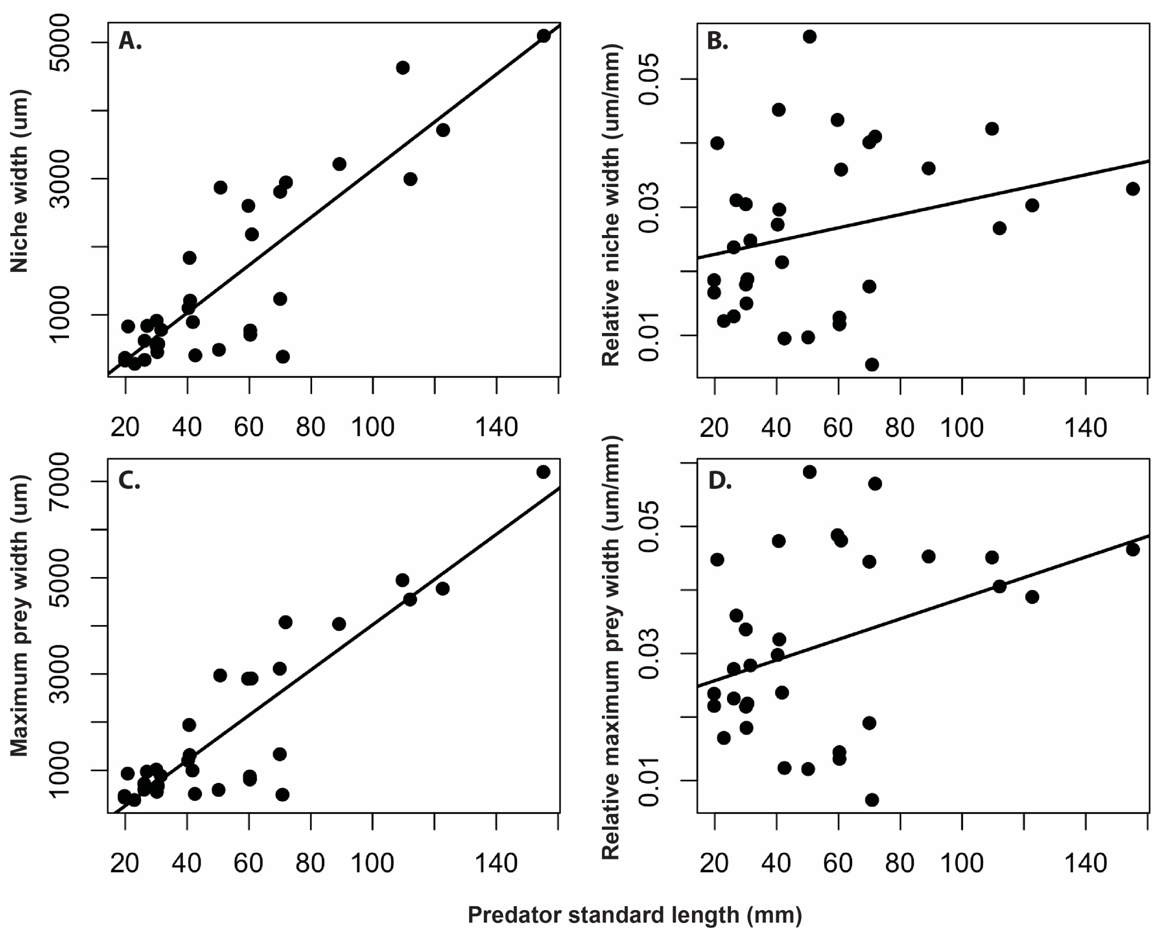


Figure 2.5. Scatter plots with linear regression lines: (A) niche breadth, (B) relative niche breadth, (C) maximum prey width, and (D) relative maximum prey width versus predator SL for 32 predator groups. Regression analyses were based upon measurements of 10,674 prey items from 511 individual fish.

CHAPTER 3

Phylogenetic analysis of trophic niche evolution reveals a latitudinal herbivory gradient in Clupeoidei (herrings, anchovies, and allies)

1. Introduction

Trophic niche evolution can profoundly impact ecological and evolutionary processes, including phenotypic evolution, speciation, and community assembly (Kalko et al. 1998; Duda and Palumbi 2004; Day et al. 2011; Pekár et al. 2011; Davis et al. 2012; Chubaty et al. 2014; Goldman-Huertas et al. 2015; Burin et al. 2016). Understanding biotic and abiotic forces that govern the evolution of trophic niches offers critical insight into biogeographic patterns (Futuyma and Moreno 1988; Floeter et al. 2005; Slatyer et al. 2013; Brown 2014). Herbivory is a particularly interesting trophic niche because there are theorized trade-offs associated with diets containing large quantities of low quality food (little energy per unit mass) and it has been identified as a potential evolutionary "dead-end" that hinders subsequent trophic diversification (Gaines and Lubchenco 1982; Floeter et al. 2005; Lobato et al. 2014; Burin et al. 2016; Sanchez and Trexler 2016). If trade-offs restrict the evolution of herbivory in certain environments and herbivory constrains trophic diversification, there may be predictable geographic patterns of herbivory and trophic evolution (Floeter et al. 2005; 2004; González-Bergonzoni et al. 2012; Chubaty et al. 2014; Sanchez and Trexler 2016).

There are trade-offs associated with herbivory. To meet metabolic demands, herbivores may spend more time foraging, have reduced activity levels, slower digestion, and higher energy allocation to digestive tissues, relative to species consuming primarily high quality prey (Ralston and Horn 1986; Elliott and Bellwood 2003; Floeter et al. 2005; Sanchez and Trexler 2016). Proposed advantages of herbivory include increased prey encounter rates, little energy required to capture prey, and utilization of suboptimal habitats (Floeter et al. 2005). Herbivorous fishes are abundant in many marine and freshwater aquatic communities (Nakamura et al. 2003; Ibañez et al. 2009; González-Bergonzoni et al. 2012; Hundt et al. 2014; Egan et al. 2017, Ch1) and consume low quality prey such as detritus, algae, macrophytes, and phytoplankton (Wilson et al. 2003; Heck et al. 2008; Hundt et al. 2014).

Abiotic environmental gradients might determine geographic patterns of herbivory. High salinity and cold temperature may decrease the probability of herbivory arising in fishes by preventing them from obtaining enough energy to meet metabolic demands (Gaines and Lubchenco 1982; Floeter et al. 2005; González-Bergonzoni et al. 2012). Cold temperatures slow production of detritus and algae and decrease digestion rates, which may limit the evolution of herbivory (Gaines and Lubchenco 1982; Floeter et al. 2005; Behrens and Lafferty 2007; Clements et al. 2009; González-Bergonzoni et al. 2012). The influential “digestion constraint” hypothesis (Gaines and Lubchenco 1982) states that in ectotherms energy requirements are difficult to meet at low temperatures when low quality materials comprise a substantial portion of the diet because digestion rate decreases more quickly than metabolic rate with declining temperature (Brett and Higgs

1970; Horn and Gibson 1990; Floeter et al. 2005). There may be low availability of detrital, algal, and plant matter in marine relative to freshwater habitats (Winemiller and Leslie 1992), a scenario that predicts a negative relationship between salinity and herbivory. Previous studies found negative correlations between herbivory and salinity and herbivory and latitude in fishes, supporting the existence of environmental constraints on herbivory, although herbivores are present in both marine and temperate areas (Floeter et al. 2005; González-Bergonzoni et al. 2012).

Evolutionary transition rates between trophic niches are variable and different trophic niches can have distinct consequences for subsequent ecological diversification (Price et al. 2012; Burin et al. 2016). Some trophic niches may act as "cradles" of diversity from which different trophic niches frequently evolve while others may act as evolutionary "dead-ends" that, once evolved, rarely give rise to additional trophic diversity (Dennis et al. 2011; Price et al. 2012; Lobato et al. 2014; Santini et al. 2015; Burin et al. 2016). Studies describing the evolution of diet in bony fishes find that herbivory may be an evolutionary dead-end because there are frequent transitions to herbivory, but infrequent transitions from herbivory to other diets (Davis et al. 2012; Price et al. 2012; Lobato et al. 2014; Santini et al. 2015; Burin et al. 2016; Lavoué et al. 2017a). Only a handful of studies have investigated the consequences of herbivory for diversification, and few studies have focused on actinopterygian fishes (Lobato et al. 2014).

For this study I investigated trophic niche evolution in Clupeoidei (anchovies, sardines, herrings, and their relatives). Clupeoidei contains over 30 herbivorous species and freshwater, marine, temperate, and tropical species (Whitehead et al. 1988; Lavoué et al. 2013; Bloom and Lovejoy 2014). Recent studies have identified strongly supported lineages within Clupeodei, but failed to resolve relationships among these lineages, in part because they used a small number of loci and relied heavily on mitochondrial DNA (Bloom and Lovejoy 2012; Lavoué et al. 2013; Bloom and Lovejoy 2014; Lavoué et al. 2017b,c). The most comprehensive phylogenetic hypothesis for Clupeoidei contains 153 of approximately 400 clupeoid species (Bloom and Lovejoy 2014). This phylogeny contains robust sampling of South American taxa, but poor sampling of several trophically diverse Indo-Pacific lineages. For example, the herring genus *Herklotsichthys* (12 species) is entirely missing and the diverse anchovy genera *Stolephorus* (20 species) and *Thryssa* (24 species) and sardines in the genus *Sardinella* (22 species) are each represented by only three species.

In this study, I investigated the evolution of herbivory and associations between herbivory and habitat in clupeoid fishes. My first objective was to use an updated molecular dataset to reconstruct a new clupeoid phylogeny with more representative sampling of Indo-Pacific trophic diversity. I then used this phylogeny to estimate the history of trophic niche evolution in clupeoids and test the hypotheses that herbivory is negatively correlated with salinity and latitude (proxy for temperature).

2. Materials and methods

2.1 Taxon sampling and molecular data collection

This study adhered to the Lavoué et al. (2014) classification of Clupeoidei and revisions suggested for the genus *Encrasicholina* (Hata and Motomura 2017), genus *Sardinella* (Stern et al. 2017), and genera *Pseudosetipinna*, *Setipinna*, and *Lycothrissa* (Lavoué and Ho 2017). I acquired DNA sequences for 191 individuals from 190 clupeoids and the denticle herring *Denticeps clupeoides* to serve as an out-group (Table 3.1). My sampling included all major clupeoid lineages and 67 of 82 genera. I downloaded sequences from GenBank and generated additional sequences from specimens I collected. I extracted total genomic DNA using Qiagen® DNAeasy Blood and Tissue Kits (Qiagen, Valencia, CA) following the manufacturer's protocol. I used polymerase chain reaction (PCR) to amplify four nuclear (*rag1*, *rag2*, *slc, zic1*) and two mitochondrial loci (*cytb, 16s*) that have been used extensively for actinopterygian systematics (Li et al. 2007; Li et al. 2010; Near et al. 2012). PCR reactions contained 2.75 µl water, 1.5 µl genomic DNA, 6.25 µl GoTaq® Green Master Mix (Promega, Madison, WI), 1.0 µl primers and were conducted using published PCR cycling protocols and amplification primers (López et al. 2004; Li et al. 2007; Li et al. 2010; Bloom and Lovejoy 2012). I used Exosap to remove excess primers and nucleotides from PCR products (Werle et al. 1994). I sequenced purified PCR products using ABI Prism® BigDye Terminator version 3.1 chemistry (Applied Biosystems, Foster City, CA) at the University of Minnesota Biomedical Genomics Center DNA Sequencing and Analysis Facility. I edited sequences, produced contigs and consensus sequences, and aligned consensus sequences using the MUSCLE algorithm (Edgar 2004) in Geneious v. 6.0.3 (www.geneious.com; Biomatters Ltd., Auckland, New Zealand). I confirmed the quality of alignments by visual inspection of sequences and their amino acid translation and comparing my alignments to alignments previously published by Bloom and Lovejoy (2014), then trimmed sequences to the following lengths (in base pairs): *rag1* 1571, *rag2* 1269, *slc* 770, *zic1* 902, *cytb* 1143, *16s* 1480.

2.2 Phylogenetic analyses

I generated two datasets for phylogenetic analyses. A "6-gene" dataset contained all six loci for a subset of 49 species from major clupeoid lineages for which I had sequences for at least five genes and the outgroup *D. clupeoides*. The purpose of the 6-gene dataset was to resolve higher-level clupeoid relationships. A "4-gene" dataset maximized taxon sampling, containing all 191 individuals and *rag1*, *rag2*, *slc*, and *cytb* gene sequences. The 4-gene dataset excluded *zic1* and *16s* because I did not have these sequences for most species (Table 3.1).

I tested for substitution saturation for each locus in my datasets using the Xia et al. (2003) method in DAMBE6 (Xia 2017). *Rag1* codon positions two and three and all *rag2* codon positions were saturated. I removed *rag1* and *rag2* third codon positions for downstream analyses, but retained *rag1* position two and *rag2* positions one and two because the latter sites were only slightly above the critical saturation index value and preliminary analyses and previous research suggested these positions contained valuable information for resolving recent clupeoid branching events (Bloom and Lovejoy 2012; Bloom and Lovejoy 2014). For all analyses, I selected partitioning schemes and nucleotide substitution models using Bayesian information criterion (BIC) scores in PartitionFinder

v. 1.01 (Lanfear et al. 2012). I did not implement the invariant sites parameter because it is redundant with the gamma distribution parameter (Yang 2006). The best fitting partitioning scheme identified by PartitionFinder for both datasets partitioned by gene and codon position and assigned GTR + gamma nucleotide substitution models to all partitions.

To time-calibrate my phylogeny I used six exponential calibration priors based upon previous reviews of clupeoid fossils and priors implemented by Bloom and Lovejoy (2014) and Lavoué et al. (2017b): (1) I used the crown clupeoid †*Cynoclupea nelsoni* (Malabarba and Dario 2017) to set a minimum age of 125 Ma for the most recent common ancestor (MRCA) of Clupeoidei and set a soft 95% maximum age of 145 Ma due to the absence of Jurassic Clupeomorpha fossils, (2) a *Dorosoma petenense* fossil (Miller 1982) to set a minimum age of 2.5 Ma for the MRCA of *Dorosoma* and set a soft 95% maximum age of 86.3 because most crown clupeoid fossils are younger, (3)-(5) a minimum age of 3.0 Ma and soft 95% maximum age of 86.3 for three sister pairs of anchovies separated by the Isthmus of Panama, and (6) †*Eoengraulis fasolo* (Marramà and Carnevale 2016) to set a minimum age of 50 Ma for the MRCA of Engraulidae and set a soft 95% maximum age of 86.3 Ma. I implemented all six priors when analyzing the 4-gene dataset, but only used the Clupeoidei and Engraulidae priors (priors 1 and 6) when analyzing the 6-gene dataset due to the reduced taxon sampling.

I conducted Bayesian phylogenetic analyses in BEAST v.2.4.5 (Bouckaert et al. 2014) via the CIPRES Science Gateway portal (Miller et al. 2010). For both datasets I conducted concatenated analyses and species tree analyses via *BEAST and ran five or more identical, independent BEAST runs. All analyses implemented a birth-death speciation prior, an uncorrelated lognormal clock model of molecular evolution, set Markov chain Monte Carlo (MCMC) lengths of 300 million generations, and logged results every 10,000th generation. I visualized results in Tracer v.1.6.0 (Rambaut et al. 2014) to confirm that MCMC runs reached stationarity, sufficient effective sample sizes of parameters (>200), and convergence of independent runs. I checked node age ranges to confirm MCMC correctly sampled from node age calibration priors. I combined trees and removed burnin in LogCombiner v.2.4.5 and used TreeAnnotator v.2.4.5 to generate maximum clade credibility trees (Bouckaert et al. 2014).

I conducted maximum likelihood phylogenetic analyses in RAxML v.8.2.4 (Stamatakis 2014) via CIPRES using 4-gene and 6-gene datasets. All maximum likelihood analyses used the same partitioning scheme implemented in the Bayesian analyses: by gene and codon position with GTR + gamma substitution models. Tree searching and non-parametric bootstrap estimation of node support was conducted simultaneously using the rapid bootstrapping algorithm. I used the bootstopping option, which determines the number of bootstrap replicates required to obtain stable support values and halts analyses automatically.

2.3 Diet data, trophic guilds, and herbivory characters

Trophic guilds are groups of species that eat similar prey (Root 1967; Simberloff and

Dayan 1991; Garrison and Link 2000). To facilitate phylogenetic comparative analysis of herbivory evolution in clupeoids I assigned species to trophic guilds. I collected diet data from large juvenile and adult specimens for 115 clupeoid species from peer-reviewed articles and by quantifying the diet of nine clupeoid species via gut content analysis (Table 3.1; Table 3.2). I condensed 97 total prey types into sixteen prey categories for analysis (Table 3.3). Prey categories were based upon previous studies and focused on morphological and functional similarity of prey rather than taxonomy (Nakamura et al. 2003; Nakane et al. 2011; Egan et al. 2017, Ch1). Diet data were reported in the literature qualitatively and quantitatively as % volume, % number, and % occurrence of prey types. These data provide distinct, but largely congruent descriptions of the relative proportion of prey in the diets of fishes (Hyslop 1980; Baker et al. 2014). In some cases, condensing % occurrence data into prey categories resulted in categories with values over 100%. In these cases I capped the value at 100%. I treated the different quantitative data types equivalently in analyses because a coarse description of diet was sufficient to examine my questions. I used program R v.3.3.1 and a p-value of <0.05 as the threshold for statistical significance for all statistical analyses (www.r-project.org). I calculated differences in prey consumption using Czekanowski dissimilarity index matrices (Czekanowski 1909) and used hierarchical agglomerative clustering to group species based upon dietary similarity using the program R vegan package (Oksansen et al. 2016). I identified statistically significant groupings, which I designated as trophic guilds, using a bootstrap randomization approach previously described by Buchheister and Latour (2015) and Egan et al. (2017, Ch1). I identified major diet differences between trophic guilds and used this information to assign clupeoid species to trophic guilds for which only qualitative data were available.

I estimated one continuous and one binary herbivory character. I measured the continuous herbivory diet character as the proportion of prey of low nutritional value in clupeoid diets (algae, detritus, phytoplankton, plant, and pollen prey categories). I coded a binary herbivory character based upon my continuous herbivore character and considered a species herbivorous if 20% of its diet was comprised of low quality prey. When possible, I assigned binary herbivore character states for species with no diet data based upon the diets of closely related species and qualitative observations of feeding and digestive structures. The terms herbivore, detritivore, and omnivore are often used inconsistently or interchangeably due to the limited resolution of diet data and differences in research focus. I acknowledge that these can be distinct trophic guilds, but for this study I use the term herbivore to describe any species consuming significant quantities of low quality prey (Floeter et al. 2005; González-Bergonzoni et al. 2012).

2.4 Habitat and range data

I collected clupeoid range and salinity use data from compiled Ocean Biogeographic Information System (www.iobis.org; Grassle 2000) and Global Biodiversity Information Facility (www.gbif.org; GBIF 2017) occurrence records accessed via AquaMaps (Kaschner et al. 2016) and from Whitehead et al. (1988). I used these data to discretely code habitat use in two ways: (1) marine, catadromous, anadromous, or freshwater and (2) primarily feeds in freshwater habitats (catadromous or freshwater) or primarily feeds in marine habitats (anadromous or marine). I recorded the northernmost and southernmost latitude of each species' range and used the absolute value of the latitude of the furthest occurrence of each species from the equator as a continuous character to serve as a proxy for each species' temperature use.

2.5 Statistical analyses

To test my hypothesis that herbivory and latitude are negatively correlated I conducted linear regression of the proportion of herbivorous clupeoid species (binary herbivory character) versus latitude at 5^0 intervals. I did not include latitudinal transects above 80^0 in any analyses because no clupeoid species occurred above this latitude. To test my hypothesis that herbivory is positively correlated with freshwater habitats I conducted simple linear regression of salinity (binary predictor variable) versus the proportion of herbivores. I also tested for a difference in the proportion of herbivorous clupeoids between freshwater and marine habitats using the prop.test MASS function.

I also tested my hypotheses using phylogenetically informed methods. All phylogenetic comparative analyses used the time-calibrated clupeoid phylogeny produced by the 4-gene concatenated analysis after removing taxa with missing habitat or diet character data. I estimated the evolutionary history of habitat (freshwater, marine, anadromous, or catadromous) and diet (trophic guilds) using Revell's (2012) modification of Bollback's (2006) Bayesian stochastic character mapping method and the maximum likelihood re-rooting method of Yang et al. (1995) using the make.simmap (Revell 2012) and rerootingMethod phytools (Revell 2012) functions, respectively. I estimated the evolutionary history of continuous character data (herbivory and latitude) using the maximum likelihood-based contMap phytools function. I tested my hypotheses that herbivory and latitude are negatively correlated (two continuous characters) and herbivory and freshwater habitat use are positively correlated (binary discrete predictor variable vs. continuous response variable) in clupeoids using phylogenetic generalized least squares regression (PGLS) with the gls phytools function. In my PGLS analyses the assumption of normally distributed residuals was violated. I explored the consequences of violating this assumption using the MCMCglmm package (Hadfield 2010) to compare p-values obtained from fitting linear models to my data assuming either normally or exponentially distributed residuals. To examine the impact of phylogenetic correction on linear regression analyses I also conducted standard linear regression of herbivory versus salinity and latitude. I tested for differences in the proportion of evolutionary diet transitions that were from non-herbivore to herbivore (transitions to herbivory/total number of evolutionary transitions) between tropical/subtropical areas (35^{0}S> and <35^{0}N) and temperate areas (>35^{0}S and 35^{0}N<) and freshwater and marine habitats using the prop.test MASS function.

3. Results

3.1 Clupeoid phylogenetic relationships and divergence times

The Bayesian 6-gene *BEAST and BEAST concatenated analyses yielded identical topologies. Bayesian posterior probabilities indicated support for some recent clupeoid branching events, but little support for higher-level relationships. There were no strongly supported differences between Bayesian and maximum likelihood analyses so I only discuss the results of the Bayesian analyses (Figure 3.1). Engraulidae (anchovies), Dussumieriinae (round herrings, rainbow sardines), Spratelloidinae (round herrings), and the Clupeidae subfamilies Clupeinae (herrings), Ehiravinae (sprats), Dorosomatinae (gizzard shads, sardinellas, herrings), and Alosinae (shads, menhadens), were recovered as monophyletic, but not Clupeidae or Dussumieriidae (Figure 3.1). Spratelloidinae was recovered as sister to all remaining Clupeoidei and Chirocentrus (wolf herrings) was sister to all clupeoids except Spratelloidinae. Engraulidae and Pristigasteridae (longfin herrings) were recovered as sister. A lineage containing Dussumieriinae, and all Clupeidae subfamilies was sister to the Engraulidae + Pristigasteridae lineage.

The 4-gene Bayesian *BEAST analyses failed to converge so I only report results of the concatenated BEAST Bayesian analyses (Figure 3.2). There were no strongly supported differences between concatenated Bayesian and maximum likelihood analyses so I only discuss the results of Bayesian analyses (Figure 3.2). Engraulidae, Dussumieriinae, Spratelloidinae, all clupeidae subfamilies except Clupeinae, and Pristigasteridae were recovered as monophyletic, but not Clupeidae or Dussumieriidae (Figure 3.2). Spratelloidinae was recovered sister to all remaining clupeoids. In contrast to the 6-gene analysis Engraulidae was recovered sister to all clupeoids except Spratelloidinae, Chirocentridae was recovered sister to Pristigasteridae, and Pristigasteridae and Chirocentridae were placed in a lineage with Dussumieriinae and Clupeinae. The clupeid genera *Herklotsichthys*, *Sardinella*, *Pellonula*, and *Microthrissa*, pristigasterid genera Pellona and *Ilisha*, Indo-Pacific anchovy genera *Thryssa* and *Coilia*, and New World anchovy genera *Engraulis*, *Anchoa, Anchoviella,* and *Anchovia* were not monophyletic.

Age estimates from the 4-gene and 6-gene Bayesian concatenated analyses were similar (Figure 3.1; Figure 3.2). I estimated an early to middle Cretaceous (mean posterior age of 126 Ma in both analyses) MRCA of Clupeoidei (Figure 3.2). Branching events between major clupeoid lineages were estimated to occur during the middle and late Cretaceous and early Cenozoic: Spratelloidinae (4 gene MRCA = 82 Ma, 6 gene MRCA = 77 Ma), Pristigasteridae + Dussumieriinae + Clupeidae lineage (4 gene MRCA = 79 Ma, 6 gene MRCA = 74 Ma), Engraulidae (4 gene MRCA = 53 Ma; 6 gene MRCA = 50 Ma), and Pristigasteridae (4-gene MRCA = 34 Ma).

3.2 Trophic guilds and character evolution

Hierarchical agglomerative clustering and bootstrap randomization analyses identified eight trophic guilds (most important prey categories shown in parentheses): terrestrial invertivore (terrestrial invertebrates, fish), molluscivore (molluscs, fish), macroalgivore (benthic macroalgae, rotifers), detritivore (detritus, zooplankton), phytoplanktivore (phytoplankton, detritus), piscivore (fish, crustaceans), crustacivore (crustaceans, zooplankton), and zooplanktivore (zooplankton, crustaceans). The zooplanktivore guild contained the most species and the molluscivore and algivore guilds contained the fewest (one species each; Table 3.1). No species in my dataset consumed exclusively low quality prey. Most zooplanktivores occurred in marine environments (~79%). The only macroalgivore inhabits tropical freshwater environments, the only molluscivore is tropical and marine, and all three terrestrial invertivore species inhabit freshwater with two species occurring in the tropics and one in the subtropics. The remaining trophic guilds were found in both freshwater and marine habitats.

Stochastic character mapping and ancestral state reconstruction yielded congruent results regarding the evolutionary history of habitat and diet in clupeoidei so I only discuss the results of stochastic character mapping. Character mapping favored a zooplanktivore trophic guild and marine habitat use as the root character states for Clupeoidei and identified 43.0 and 31.8 average changes between diet and habitat character states, respectively (Figure 3.3 and Figure 3.4). Zooplanktivore to crustacivore (8 transitions) and zooplanktivore to piscivore (8 transitions) were the most common transitions between trophic guilds and marine to freshwater were the most frequent habitat transitions (13 transitions; Figure 3.3). Herbivore trophic guilds evolved three times in tropical freshwater environments, three times is subtropical marine environments, and twice in tropical marine environments (Figure 3.4; Figure 3.5). Character mapping identified an additional origin of herbivory when using binary herbivory coding, rather than trophic guilds because the white sardinella (*Sardinella albella*) was assigned to the zooplanktivore trophic guild, but also consumed substantial quantities of phytoplankton. There were three transitions between herbivore trophic guilds (phytoplanktivore to detritivore, detritivore to phytoplanktivore, and either detritivore or phytoplanktivore to algivore) and no transitions from an herbivore to non-herbivore guild (Figure 3.3 and

Figure 3.4).

3.2 Spatial patterns of herbivory

Linear regression found a statistically significant negative correlation between latitude and the proportion of herbivorous clupeoid species (p=0.003; Figure 3.5). Linear regression did not find a correlation between salinity and the proportion of herbivores (p=0.108) and the prop.test analysis found no significant difference in the proportion of herbivores between freshwater (9% of species) and marine habitats (14% of species; p=0.107). The PGLS regressions did not identify statistically significant correlations between herbivory and latitude (p=0.588) or herbivory and salinity (p=0.794) and MCMCglmm analyses confirmed that non-significant p-values are obtained in both models assuming exponentially distributed residuals and models assuming normally distributed residuals. Standard linear regression yielded a higher p-value than PGLS for latitude versus herbivory (p=0.927) and a lower p-value than PGLS for salinity vs herbivory (p=0.683). The proportion of total diet transitions that were from non-herbivore to herbivore was significantly greater in tropical/subtropical areas (6 of 21 transitions with *S. albella* transition included) than temperate areas (0 of 10 transitions; p=0.017). There was no significant difference in the proportion of diet transitions that were from non-herbivore to herbivore in freshwater versus marine habitats (3 transitions in each habitat with *S. albella* transition included; p=1.0).

4. Discussion

4.1 Clupeoid phylogenetic relationships and divergence times

My phylogenetic hypothesis for Clupeoidei recovers the same major lineages identified by previous studies (reviewed by Lavoué et al. 2014), but relationships among these lineages remain problematic (Bloom and Lovejoy 2012; Lavoué et al. 2013; Bloom and Lovejoy 2014; Lavoué et al. 2017b,c). The 6-gene and 4-gene analyses did find strong support for the position of Spratelloidinae sister to all remaining clupeoids. Bloom and Lovejoy (2014) also recovered Spratelloidinae in this position using nuclear and mitochondrial loci, but using mitochondrial datasets Lavoué et al. (2013) and Lavoué et al. (2017c) placed Spratelloidinae sister all clupeoids except Engraulidae and sister to Chirocentridae, respectively. My 6-gene phylogeny did not confidently place Pristigasteridae, but the 4-gene analysis found strong support for a close affiliation with Clupeinae and Dussumieriinae (Figures 1 and 2). One recent molecular study also recovered Pristigasteridae in a clade with Dussumieriinae and Clupeinae (Li and Ortí 2007), but Lavoué et al. (2013) and Bloom and Lovejoy (2014) recovered Pristigasteridae as sister to Clupeidae with weak support. The minor differences between my phylogenetic hypothesis and previous studies are likely due to my exclusion of the 3rd codon positions of *rag1* and *rag2* due to substitution saturation, inclusion of additional nuclear markers, and more representative taxon sampling.

Divergence times of major clades estimated by the 4-gene and 6-gene analyses were congruent, but differed from previous studies and were often younger (Figure 3.2; Lavoué et al. 2013; Bloom and Lovejoy 2014; Lavoué et al. 2017b). For example, this study estimated a Cretaceous rather than Jurassic MRCA of Clupeoidei and ages of 34 Ma, 50-53 Ma, and 77-83 Ma, for Pristigasteridae, Engraulidae, and Spratelloidinae. Bloom and Lovejoy (2014) estimated ages of and 71 Ma (Pristigasteridae), 88 Ma (Engraulidae), 108 Ma (Spratelloidinae) and Lavoué et al. (2013) estimated ages of 53 Ma (Pristigasteridae), 73 Ma (Engraulidae), and 57 Ma (Spratelloidinae). These differences are likely largely due to my use of both mitochondrial and nuclear loci and exclusion of two fossils used in previous studies due to controversy regarding their placement (Lavoué et al. 2017b): †*Gasteroclupea branisai*, previously used to set a minimum age of 67 Ma for the MRCA of Pristigasteridae, †*Nolfia riachuelensis*, previously used to set a minimum age of 99 Ma for the MRCA of Clupeidae (Bloom and Lovejoy 2014), †*Lecceclupea ehiravaensis* to set a minimum age of 74 Ma for the MRCA of the clupeid lineage Ehiravini (*Gilchristella* + *Clupeichthys*; Lavoué et al. 2013).

4.2 Trophic guilds and character evolution

The digestion constraint hypothesis suggests that cold temperatures constrain the evolution of herbivory and predicts a negative relationship between herbivory and latitude (Gaines and Lubchenco 1982; Floeter et al. 2005). My linear regression and prop.test analyses support the existence of a latitudinal herbivory gradient, finding a significant negative correlation between the proportion of herbivorous clupeoids and latitude and a grater proportion of transitions from non-herbivore to herbivore in tropical/subtropical (six transitions) than temperate areas (no transitions; Figures 3.5 and

3.6). PGLS analysis found no significant correlation between herbivory and latitude. Keeping in mind the strengths and weaknesses of my various statistical analyses taken together, these findings provide some support for the temperature constraint hypothesis. All clupeid species in herbivorous trophic guilds were historically assigned to one of the two “shad” Clupeidae subfamilies (Dorosomatinae and Alosinae) based on morphology, suggesting this niche evolved rarely. My phylogeny suggests that herbivory evolved multiple times and that herbivorous clupeids and anchovies convergently evolved similar morphologies such as deep, laterally compressed bodies and long digestive tracts (Whitehead et al. 1988).

The detritivorous gizzard shads (*Dorosoma* spp.) and the phytoplanktivorous menhadens (*Brevoortia*) were the only clupeoids in herbivorous trophic guilds with ranges extending into temperate areas. Most species in the gizzard shad and menhaden lineages have primarily subtropical or tropical ranges (Table 3.2) and herbivory was inferred to have evolved in the subtropics prior to colonization of temperate regions in both lineages (Figures 3.4 and 3.5). The long digestive tracts characteristic of *Brevoortia* and *Dorosoma* spp. are an apparent adaptation to digest detritus in addition to zooplankton, potentially allowing them to circumvent temperature constraints of herbivory (Haskell 1959; Schmitz and Baker 1969; Mundahl and Wissing 1987; Smoot and Findlay 2010; Chubaty et al. 2014). *Dorosoma cepedianum* can survive on a strictly detritivorous diet (low quality), but exhibit reduced growth and condition relative to periods when an omnivorous diet (high quality) is consumed, and consume little detritus when zooplankton are abundant (Mundahl and Wissing 1987). Omnivorous herbivory may be adaptive because it allows *Dorosoma* spp. to maintain energy intake in seasonal temperate environments characterized by fluctuating prey availability (Mundahl and Wissing 1987; Frederiksen et al. 2006; Ayón et al. 2011). Further description and comparison of the digestive physiology and morphology, life history, and behavior of temperate herbivorous fishes may illustrate how these fishes satisfy metabolic demands with diets containing large proportions of poor quality food.

None of my statistical analyses supported the hypothesis that herbivory is negatively correlated with salinity. Clupeoids evolved herbivorous trophic guilds three times in freshwater and five times in marine environments with three of these transitions occurring between herbivorous trophic guilds (Figures 3.3 and 3.4). Previous research that shoId a correlation between herbivory and salinity used data from both offshore and nearshore fish communities (González-Bergonzoni et al. 2012). The majority of marine clupeoid species inhabit nearshore environments (Whitehead et al. 1988). The lack of support for a relationship between freshwater environments and herbivory in clupeoids could be because detrital, algal, and plant material is readily available in nearshore habitats in contrast to offshore habitats (Coates 1993).

My data suggest certain trophic guilds are evolutionary cradles that give rise to ecological diversity, while others are evolutionary dead-ends. Although approximately 50% of the clupeoids included in my study were zooplanktivores, there were no evolutionary transitions to this trophic guild in Clupeoidei (Figures 3.3 and 3.4). Interestingly, zooplanktivory gave rise to all other trophic guilds, except algivory, at least once, which indicates zooplanktivory acts as an evolutionary cradle capable of giving rise to a diversity of trophic niches. There were three transitions between herbivore guilds and no transitions from an herbivore to non-herbivore guild (Figsures 3.3 and 3.4). These findings are consistent with a general pattern of more transitions to herbivory than from herbivory in fishes, birds, and mammals, and suggests that sometimes herbivory acts as an evolutionary dead-end, limiting subsequent trophic diversification (Davis et al. 2012; Price et al. 2012; Lobato et al. 2014; Santini et al. 2015; Burin et al. 2016). The ecologies of herbivorous clupeoids are diverse. There are catadromous, anadromous, marine, freshwater, tropical, subtropical, and temperate herbivores, with maximum body lengths and lifespans ranging from 18.2 cm (Atlantic anchoveta, *Cetengraulis edentulus*) to 60 cm (Hilsa shad, *Tenualosa ilisha*) and three years (Pacific anchoveta, *Cetengrualis mysticetus*) to 10 years (Gizzard shad, *Dorosoma cepedianum*), respectively (Whitehead et al. 1988). Although herbivory may hinder trophic diversification, it might not limit other types of ecological diversification. The repeated evolution of herbivory, piscivory, and crustacivory in both freshwater and marine environments suggests that biotic forces such as prey availability and presence or absence of niche overlap with incumbent predators may play an important role in diet evolution within Clupeoidei (Case 1983; Bloom and Lovejoy 2012; Donoghue and Edwards 2014).

The clupeoid trophic guilds I identified will be useful for fisheries management and future ecological and evolutionary research. These trophic guilds can be refined with additional diet data obtained using complementary methods such as stable isotope and gut content analysis. Collecting prey size data may provide valuable insight into clupeoid ecology and evolution because prey size consumption appears to vary within and between trophic guilds (Table 3.2; Egan et al. 2017, Ch1) and size distributions of prey appear to regulate clupeoid population sizes in some ecosystems (Ayón et al. 2011). The species in the algivore and molluscivore trophic guilds should be subjected to additional gut content analysis given the apparent rarity of these guilds within clupeoids and their designation based upon a small number of diet studies (Blaber et al. 1998; Mondal and Kaviraj 2010; Phukan et al. 2012; Shahraki et al. 2014).

Table 3.1. Taxon and locus sampling is shown for 4-gene and 6-gene (indicated with *) phylogenetic analyses. Museum catalog numbers (Catalog #), when available, and Genbank accession numbers are provided for specimens and loci sampled in this study. Sequences generated by this study have bold Genbank accession numbers. Institution codes: James Ford Bell Museum of Natural History (JFBM), French National Museum of Natural History (MNHN-IC), University of Hamburg Zoological Museum (ZMH), Florida Museum of Natural History (FLMNH), Museum and Art Gallery of the Northern Territory (NTM), South Australian Museum (ABTC), American Museum of Natural History (AMNH), and Academia Sinica Biodiversity Research Museum (ASIZP).

Family	Species	Catalog #	*slc*	*rag1*	*rag2*	*zic1*	*16s*	*cytb*
Chirocentridae	*Chirocentrus dorab**	JFBM 48145	**MG958334**	**MG958449**	**MH028406**		AP006229	AP006229
Clupeidae	*Alosa aestivalis*				DQ912146			EU552615
Clupeidae	*Alosa alabamae**	JFBM 47422	**MG958366**	**MG958433**	**MG958300**	**MG958149**	KJ158129	KJ158091
Clupeidae	*Alosa algeriensis**	MNHN-IC 2017-0493	**MG958368**	**MG958432**	**MG958299**	**MG958148**	**MG958235**	**MG958211**
Clupeidae	*Alosa alosa**	MNHN-IC 2004-1477	**MG958367**	**MG958431**	**MG958301**	**MG958164**	AP009131	**MG958210**
Clupeidae	*Alosa chrysochloris**	JFBM 48452	**MG958365**	**MG958430**	**MG958298**	**MG958147**	DQ912081	**MG958209**
Clupeidae	*Alosa fallax**	ZMH 200071	**MG958369**	**MG958381**	**MG958302**	**MG958163**	EU552737	**MG958212**
Clupeidae	*Alosa mediocris*			KJ158146	KJ158110			KJ158093
Clupeidae	*Alosa pseudoharengus*			DQ912115	DQ912149			AP009132
Clupeidae	*Alosa sapidissima*			DQ912116	DQ912150			EU552616
Clupeidae	*Amblygaster sirm*							NC035064
Clupeidae	*Anodontostoma chacunda**	JFBM 48111	**MG958353**	**MG958380**	**MG958280**	**MG958155**	AP011614	**MG958218**
Clupeidae	*Brevoortia aurea*							EF564665
Clupeidae	*Brevoortia patronus**	JFBM 47414	**MG958364**	**MG958435**	**MG958297**	**MG958146**	DQ912068	**MG958213**
Clupeidae	*Brevoortia smithi**	FLMNH 2011-0632		**MG958434**	**MG958296**	**MG958145**	KJ158131	**MG958214**
Clupeidae	*Brevoortia tyrannus*			DQ912106	DQ912139			EU552614
Clupeidae	*Clupea harengus**	MNHN-IC 2017-0506	**MG958329**	**MG958419**	**MG958288**	**MG958150**	DQ912078	**MG958195**
Clupeidae	*Clupea pallasii**	JFBM 47412	**MG958372**	**MG958420**	**MG958287**	**MG958139**	DQ912082	**MG958194**
Clupeidae	*Clupeichthys aesarnensis**	FLMNH 2015-0015	**MG958333**	**MG958402**	**MG958305**		AP011584	**MG958202**
Clupeidae	*Clupeichthys goniognathus*							AP011589
Clupeidae	*Clupeichthys perakensis**	FLMNH 2014-0249	**MG958332**	**MG958403**	**MG958304**		AP011585	**MG958201**
Clupeidae	*Clupeoides borneensis*							AP011586
Clupeidae	*Clupeonella cultriventris*							AP009615
Clupeidae	*Corica soborna*	FLMNH 2005-0909	**MG958331**	**MG958401**	**MG958303**			**MG958207**
Clupeidae	*Dorosoma cepedianum**	JFBM 47667	**MG958356**	**MG958450**	**MG958284**	**MG958157**	DQ912062	**MG958215**
Clupeidae	*Dorosoma petenense*			KJ158147	KJ158111			EU552581
Clupeidae	*Ehirava fluviatilis*							AP011588
Clupeidae	*Escualosa thoracata**	JFBM 48638	**MG958357**		**MG958268**		AP011601	**MG958171**
Clupeidae	*Ethmalosa fimbriata*							AP009138
Clupeidae	*Ethmidium maculatum*							AP011602
Clupeidae	*Gilchristella aestuaria*							EU552578
Clupeidae	*Gudusia chapra*			KJ158145	KJ158108			KJ158090
Clupeidae	*Harengula humeralis*			KJ158135	KJ158098			
Clupeidae	*Harengula jaguana**	FLMNH 2007-0255		DQ912122	DQ912156		DQ912086	AP011592
Clupeidae	*Herklotsichthys blackburni**	NTM 268	**MG958362**	**MG958427**		**MG958140**	**MG958237**	**MG958191**
Clupeidae	*Herklotsichthys castelnaui*	JFBM 48081	**MG958359**	**MG958424**	**MG958271**			
Clupeidae	*Herklotsichthys dispilonotus*	JFBM 48613	**MG958355**	**MG958404**	**MG958263**			**MG958190**
Clupeidae	*Herklotsichthys gotoi**	NTM 166	**MG958361**	**MG958428**	**MG958270**	**MG958153**	**MG958238**	**MG958192**
Clupeidae	*Herklotsichthys koningsbergeri*	NTM 269	**MG958363**	**MG958426**				
Clupeidae	*Herklotsichthys lippa*	NTM 270	**MG958360**	**MG958425**				
Clupeidae	*Herklotsichthys quadrimaculatus*	MNHN-IC 2005-2586	**MG958358**	**MG958423**	**MG958269**			
Clupeidae	*Hilsa kelee**	JFBM 48560	**MG958327**	**MG958393**	**MG958272**		AP011613	**MG958224**
Clupeidae	*Hyperlophus vittatus*							AP011593
Clupeidae	*Konosirus punctatus*							AB548682
Clupeidae	*Lile stolifera*			KJ158137	KJ158100			KJ158080
Clupeidae	*Limnothrissa miodon*							EU552553
Clupeidae	*Microthrissa congica*							EU552625

Clupeidae	*Microthrissa royauxi**	AMNH 239608	**MG958349**	**MG958412**	**MG958266**		EU552790	**MG958217**
Clupeidae	*Nematalosa come**	JFBM 48018	**MG958326**	**MG958440**	**MG958281**	**MG958154**		**MG958204**
Clupeidae	*Nematalosa erebi**	NTM A00944	**MG958325**	**MG958441**	**MG958283**		EU552755	**MG958205**
Clupeidae	*Nematalosa japonica**	JFBM 47453	**MG958354**	**MG958392**	**MG958282**		AP009142	**MG958203**
Clupeidae	*Nematalosa nasus*							KC466692
Clupeidae	*Odaxothrissa vittata*			DQ912131	DQ912167			AP009231
Clupeidae	*Odaxothrissa losera*						AP011595	AP011595
Clupeidae	*Opisthonema libertate*				KJ158101			KJ158081
Clupeidae	*Opisthonema oglinum**	FLMNH 2007-0164	**MG958324**	**MG958391**	**MG958285**		DQ912074	**MG958219**
Clupeidae	*Pellonula leonensis**	AMNH 258349	**MG958323**	**MG958413**	**MG958264**		DQ912095	EU552624
Clupeidae	*Pellonula vorax*							EU552628
Clupeidae	*Potamalosa richmondia**	ABTC 78102	**MG958319**	**MG958417**	**MG958289**		AP011594	**MG958197**
Clupeidae	*Potamothrissa acutirostris*	AMNH 239604	**MG958318**	**MG958389**	**MG958265**			**MG958216**
Clupeidae	*Potamothrissa obtusirostris*							EU552623
Clupeidae	*Ramnogaster sp.*							GQ890211
Clupeidae	*Rhinosardinia amazonica*							EU552550
Clupeidae	*Rhinosardinia bahiensis*			KJ158149	KJ158113			KJ158095
Clupeidae	*Sardina pilchardus**	MNHN-IC 2017-0505	**MG958322**	**MG958429**	**MG958294**	**MG958144**	AP009233	**MG958189**
Clupeidae	*Sardinella albella*							AP011605
Clupeidae	*Sardinella aurita* Genbank			KJ158136				KJ158078
Clupeidae	*Sardinella aurita* Thailand	JFBM 48669	**MG958376**	**MG958448**	**MG958277**			**MG958223**
Clupeidae	*Sardinella aurita**	MNHN-IC 2017-0508	**MG958321**	**MG958416**		**MG958159**	DQ912067	**MG958208**
Clupeidae	*Sardinella gibbosa*	JFBM 48174, 47442	**MG958306**	**MG958421**	**MG958274**			
Clupeidae	*Sardinella hualiensis*	ASIZP 911005	**MG958317**		**MG958275**			
Clupeidae	*Sardinella maderensis*	MNHN-IC 2013-0981		**MG958422**	**MG958273**			**MG958221**
Clupeidae	*Sardinella melanura**	JFBM 47431	**MG958315**	**MG958377**	**MG958276**	**MG958156**	**MG958239**	
Clupeidae	*Sardinella* sp.*	JFBM 47434	**MG958316**	**MG958415**	**MG958278**	**MG958158**	**MG958240**	**MG958220**
Clupeidae	*Sardinops sagax*	ABTC 120558	**MG958307**		**MG958295**			**MG958226**
Clupeidae	*Sauvagella madagascariensis*							EU552610
Clupeidae	*Sauvagella robusta*							EU552608
Clupeidae	*Sierrathrissa leonensis*							EU552593
Clupeidae	*Sprattus antipodum*							AP011608
Clupeidae	*Sprattus muelleri*							AP011607
Clupeidae	*Sprattus sprattus*	MNHN-IC 2017-0507		**MG958418**	**MG958286**			**MG958193**
Clupeidae	*Stolothrissa tanganicae*							EU552552
Clupeidae	*Tenualosa ilisha*							EU552622
Clupeidae	*Tenualosa thibaudeaui*	JFBM 48960		**MG958385**	**MG958279**			**MG958229**
Denticipitidae	*Denticeps clupeoides**			DQ912100	DQ912133		DQ912063	EU552629
Dussumieriidae	*Dussumieria acuta**	JFBM 48214, 47630		**MG958379**	**MG958267**	**MG958165**	**MG958236**	**MG958206**
Dussumieriidae	*Dussumieria elopsoides*							AP017947
Dussumieriidae	*Etrumeus golanii**	MNHN-IC 2014-2877	**MG958373**	**MG958436**	**MG958290**	**MG958152**		**MG958196**
Dussumieriidae	*Etrumeus micropus**	ASIZP 0911923	**MG958374**	**MG958394**	**MG958291**	**MG958151**		**MG958169**
Dussumieriidae	*Etrumeus whiteheadi*							EU552567
Dussumieriidae	*Jenkinsia lamprotaenia*			DQ912107	DQ912140			EU552613
Dussumieriidae	*Spratelloides delicatulus**	MNHN-IC 2014-2905	**MG958312**	**MG958400**	**MG958241**		AP009144	**MG958173**
Dussumieriidae	*Spratelloides gracilis**	JFBM 47427	**MG958330**	**MG958399**	DQ912165.1		AP009145	**MG958172**
Dussumieriidae	*Spratelloides robustus**	ABTC 71316	**MG958311**	**MG958398**	**MG958242**		EU552786	**MG958170**
Engraulidae	*Amazonsprattus scintilla*			JQ012538	JQ012667			JQ012351
Engraulidae	*Anchoa cayorum*			JQ012555	JQ012700			JQ012347
Engraulidae	*Anchoa chamensis*			JQ012563	JQ012718			JQ012375
Engraulidae	*Anchoa colonensis*			JQ012559	JQ012716			JQ012383
Engraulidae	*Anchoa cubana*			JQ012550	JQ012705			JQ012342
Engraulidae	*Anchoa delicatissima*			JQ012557	JQ012704			JQ012348
Engraulidae	*Anchoa filifera*			JQ012542	JQ012722			JQ012387
Engraulidae	*Anchoa hepsetus*	JFBM 47609	**MG958342**	**MG958407**	**MG958258**			
Engraulidae	*Anchoa lamprotaenia*			JQ012630	JQ012696			JQ012379
Engraulidae	*Anchoa lyolepis*			JQ012573	JQ012688			JQ012344
Engraulidae	*Anchoa mitchilli**	JFBM 47359	**MG958343**	JQ012553	**MG958257**	**MG958141**	JQ012462	**MG958186**
Engraulidae	*Anchoa mundeoloides*			JQ012565	JQ012715			JQ012419
Engraulidae	*Anchoa nasus*			JQ012575	JQ012690			JQ012373
Engraulidae	*Anchoa panamensis*			JQ012570	JQ012712			JQ012392
Engraulidae	*Anchoa parva*			JQ012558	JQ012702			JQ012377
Engraulidae	*Anchoa scofieldi*			JQ012571	JQ012711			JQ012349
Engraulidae	*Anchoa spinifer*			KJ158140	KJ158104			KJ158085
Engraulidae	*Anchoa walkeri*			JQ012568	JQ012713			JQ012369
Engraulidae	*Anchovia clupeoides*			KJ158142	KJ158106			KJ158087
Engraulidae	*Anchovia macrolepidota*			JQ012561	JQ012709			JQ012394
Engraulidae	*Anchovia surinamensis*			JQ012613	JQ012665			JQ012402
Engraulidae	*Anchoviella alleni*			JQ012598	JQ012655			JQ012333
Engraulidae	*Anchoviella balboae*			JQ012566	JQ012720			JQ012371
Engraulidae	*Anchoviella brevirostris*			JQ012608	JQ012686			JQ012412
Engraulidae	*Anchoviella carrikeri*			JQ012605	JQ012659			JQ012339
Engraulidae	*Anchoviella elongata*			JQ012548	JQ012707			JQ012381
Engraulidae	*Anchoviella guianensis*			JQ012606	JQ012657			JQ012324
Engraulidae	*Anchoviella guianensis* cf.			JQ012585	JQ012673			JQ012400
Engraulidae	*Anchoviella jamesi*			KJ158138	KJ158102			KJ158083
Engraulidae	*Anchoviella lepidentostole*			JQ012596	JQ012634			JQ012414
Engraulidae	*Anchoviella manamensis*			KJ158139	KJ158103			KJ158084
Engraulidae	*Anchoviella* sp.1			JQ012589	JQ012677			JQ012353
Engraulidae	*Anchoviella* sp.2			JQ012581	JQ012648			JQ012337
Engraulidae	*Anchoviella* sp.3			JQ012593	JQ012632			JQ012404

Engraulidae	*Cetengraulis edentulus*			JQ012577	JQ012692			JQ012385
Engraulidae	*Cetengraulis mysticetus*			JQ012579	JQ012694			JQ012390
Engraulidae	*Coilia brachygnathus*			DQ912124	DQ912159			EU694410
Engraulidae	*Coilia dussumieri*	NTM A01796	**MG958351**	**MG958445**	**MG958247**			**MG958179**
Engraulidae	*Coilia lindmani*							AP011558
Engraulidae	*Coilia mystus*			DQ912126	DQ912162			EU694407
Engraulidae	*Coilia nasus*			DQ912123	DQ912157			AP009135
Engraulidae	*Coilia reynaldi*							AP011559
Engraulidae	*Encrasicholina heteroloba*	JFBM 47433, 48224	**MG958335**	**MG958405**	**MG958256**			**MG958168**
Engraulidae	*Encrasicholina punctifer*	JFBM 47659	**MG958328**	**MG958395**				**MG958174**
Engraulidae	*Engraulis albidus*		**MG958348**	**MG958409**	**MG958261**			**MG958167**
Engraulidae	*Engraulis anchoita*							JQ012416
Engraulidae	*Engraulis australis*	ABTC 82219	**MG958345**	**MG958410**				**MG958188**
Engraulidae	*Engraulis encrasicolus**	MNHN-IC 2017-0492	**MG958346**	**MG958411**	**MG958262**	**MG958143**	JQ012464	**MG958187**
Engraulidae	*Engraulis eurystole*			DQ912121	DQ912155			JQ012427
Engraulidae	*Engraulis japonicus**	ASIZP 0910621; JFBM 48201	**MG958347**	**MG958408**	**MG958260**	**MG958142**	AB040676	**MG958166**
Engraulidae	*Engraulis mordax**	JFBM 47413	**MG958344**	**MG958406**	**MG958259**		JQ012455	**MG958185**
Engraulidae	*Engraulis ringens*			JQ012533	JQ012731			JQ012426
Engraulidae	*Jurengraulis juruensis*			JQ012610	JQ012732			JQ012329
Engraulidae	*Lycengraulis batesii*			JQ012619	JQ012643			JQ012411
Engraulidae	*Lycengraulis grossidens*			JQ012622	JQ012639			JQ012396
Engraulidae	*Lycengraulis poeyi*			JQ012621	JQ012642			JQ012370
Engraulidae	*Pterengraulis atherinoides*			JQ012616	JQ012636			JQ012323
Engraulidae	*Setipinna crocodilus*			JQ012534	JQ012683			JQ012420
Engraulidae	*Setipinna melanochir**	FLMNH 2008-0492	**MG958314**	**MG958388**	**MG958246**		AP011565	**MG958227**
Engraulidae	*Setipinna taty**	JBM 48665	**MG958313**	**MG958387**	**MG958244**		JQ012470	**MG958183**
Engraulidae	*Setipinna tenuifilis**	NTM A01240		**MG958386**	**MG958245**		JQ012503	**MG958184**
Engraulidae	*Stolephorus brachycephalus*	JFBM 48023	**MG958338**	**MG958446**				**MG958178**
Engraulidae	*Stolephorus carpentariae*	NTM A03639	**MG958339**	**MG958451**	**MG958253**			
Engraulidae	*Stolephorus chinensis*	JFBM 48656	**MG958310**	**MG958452**				**MG958228**
Engraulidae	*Stolephorus chinensis* Genbank							AP011566
Engraulidae	*Stolephorus commersonnii*							KX753639
Engraulidae	*Stolephorus indicus**	JFBM 47464	**MG958337**	**MG958396**	**MG958254**	**MG958160**		**MG958176**
Engraulidae	*Stolephorus insularis*	JFBM 47504, 47623	**MG958336**	**MG958414**				**MG958233**
Engraulidae	*Stolephorus nelsoni*	JFBM 48063	**MG958340**	**MG958443**				**MG958177**
Engraulidae	*Stolephorus sp.*			JQ012536	JQ012671			JQ012361
Engraulidae	*Stolephorus waitei*	JFBM 47459	**MG958341**	**MG958442**	**MG958255**			**MG958175**
Engraulidae	*Stolephorus waitei* Genbank							AP011567
Engraulidae	*Thryssa baelama*	NTM A01284		**MG958378**	**MH028407**			
Engraulidae	*Thryssa brevicauda*	NTM A01244						**MG958181**
Engraulidae	*Thryssa chefuensis*	JFBM 47443	**MG958350**	**MG958384**	**MG958243**			**MG958230**
Engraulidae	*Thryssa dussumieri**	JFBM 48211	**MG958352**	**MG958453**	**MG958248**		JQ012468	JQ012363
Engraulidae	*Thryssa hamiltonii**	JFBM 47458	**MG958309**	**MG958439**	**MG958251**	**MG958162**	**MG958234**	**MG958231**
Engraulidae	*Thryssa kammalensis*	JFBM 48657	**MG958308**	**MG958383**	**MG958250**			**MG958232**
Engraulidae	*Thryssa mystax*			JQ012537	JQ012680			JQ012366
Engraulidae	*Thryssa scratchleyi*	NTM A3688		**MG958397**				**MG958182**
Engraulidae	*Thryssa setirostris*	JFBM 47439		**MG958444**	**MG958249**			**MG958222**
Engraulidae	*Thryssa spinidens**	JFBM 48784		**MG958382**	**MG958252**	**MG958161**		**MG958180**
Pristigasteridae	*Ilisha africana*							AP009140
Pristigasteridae	*Ilisha amazonica*			KJ158151	KJ158115			KJ158097
Pristigasteridae	*Ilisha elongata**	ASIZP 0915694	**MG958371**	**MG958437**	**MG958293**		DQ912090	**MG958200**
Pristigasteridae	*Ilisha megaloptera*				KJ158099			KJ158079
Pristigasteridae	*Ilisha melastoma*	JFBM 47462	**MG958370**	**MG958438**				**MG958199**
Pristigasteridae	*Ilisha* sp. Thailand	JFBM 48782	**MG958320**	**MG958447**	**MH028408**			**MG958225**
Pristigasteridae	*Odontognathus mucronatus*							KJ158082
Pristigasteridae	*Opisthopterus tardoore*	JFBM 48658	**MG958375**	**MG958390**	**MG958292**			**MG958198**
Pristigasteridae	*Pellona castelnaeana*			DQ912102	DQ912135			EU552554
Pristigasteridae	*Pellona ditchela*							AP011609
Pristigasteridae	*Pellona flavipinnis*			DQ912101	DQ912134			EU552551
Pristigasteridae	*Pellona harroIri*			KJ158143	KJ158107			KJ158088
Pristigasteridae	*Pristigaster cayana*			KJ158150	KJ158114			KJ158096
Pristigasteridae	*Pristigaster whiteheadi*			KJ158144				KJ158089
Sundasalangidae	*Sundasalanx mekongensis*							AP006232

Table 3.2. Clupeoid trophic guilds (guild): detritivore = detr, zooplanktivore = zoop, terrestrial invertivore = terr, piscivore = pisc, crustacivore = crus, Macroalgivore = algi, molluscivore = moll, Phytoplanktivore = phyt). Habitat character states: freshwater (FW), marine (M), anadromous (A), and catadromous (C). Latitudinal extremes of each species' geographic range (Lat). Herbivory characters: continuous (C; score of 1.0 = diet entirely herbivorous) and binary (B; 0 = not herbivorous, 1 = herbivorous). Citations for diet data (Diet Citations).

Family	Species	Guild	Hab	Lat	Herbivory		Diet Citations
					C	B	
Chirocentridae	*Chirocentrus dorab*	Pisc	M	35N-20S	0.00	0	Chacko 1949; Venkataraman 1960
Chirocentridae	*Chirocentrus nudus*		M	30N-30S		0	
Clupeidae	*Alosa aestivalis*	Zoop	A	41N-25N	0.00	0	Stone and Daborn 1987; Winkelman and Van Den Avyle 2002; Buchheister and Latour 2015
Clupeidae	*Alosa agone*		FW	47N-45N		0	
Clupeidae	*Alosa alabamae*	Terr	A	44N-24N	0.07	0	Mickle et al. 2013
Clupeidae	*Alosa algeriensis*		A	41N-36N		0	
Clupeidae	*Alosa alosa*	Zoop	A	61N-20N	0.11	0	Correia et al. 2001; Maitland and Lyle 2005
Clupeidae	*Alosa braschnikowi*		S	48N-35N		0	
Clupeidae	*Alosa caspia*		A	48N-37N		0	
Clupeidae	*Alosa chrysochloris*	Pisc	FW	45N-23N	0.00	0	Whitehead et al. 1988
Clupeidae	*Alosa curensis*		S	41N-37N		0	
Clupeidae	*Alosa fallax*	Pisc	A	66N-27N	0.09	0	Aprahamian 1989; Assis et al. 1992; Maitland and Lyle 2005; Skóra et al. 2012; Nachón et al. 2013
Clupeidae	*Alosa immaculata*		A	50N-41N		0	
Clupeidae	*Alosa kessleri*		A	55N-35N		0	
Clupeidae	*Alosa killarnensis*		FW	55N-51N		0	
Clupeidae	*Alosa macedonica*		FW	41N-40N		0	
Clupeidae	*Alosa maeotica*		S	48N-40N		0	
Clupeidae	*Alosa mediocris*	Pisc	A	46N-25N	0.00	0	Buchheister and Latour, 2015
Clupeidae	*Alosa pseudoharengus*	Zoop	A	55N-34N	0.04	0	Kohler and Ney 1980; Stone and Daborn 1987; Buchheister and Latour 2015; Malek et al. 2016
Clupeidae	*Alosa sapidissima*	Crus	A	61N-22N	0.00	0	Buchheister and Latour 2015; Malek et al. 2016
Clupeidae	*Alosa saposchnikowii*		A	49N-35N		0	Malkin and Andrianova 2008
Clupeidae	*Alosa sphaerocephala*		S	48N-36N		0	
Clupeidae	*Alosa tanaica*		A	49N-36N		0	Kottelat and Freyhof 2007
Clupeidae	*Alosa vistonica*		FW	42N-41N		0	
Clupeidae	*Alosa volgensis*		A			0	Kottelat and Freyhof 2007
Clupeidae	*Amblygaster clupeoides*		M	17N-19S		0	Froese and Pauly 2019
Clupeidae	*Amblygaster leiogaster*		M	30N-23S		0	
Clupeidae	*Amblygaster sirm*	Zoop	M	35N-28S	0.11	0	Whitehead et al. 1988
Clupeidae	*Anodontostoma chacunda*	Detr	A	31N-23S	0.70	1	Chacko 1949; Venkataraman 1960; Abrantes et al. 2009
Clupeidae	*Anodontostoma selangkat*		M	15N-8S		1	
Clupeidae	*Anodontostoma thailandiae*		M	24N-0N		1	
Clupeidae	*Brevoortia aurea*	Phyt	M	22S-38S		1	Sanchez 1989; Froese and Pauly 2017
Clupeidae	*Brevoortia gunteri*		M	30N-17N		1	Castillo-Rivera et al. 1996
Clupeidae	*Brevoortia patronus*	Phyt	M	31N-19N	0.70	1	Castillo-Rivera et al. 1996; Winemiller et al. 2007
Clupeidae	*Brevoortia pectinata*		M	30S-40S		1	Garcia et al. 2007
Clupeidae	*Brevoortia smithi*	Phyt	M	37N-23N	0.70	1	Whitehead et al. 1988
Clupeidae	*Brevoortia tyrannus*	Detr	M	46N-30N	0.80	1	Lewis and Peters 1994
Clupeidae	*Clupanodon thrissa*		A	41N-6N			
Clupeidae	*Clupea harengus*	Zoop	M	80N-33N	0.00	0	Gorokhova et al. 2004; Malek et al. 2016
Clupeidae	*Clupea pallasii*	Zoop	M	77N-33N	0.00	0	Wailes et al. 1935; Barry et al. 1996
Clupeidae	*Clupeichthys aesarnensis*	Zoop	FW	17N-13N	0.04	0	Sirimongkonthaworn and Fernando 1994; Ariyaratne et al. 2008

Clupeidae	*Clupeichthys bleekeri*		FW	2N-3S		0	
Clupeidae	*Clupeichthys goniognathus*		FW	18N-4S		0	Lim et al. 1999
Clupeidae	*Clupeichthys perakensis*		FW	6N-3N		0	Froese and Pauly 2019
Clupeidae	*Clupeoides borneensis*		FW	14N-4S		0	Rainboth 1996
Clupeidae	*Clupeoides hypselosoma*		FW	1N-4S		0	
Clupeidae	*Clupeoides papuensis*		FW	4S-8S		0	Allen 1991
Clupeidae	*Clupeoides venulosus*		FW	5S-8S		0	Allen 1991
Clupeidae	*Clupeonella abrau*		FW	43N-37N		0	Froese and Pauly 2019
Clupeidae	*Clupeonella caspia*		A	46N-36N		0	Froese and Pauly 2019
Clupeidae	*Clupeonella cultriventris*	Zoop	A	60N-36N	0.00	0	Kiyashko et al. 2007
Clupeidae	*Clupeonella engrauliformis*		S	44N-35N		0	
Clupeidae	*Clupeonella grimmi*		S	43N-35N		0	Froese and Pauly 2019
Clupeidae	*Clupeonella muhlisi*		FW	40N		0	Froese and Pauly 2019
Clupeidae	*Clupeonella tscharchalensis*		FW			0	Froese and Pauly 2019
Clupeidae	*Congothrissa gossei*		FW	7N-2S		0	Whitehead et al. 1988
Clupeidae	*Corica laciniata*		FW	12N-2S		0	
Clupeidae	*Corica soborna*		FW	24N-3S		0	
Clupeidae	*Dayella malabarica*		FW, M	13N-6N		0	
Clupeidae	*Dorosoma anale*		FW	21N-14N		1	
Clupeidae	*Dorosoma chavesi*		FW	14N-11N		1	
Clupeidae	*Dorosoma cepedianum*	Detr	FW	49N-21N	0.14	1	Kutkuhn 1958; Jude 1973; Mundahl and Wissing 1987
Clupeidae	*Dorosoma petenense*	Detr	FW	42N-15N	0.44	1	Haskell 1959; Winkelman and Van Den Avyle 2002
Clupeidae	*Dorosoma smithi*		FW	29N-20N		1	
Clupeidae	*Ehirava fluviatilis*	Zoop	M	14N-4N	0.53	0	Mihindukulasooriya and Amarasinghe 2014
Clupeidae	*Escualosa elongata*		M	15N-8N		0	
Clupeidae	*Escualosa thoracata*	Zoop	M	27N-22S	0.02	0	Hajisamae et al. 2004; Hajisamae and Ibrahim 2008
Clupeidae	*Ethmalosa fimbriata*	Phyt	C	25N-8S	0.65	1	Fagade and Olaniyan 1972; Blay and Eyeson 1982
Clupeidae	*Ethmidium maculatum*	Zoop	M	0-37S		0	Froese and Pauly 2019
Clupeidae	*Gilchristella aestuaria*	Zoop	FW	25S-36S	0.02	0	Blaber 1979; Bennett and Branch 1990
Clupeidae	*Gonialosa manmina*		FW	29N-21N		1	
Clupeidae	*Gonialosa modesta*		FW	24N-14N		1	
Clupeidae	*Gonialosa whiteheadi*		FW	7N-4N		1	
Clupeidae	*Gudusia chapra*	Algi	FW	30N-17N	0.64	1	Mondal and Kaviraj 2010; Phukan et al. 2012
Clupeidae	*Gudusia variegata*		FW	26N-17N		1	
Clupeidae	*Harengula clupeola*		M	31N-7S		0	
Clupeidae	*Harengula humeralis*		M	34N-15N		0	
Clupeidae	*Harengula jaguana*	Pisc	M	43N-37S	0.04	0	Vega-Cendejas et al. 1994
Clupeidae	*Harengula thrissina*		M	33N-17S		0	Froese and Pauly 2019
Clupeidae	*Herklotsichthys blackburni*		M	14S-21S		0	
Clupeidae	*Herklotsichthys castelnaui*	Zoop	M	24S-39S	0.00	0	Abrantes et al. 2009; This study
Clupeidae	*Herklotsichthys collettei*		M	21S-25S		0	
Clupeidae	*Herklotsichthys dispilonotus*		M	20N-9S		0	
Clupeidae	*Herklotsichthys gotoi*		M	4S-19S		0	
Clupeidae	*Herklotsichthys koningsbergeri*	Zoop	M	13S-27S	0.00	0	Abrantes et al. 2009
Clupeidae	*Herklotsichthys lippa*		M	9S-24S		0	
Clupeidae	*Herklotsichthys lossei*		M	31N-24N		0	
Clupeidae	*Herklotsichthys ovalis*		M			0	
Clupeidae	*Herklotsichthys punctatus*		M	37N-12N		0	
Clupeidae	*Herklotsichthys quadrimaculatus*	Zoop	M	39N-33S	0.06	0	Milton et al. 1994
Clupeidae	*Herklotsichthys spilurus*		M	11N-23S		0	
Clupeidae	*Hilsa kelee*	Zoop	M	25N-18S	0.00	0	Blaber 1979
Clupeidae	*Hyperlophus translucidus*		M	24S-34S		0	
Clupeidae	*Hyperlophus vittatus*		M	25S-40S		0	
Clupeidae	*Jenkinsia lamprotaenia*		M	34N-8N		0	Froese and Pauly 2019
Clupeidae	*Jenkinsia majua*		M	28N-9N		0	Froese and Pauly 2019
Clupeidae	*Jenkinsia parvula*		M	14N-8N		0	Froese and Pauly 2019
Clupeidae	*Jenkinsia stolifera*		M	31N-8N		0	Froese and Pauly 2019
Clupeidae	*Konosirus punctatus*	Detr	M	42N-23N	0.60	1	Kanou et al. 2004; Inoue et al. 2005
Clupeidae	*Laeviscutella dekimpei*		FW	10N-7S		0	
Clupeidae	*Lile gracilis*		M	33N-5S		0	Froese and Pauly 2019
Clupeidae	*Lile nigrofasciata*		M			0	
Clupeidae	*Lile piquitinga*		M	13N-20S		0	
Clupeidae	*Lile stolifera*		M	33N-5S		0	
Clupeidae	*Limnothrissa miodon*	Zoop	FW	3S-18S	0.00	0	Longh et al. 1983
Clupeidae	*Microthrissa congica*	Terr	FW	10N-10S	0.00	0	Kimbembi-ma-Ibaka and Nzuki 2001
Clupeidae	*Microthrissa minuta*		FW	3N-7S		0	
Clupeidae	*Microthrissa moeruensis*		FW	6S-10S		0	
Clupeidae	*Microthrissa royauxi*		FW	8N-7N		0	
Clupeidae	*Microthrissa whiteheadi*		FW	10N-10S		0	
Clupeidae	*Minyclupeoides dentibranchialus*		FW			0	
Clupeidae	*Nannothrissa parva*		FW	6N-3S		0	Froese and Pauly 2019
Clupeidae	*Nannothrissa stewarti*		FW	0-3S		0	
Clupeidae	*Nematalosa arabica*		M	27N-10N		1	

Clupeidae	*Nematalosa come*	Detr	M	30N-21S	0.70	1	Nanjo et al. 2008; Abrantes et al. 2009
Clupeidae	*Nematalosa erebi*	Detr	FW	11S-37S	0.93	1	Pusey et al. 1995; Medeiros and Arthington 2008
Clupeidae	*Nematalosa flyensis*		FW	4S-7S		1	
Clupeidae	*Nematalosa galatheae*		A	24N-0		1	
Clupeidae	*Nematalosa japonica*	Detr	M	37N-4N	0.70	1	Froese and Pauly 2019
Clupeidae	*Nematalosa nasus*	Zoop	M	38N-1N	0.70	1	Froese and Pauly 2019
Clupeidae	*Nematalosa papuensis*		FW	4S-7S		1	
Clupeidae	*Nematalosa persara*		M			1	
Clupeidae	*Nematalosa resticularia*		M			1	
Clupeidae	*Nematalosa vlaminghi*		M	16S-32S		1	
Clupeidae	*Odaxothrissa ansorgii*		FW	16N-15S		0	
Clupeidae	*Odaxothrissa losera*		FW	7N-14S		0	
Clupeidae	*Odaxothrissa mento*		FW	13N-2S		0	
Clupeidae	*Opisthonema berlangai*		M	3N-4S		0	
Clupeidae	*Opisthonema bulleri*		M	25N-5S		0	Froese and Pauly 2019
Clupeidae	*Opisthonema libertate*		M	28N-3S		0	
Clupeidae	*Opisthonema medirastre*		M	36N-6S		0	Froese and Pauly 2019
Clupeidae	*Opisthonema oglinum*	Crus	M	41N-37S	0.32	1	Vega-Cendejas et al. 1994
Clupeidae	*Pellonula leonensis*		A	17N-5S		0	
Clupeidae	*Pellonula vorax*	Pisc	A	13N-13S	0.20	0	Offem et al. 2009
Clupeidae	*Platanichthys platana*		FW	25S-36S		0	
Clupeidae	*Potamalosa richmondia*	Crus	C	32S-39S	0.00	0	Froese and Pauly 2019
Clupeidae	*Potamothrissa acutirostris*		FW	7N-5S		0	
Clupeidae	*Potamothrissa obtusirostris*		FW	7N-8S		0	
Clupeidae	*Potamothrissa whiteheadi*		FW	2S-5S		0	
Clupeidae	*Ramnogaster arcuata*		M	33S-42S		0	
Clupeidae	*Ramnogaster melanostoma*		FW	31S-38S		0	
Clupeidae	*Rhinosardinia amazonica*	Zoop	FW	10N-8S	0.00	0	Froese and Pauly 2019
Clupeidae	*Rhinosardinia bahiensis*		FW	10N-20S		0	
Clupeidae	*Sardina pilchardus*	Zoop	M	68N-14N	0.09	0	Garrido et al. 2008; Nikolioudakis et al. 2012; Costalago 2012; Costalago et al. 2015
Clupeidae	*Sardinella albella*	Zoop	M	31N-30S	0.27	1	Venkataraman 1960; Horinouchi et al. 2012
Clupeidae	*Sardinella atricauda*		M	1N-9S		0	
Clupeidae	*Sardinella aurita*	Zoop	M	47N-40S	0.02	0	Tsikliras et al. 2005; Lomiri et al. 2008
Clupeidae	*Sardinella brachysoma*		M	25N-23S		0	
Clupeidae	*Sardinella fiijiense*		M	5S-19S		0	
Clupeidae	*Sardinella fimbriata*		M	30N-11S		0	
Clupeidae	*Sardinella gibbosa*	Zoop	M	41N-37S	0.00	0	Chacko 1949; Nyunja et al. 2002; Mavuti et al. 2004; Abrantes et al. 2009; Shahraki et al. 2014
Clupeidae	*Sardinella hualiensis*		M	29N-17N		0	
Clupeidae	*Sardinella jussieu*		M	20N-27S		0	
Clupeidae	*Sardinella maderensis*	Zoop	M	46N-23S	0.09	0	Fagade and Olaniyan 1973; Faye et al. 2012
Clupeidae	*Sardinella marquesensis*		M	24N-19S		0	
Clupeidae	*Sardinella melanura*	Zoop	M	26N-23S	0.03	0	Kuthalingam 1961
Clupeidae	*Sardinella richardsoni*		M	30N-17N		0	
Clupeidae	*Sardinella rouxi*		M	18N-10S		0	
Clupeidae	*Sardinella sindensis*		M	30N-10N		0	
Clupeidae	*Sardinella tawilis*		FW	18N-14N		0	
Clupeidae	*Sardinella zunasi*		M	38N-22N		0	
Clupeidae	*Sardinops sagax*	Zoop	M	61N-47S	0.08	0	Burchmore et al. 1984; Van de Lingen 2002; Mketsu 2008; Espinoza et al. 2009
Clupeidae	*Sauvagella madagascariensis*		FW	11S-26S		0	
Clupeidae	*Sauvagella robusta*		FW	15S		0	
Clupeidae	*Sierrathrissa leonensis*		FW	18N-0		0	Whitehead et al. 1988
Clupeidae	*Spratelloides delicatulus*	Zoop	M	40N-29S	0.00	0	Milton et al. 1990; Nakamura et al. 2003; Mavuti et al. 2004; Gajdzik et al. 2014
Clupeidae	*Spratelloides gracilis*	Zoop	M	33N-30S	0.00	0	Nakane et al. 2011
Clupeidae	*Spratelloides lewisi*		M	2N-12S		0	
Clupeidae	*Spratelloides robustus*	Zoop	M	12S-39S	0.00	0	Froese and Pauly 2019
Clupeidae	*Spratellomorpha bianalis*		M	0-26S		0	
Clupeidae	*Sprattus antipodum*		M	37S-48S		0	
Clupeidae	*Sprattus fuegensis*		M	38S-58S		0	
Clupeidae	*Sprattus muelleri*		M	33S-51S		0	
Clupeidae	*Sprattus novaehollandiae*		M	38S-45S		0	
Clupeidae	*Sprattus sprattus*	Zoop	M	66N-30N	0.00	0	Moore and Moore 1976; Köster and Möllmann 2000; Gorokhova et al. 2004
Clupeidae	*Stolothrissa tanganicae*	Zoop	FW	1S-10S	0.00	0	Froese and Pauly 2019
Clupeidae	*Strangomera bentincki*		M	30S-37S		1	Arrizaga et al. 1993
Clupeidae	*Sundasalanx malleti*		FW	0		0	Froese and Pauly 2019
Clupeidae	*Sundasalanx megalops*		FW	0		0	
Clupeidae	*Sundasalanx mekongensis*		FW	16N-17N		0	
Clupeidae	*Sundasalanx mesops*		FW	0		0	
Clupeidae	*Sundasalanx microps*		FW	2N-0		0	
Clupeidae	*Sundasalanx platyrhynchus*		FW	0		0	
Clupeidae	*Sundasalanx praecox*		FW	2N-18N		0	

Clupeidae	*Tenualosa ilisha*	Phyt	A	34N-5N	0.70	1	De and Datta 1990; Dutta et al. 2014
Clupeidae	*Tenualosa macrura*		A	7N-9S		0	Froese and Pauly 2019
Clupeidae	*Tenualosa reevesii*		A	31N-5N		0	Froese and Pauly 2019
Clupeidae	*Tenualosa thibaudeaui*	Phyt	FW	20N-10N	0.70	1	Froese and Pauly 2019
Clupeidae	*Tenualosa toli*		A	23N-7S		0	Froese and Pauly 2019
Clupeidae	*Thrattidion noctivagus*		FW	6N-3N		0	Whitehead et al. 1988
Dussumieriidae	*Dussumieria acuta*		M	31N-7S		0	
Dussumieriidae	*Dussumieria elopsoides*	Crus	M	36N-19S	0.00	0	Chacko 1949; Venkataraman 1960
Dussumieriidae	*Etrumeus acuminatus*		M	36N-18S		0	
Dussumieriidae	*Etrumeus golanii*	Zoop	M	18N-2N	0.00	0	Tanaka et al. 2006
Dussumieriidae	*Etrumeus makiawa*		M	21N		0	
Dussumieriidae	*Etrumeus micropus*		M	35N-21N		0	
Dussumieriidae	*Etrumeus sadina*		M	45N-8N		0	Froese and Pauly 2019
Dussumieriidae	*Etrumeus whiteheadi*	Zoop	M	17S-35S	0.00	0	Froese and Pauly 2019
Dussumieriidae	*Etrumeus wongratanai*		M	1S-34S		0	
Engraulidae	*Amazonsprattus scintilla*	Terr	FW	0S-3S	0.00	0	Whitehead et al. 1988
Engraulidae	*Anchoa analis*		M	27N-21N		0	
Engraulidae	*Anchoa argentivittata*		M	28N-5S		0	
Engraulidae	*Anchoa belizensis*		M	20N-14S		0	
Engraulidae	*Anchoa cayorum*		M	28N-10N		0	
Engraulidae	*Anchoa chamensis*		M	10N-5N		0	
Engraulidae	*Anchoa choerostoma*		M	34N-30N		0	
Engraulidae	*Anchoa colonensis*	Crus	M	23N-7N	0.00	0	This study
Engraulidae	*Anchoa compressa*		M	36N-20N		0	
Engraulidae	*Anchoa cubana*		M	36N-30S		0	
Engraulidae	*Anchoa curta*		M	28N-6S		0	
Engraulidae	*Anchoa delicatissima*		M	34N-20N		0	
Engraulidae	*Anchoa eigenmannia*		M	14N-5N		0	
Engraulidae	*Anchoa exigua*		M	28N-5N		0	
Engraulidae	*Anchoa filifera*		M	23N-27S		0	
Engraulidae	*Anchoa helleri*		M	32N-25N		0	
Engraulidae	*Anchoa hepsetus*	Zoop	M	44N-36S	0.00	0	Carr and Adams 1973
Engraulidae	*Anchoa ischana*		M	33N-3S		0	
Engraulidae	*Anchoa januaria*		M	4S-29S		0	
Engraulidae	*Anchoa lamprotaenia*		M	28N-7S		0	
Engraulidae	*Anchoa lucida*		M	29N-6S		0	
Engraulidae	*Anchoa lyolepis*		M	38N-27S		0	
Engraulidae	*Anchoa marinii*		M	22S-40S		0	
Engraulidae	*Anchoa mitchilli*	Zoop	M	42N-16N	0.12	0	Carr and Adams 1973; Odum and Heald 1972; Livingston 1982
Engraulidae	*Anchoa mundeola*		M	28N-5N		0	
Engraulidae	*Anchoa mundeoloides*		M	32N-28N		0	
Engraulidae	*Anchoa nasus*		M	31N-14S		0	
Engraulidae	*Anchoa panamensis*		M	10N-5N		0	
Engraulidae	*Anchoa parva*		M	23N-7N		0	
Engraulidae	*Anchoa pectoralis*		M	1N-27S		0	
Engraulidae	*Anchoa scofieldi*		M	25N-20N		0	
Engraulidae	*Anchoa spinifer*		M	14N-26S		0	
Engraulidae	*Anchoa starksi*		M	14N-4S		0	
Engraulidae	*Anchoa tricolor*		M	2S-39S		0	
Engraulidae	*Anchoa trinitatis*		M	14N-7N		0	
Engraulidae	*Anchoa walkeri*		M	31N-5N		0	
Engraulidae	*Anchovia clupeoides*	Zoop	M	23N-25S	0.00	0	Whitehead et al. 1988
Engraulidae	*Anchovia macrolepidota*	Zoop	M	30N-5S	0.00	0	Whitehead et al. 1988
Engraulidae	*Anchovia surinamensis*	Zoop	FW	11N-1S	0.09	0	Mérona et al. 2001; Mérona et al. 2008
Engraulidae	*Anchoviella alleni*		FW	2S-8S		0	
Engraulidae	*Anchoviella balboae*		M	10N-4N		0	
Engraulidae	*Anchoviella blackburni*		M	15N-9N		0	
Engraulidae	*Anchoviella brevirostris*	Zoop	M	10N-27S	0.00	0	Wakabara et al. 1996
Engraulidae	*Anchoviella carrikeri*		FW	0-15S		0	
Engraulidae	*Anchoviella cayennensis*		M	12N-21S		0	
Engraulidae	*Anchoviella elongata*		M	19N-9N		0	
Engraulidae	*Anchoviella guianensis*		FW	9N-4S		0	
Engraulidae	*Anchoviella jamesi*	Zoop	FW	9N-6S	0.00	0	Ropke et al. 2013
Engraulidae	*Anchoviella juruasanga*		FW			0	
Engraulidae	*Anchoviella lepidentostole*		A	9N-27S		0	Froese and Pauly 2019
Engraulidae	*Anchoviella manamensis*		FW	10N-6N		0	
Engraulidae	*Anchoviella nattereri*		M	0-4S		0	
Engraulidae	*Anchoviella perezi*		M			0	
Engraulidae	*Anchoviella perfasciata*		M	32N-10N		0	
Engraulidae	*Anchoviella vaillanti*		M	7S-15S		0	
Engraulidae	*Cetengraulis edentulus*	Phyt	M	23N-28S	1.00	1	Gay et al. 2002; Krumme et al. 2008
Engraulidae	*Cetengraulis mysticetus*	Phyt	M	32N-4S	0.98	1	Bayliff 1963
Engraulidae	*Coilia borneensis*		FW	6N-7S		0	
Engraulidae	*Coilia brachygnathus*	Crus	FW	32N-27N	0.00	0	Zhang et al. 2013
Engraulidae	*Coilia coomansi*		FW	2N-6S		0	
Engraulidae	*Coilia dussumieri*	Zoop	M	24N-9S	0.00	0	Rao 1967
Engraulidae	*Coilia grayii*		M	33N-7N		0	
Engraulidae	*Coilia lindmani*		FW	14N-4S		0	
Engraulidae	*Coilia macrognathos*		FW	10N-5S		0	

Engraulidae	*Coilia mystus*	Zoop	M	42N-4N	0.00	0	Cheng 1956
Engraulidae	*Coilia nasus*	Zoop	A	42N-21N	0.00	0	Islam and Tanaka 2006
Engraulidae	*Coilia neglecta*		M	25N-5S		0	
Engraulidae	*Coilia ramcarati*		M	25N-13N		0	
Engraulidae	*Coilia rebentischii*		M	14N-1N		0	
Engraulidae	*Coilia reynaldi*		M	26N-7N		0	
Engraulidae	*Encrasicholina heteroloba*	Zoop	M	32N-26S	0.01	0	Venkataraman 1960; Rao 1967; Milton et al. 1990; Nair 1998; Abrantes et al. 2009
Engraulidae	*Encrasicholina oligobranchus*		M	17N-4N		0	
Engraulidae	*Encrasicholina pseudoheteroloba*		M			0	
Engraulidae	*Encrasicholina punctifer*	Zoop	M	42N-35S	0.11	0	Nair 1998; Salarpmy et al. 2008
Engraulidae	*Encrasicholina purpurea*		M	25N-14N		0	Froese and Pauly 2019
Engraulidae	*Engraulis albidus*		M	43N		0	
Engraulidae	*Engraulis anchoita*	Zoop	M	21S-50S	0.00	0	Capitanio et al. 2005
Engraulidae	*Engraulis australis*		M	20S-47S		0	
Engraulidae	*Engraulis capensis*		M	16S-26S		0	
Engraulidae	*Engraulis encrasicolus*	Zoop	M	62N-37S	0.00	0	Plounevez and Champalbert 1999; Mketsu 2008; Borme et al. 2009; Costalago et al. 2012
Engraulidae	*Engraulis eurystole*		M	45N-0		0	
Engraulidae	*Engraulis japonicus*	Zoop	M	49N-2N	0.00	0	Inoue et al. 2005; Tanaka et al. 2006
Engraulidae	*Engraulis mordax*	Zoop	M	51N-21N	0.15	0	Koslow 1981; Whitehead et al. 1988; Barry et al. 1996
Engraulidae	*Engraulis ringens*	Crus	M	5S-43S	0.02	0	Espinoza and Bertrand 2008
Engraulidae	*Jurengraulis juruensis*		FW	0-14S			
Engraulidae	*Lycengraulis batesii*	Pisc	FW	9N-7S	0.08	0	Mérona et al. 2001; Mérona et al. 2008; Ropke et al. 2013
Engraulidae	*Lycengraulis figueiredoi*		FW	1N		0	
Engraulidae	*Lycengraulis grossidens*	Pisc	A	19N-41S	0.00	0	Froese and Pauly 2019
Engraulidae	*Lycengraulis limnichthys*		FW	9S		0	
Engraulidae	*Lycengraulis poeyi*	Pisc	M	14N-6N	0.00	0	Froese and Pauly 2019
Engraulidae	*Papuengraulis micropinna*		M	6S-11S		0	
Engraulidae	*Pterengraulis atherinoides*	Pisc	FW	11N-7S	0.00	0	Mérona et al. 2001; Krumme et al. 2005
Engraulidae	*Setipinna breviceps*		M	9N-5S		0	
Engraulidae	*Setipinna brevifilis*		FW	28N-23N		0	
Engraulidae	*Setipinna crocodilus*	Pisc	FW	17N-5S	0.00	0	Froese and Pauly 2019
Engraulidae	*Setipinna melanochir*	Pisc	M	19N-8S	0.00	0	Froese and Pauly 2019
Engraulidae	*Setipinna paxtoni*		M	11S-18S		0	
Engraulidae	*Setipinna phasa*		FW	30N-18N		0	
Engraulidae	*Setipinna taty*	Crus	M	24N-9S	0.11	0	Rao 1967; Hong 1990; Chaudhuri et al. 2014
Engraulidae	*Setipinna tenuifilis*	Pisc	M	42N-17S	0.00	0	Froese and Pauly 2019
Engraulidae	*Setipinna wheeleri*		FW	22N-16N		0	
Engraulidae	*Stolephorus advenus*		M	7S-14S		0	
Engraulidae	*Stolephorus andhraensis*		M	22N-15S		0	
Engraulidae	*Stolephorus apiensis*		M	2S-20S		0	
Engraulidae	*Stolephorus baganensis*		M	16N-7S		0	
Engraulidae	*Stolephorus brachycephalus*	Crus	M	5S-15S	0.00	0	This study
Engraulidae	*Stolephorus carpentariae*		M	3S-32S		0	
Engraulidae	*Stolephorus chinensis*	Zoop	M	29N-1N	0.01	0	This study
Engraulidae	*Stolephorus commersonnii*	Zoop	M	27N-24S	0.00	0	Venkataraman 1960; Blaber 1979; Hayase et al. 1999; Hajisamae and Ibrahim 2008
Engraulidae	*Stolephorus dubiosus*		M	25N-9S		0	
Engraulidae	*Stolephorus holodon*		M	24S-40S		0	
Engraulidae	*Stolephorus indicus*	Zoop	M	30N-37S	0.00	0	Chacko 1949; De Troch et al. 1998; Hajisamae et al. 2003; Hajisamae and Ibrahim 2008; Horinouchi et al. 2012
Engraulidae	*Stolephorus insularis*	Zoop	M	28N-9S	0.00	0	Rao 1967; Hayase et al. 1999
Engraulidae	*Stolephorus multibranchus*		M	9N-3N		0	
Engraulidae	*Stolephorus nelsoni*		M	15S-20S		0	
Engraulidae	*Stolephorus pacificus*		M	17N-2N		0	
Engraulidae	*Stolephorus ronquilloi*		M	17N-7N		0	
Engraulidae	*Stolephorus shantungensis*		M			0	
Engraulidae	*Stolephorus teguhi*		M			0	
Engraulidae	*Stolephorus tri*		M	17N-11S		0	
Engraulidae	*Stolephorus waitei*	Zoop	M	25N-21S	0.00	0	Nair 1998
Engraulidae	*Thryssa adelae*		M	37N-21N		0	
Engraulidae	*Thryssa aestuaria*		M	7S-32S		0	
Engraulidae	*Thryssa baelama*	Crus	M	31N-25S	0.00	0	Marichamy 1972
Engraulidae	*Thryssa brevicauda*		M	5S-13S		0	
Engraulidae	*Thryssa chefuensis*	Crus	M	39N-21N	0.00	0	This study
Engraulidae	*Thryssa dayi*		M	27N-6N		0	
Engraulidae	*Thryssa dussumieri*	Crus	M	27N-7S	0.00	0	Chacko 1949
Engraulidae	*Thryssa encrasicholoides*		M	21N-26S		0	
Engraulidae	*Thryssa gautamiensis*		M	25N-4N		0	
Engraulidae	*Thryssa hamiltonii*	Pisc	M	31N-25S	0.00	0	This study
Engraulidae	*Thryssa kammalensis*	Crus	M	9N-11S	0.00	0	Hajisamae and Ibrahim 2008
Engraulidae	*Thryssa kammalensoides*		M	21N-13N		0	
Engraulidae	*Thryssa malabarica*		M	27N-3N		0	
Engraulidae	*Thryssa marasriae*		M	9S-15S		0	

Engraulidae	*Thryssa mystax*	Crus	M	25N-9S	0.00	0	Froese and Pauly 2019
Engraulidae	*Thryssa polybranchialis*		M	21N-4N		0	
Engraulidae	*Thryssa purava*		M	25N-5N		0	
Engraulidae	*Thryssa rastosa*		FW	6S-9S		0	Allen 1991
Engraulidae	*Thryssa scratchleyi*	Pisc	FW	5S-15S	0.00	0	Froese and Pauly 2019
Engraulidae	*Thryssa setirostris*	Crus	M	28N-40S	0.00	0	Froese and Pauly 2019
Engraulidae	*Thryssa spinidens*	Crus	M	25N-3N	0.00	0	This study
Engraulidae	*Thryssa stenosoma*		M	25N-15N		0	
Engraulidae	*Thryssa vitrirostris*		M	31N-40S		0	
Engraulidae	*Thryssa whiteheadi*		M	31N-24N		0	
Pristigasteridae	*Chirocentrodon bleekerianus*		M	24N-25S		0	
Pristigasteridae	*Ilisha africana*	Zoop	M	17N-7S	0.00	0	Fagade and Olaniyan 1973; Marcus 1986
Pristigasteridae	*Ilisha amazonica*		FW	1N-12S		0	
Pristigasteridae	*Ilisha compressa*		M	30N-23N		0	
Pristigasteridae	*Ilisha elongata*	Pisc	M	39N-1S	0.00	0	Rao 1967; Blaber et al. 1998
Pristigasteridae	*Ilisha filigera*		M	24N-0		0	
Pristigasteridae	*Ilisha fuerthii*		M	14N-4S		0	Froese and Pauly 2019
Pristigasteridae	*Ilisha kampeni*		M	24N-9S		0	
Pristigasteridae	*Ilisha lunula*		M	5S-21S		0	
Pristigasteridae	*Ilisha macrogaster*		M	9N-3S		0	
Pristigasteridae	*Ilisha megaloptera*	Pisc	M	24N-10S	0.00	0	Blaber et al. 1998
Pristigasteridae	*Ilisha melastoma*	Moll	M	29N-8S	0.00	0	Blaber et al. 1998; Shahraki et al. 2014
Pristigasteridae	*Ilisha novacula*		FW	24N-14N		0	
Pristigasteridae	*Ilisha obfuscata*		M	18N-8N		0	
Pristigasteridae	*Ilisha pristigastroides*		M	1S-7S		0	
Pristigasteridae	*Ilisha sirishai*		M	31N-0		0	
Pristigasteridae	*Ilisha striatula*		M	26N-5N		0	
Pristigasteridae	*Neoopisthopterus cubanus*		M	24N-17N		0	
Pristigasteridae	*Neoopisthopterus tropicus*		M	27N-4S		0	Froese and Pauly 2019
Pristigasteridae	*Odontognathus compressus*		M	14N-4N		0	
Pristigasteridae	*Odontognathus mucronatus*		M	12N-26S		0	
Pristigasteridae	*Odontognathus panamensis*		M	14N-5N		0	Froese and Pauly 2019
Pristigasteridae	*Opisthopterus dovii*		M	32N-5S		0	Froese and Pauly 2019
Pristigasteridae	*Opisthopterus effulgens*		M	5N-0		0	
Pristigasteridae	*Opisthopterus equatorialis*		M	13N-5S		0	
Pristigasteridae	*Opisthopterus macrops*		M	10N-4N		0	
Pristigasteridae	*Opisthopterus tardoore*	Zoop	M	29N-8S	0.00	0	Venkataraman 1960
Pristigasteridae	*Opisthopterus valenciennesi*		M	29N-8S		0	
Pristigasteridae	*Pellona altamazonica*		FW			0	
Pristigasteridae	*Pellona castelnaeana*	Pisc	FW	0-13S	0.07	0	Mérona et al. 2001; González and Vispo 2003; Pouilly et al. 2004
Pristigasteridae	*Pellona dayi*		M	18N-8N		0	
Pristigasteridae	*Pellona ditchela*	Zoop	FW	25N-30S	0.00	0	Mavuti et al. 2004
Pristigasteridae	*Pellona flavipinnis*	Pisc	FW	10N-35S	0.01	0	González and Vispo 2003; Pouilly et al. 2003; Moreira-Hara et al. 2009
Pristigasteridae	*Pellona harroIri*		M	12N-30S		0	
Pristigasteridae	*Pliosteostoma lutipinnis*		M	25N-3N		0	
Pristigasteridae	*Pristigaster cayana*		FW	1N-2S		0	
Pristigasteridae	*Pristigaster whiteheadi*		FW			0	
Pristigasteridae	*Raconda russeliana*		M	24N-9S		0	Froese and Pauly 2019

Table 3.3. Proportions of prey in the diets of ten clupeiform species expressed as percent frequency, percent number, and percent volume.

Species	n	SL (mm)	n Prey	Algae			Amphipoda			Arthropoda			Bivalva veliger			Brachyura			Centric diatom			Chaetognatha			Cirripedia cypris			Cladocera		
				% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V
Anchoa colonensis	10	35.56-58.99	154	0.100	0.006	<0.001				0.100	0.006	0.009	0.300	0.084	0.007										0.300	0.026	0.001			
Encrasicholina punctifer	10	68.18-77.47	339										0.100	0.006	<0.001							0.500	0.071	0.181	0.600	0.029	0.008			
Encrasicholina heteroloba	14	56.81-75.77	433	0.143	0.016	<0.001							0.214	0.007	0.015				0.071	0.002	<0.001				0.429	0.025	0.013	0.286	0.048	0.088
Herklotsichthys castelnaui	10	56.05-62.6	385	0.300	0.010	0.001							0.200	0.005	<0.001				1.000	0.161	0.039				0.900	0.055	0.009			
Stolephorus brachycephalus	10	63.04-81.23	67				0.100	0.015	0.001																0.300	0.060	<0.001			
Stolephorus chinensis	9	59.69-70.46	257				0.111	0.004	0.138										0.556	0.195	0.003				0.222	0.016	0.007			
Thryssa chefuensis	10	83.17-96.7	25																											
Thryssa dussumieri	15	94.81-120.51	182				0.067	0.006	0.001							0.067	0.006	0.001							0.133	0.011	<0.001			
Thryssa hamiltonii	12	98.71-188.16	98	1.000	0.020	<0.001	0.250	0.041	0.029																0.083	0.010	0.001			
Thryssa spinidens	6	79.62-121.26	199																											

Species	n	SL (mm)	n Prey	Copepoda			Crustacea nauplii			Cumacea			Cyanobacteria			megalopa			Decapoda zoea			Dinoflagellata			Egg			Fish		
				% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V
Anchoa colonensis	10	35.56-58.99	154	1.000	0.643	0.026	0.100	0.006	<0.001										0.100	0.006	0.001							0.100	0.026	0.527
Encrasicholina punctifer	10	68.18-77.47	339	1.000	0.737	0.302	0.100	0.006	<0.001							0.100	0.003	0.002	0.100	0.003	0.002				0.400	0.024	<0.001	0.200	0.021	0.177
Encrasicholina heteroloba	14	56.81-75.77	433	1.000	0.850	0.791	0.357	0.022	0.015										0.071	0.005	0.048									
Herklotsichthys castelnaui	10	56.05-62.6	385	1.000	0.740	0.942	0.200	0.005	<0.001													0.100	0.003	0.007						
Stolephorus brachycephalus	10	63.04-81.23	67	0.500	0.418	0.001																						0.100	0.015	0.043
Stolephorus chinensis	9	59.69-70.46	257	1.000	0.632	0.766	0.111	0.004	0.003	0.111	0.004	0.022				0.111	0.008	0.179	0.001	0.004	0.001									
Thryssa chefuensis	10	83.17-96.7	25																									0.400	0.240	0.301
Thryssa dussumieri	15	94.81-120.51	182	0.467	0.088	0.001																								
Thryssa hamiltonii	12	98.71-188.16	98	0.167	0.051	<0.001				0.083	0.010	<0.001				0.083	0.051	0.023	0.167	0.041	0.001									
Thryssa spinidens	6	79.62-121.26	199	0.667	0.050	0.002													0.167	0.005	<0.001									

Species	n	SL (mm)	n Prey	Gammeridea			Gastropoda veliger			Hydrozoa			Isopoda			Lucifer			Nematoda			Ostacoda			Pennate diatom			Plant		
				% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V	% F	% N	% V
Anchoa colonensis	10	35.56-58.99	154	0.100	0.006	0.001				0.100	0.006	<0.001	0.100	0.013	0.048	0.100	0.104	0.366	0.200	0.019	0.001									
Encrasicholina punctifer	10	68.18-77.47	339													0.500	0.032	0.024												
Encrasicholina heteroloba	14	56.81-75.77	433				0.143	0.007	0.009										0.143	0.009	0.003				0.143	0.005	<0.001			
Herklotsichthys castelnaui	10	56.05-62.6	385				0.400	0.010	0.003										0.100	0.003	<0.001				0.200	0.005	<0.001	0.100	0.003	<0.001
Stolephorus brachycephalus	10	63.04-81.23	67										0.200	0.030	<0.001				0.200	0.045	<0.001									
Stolephorus chinensis	9	59.69-70.46	257				0.111	0.004	0.001																					
Thryssa chefuensis	10	83.17-96.7	25										0.100	0.040	0.014															
Thryssa dussumieri	15	94.81-120.51	182													0.600	0.392	0.017				0.133	0.011	<0.001						
Thryssa hamiltonii	12	98.71-188.16	98													0.333	0.092	0.004				0.083	0.092	0.010				0.083	0.020	0.001
Thryssa spinidens	6	79.62-121.26	199	0.167	0.005	0.001										0.667	0.201	0.022				1.000	0.151	0.013						

Species	n	SL (mm)	n Prey	Polychaeta			Shrimp			Trematoda		
				% F	% N	% V	% F	% N	% V	% F	% N	% V
Anchoa colonensis	10	35.56-58.99	154				0.100	0.006	0.012	0.400	0.039	0.001
Encrasicholina punctifer	10	68.18-77.47	339	0.100	0.003	0.004	0.400	0.029	0.165			
Encrasicholina heteroloba	14	56.81-75.77	433				0.071	0.002	0.019			
Herklotsichthys castelnaui	10	56.05-62.6	385									
Stolephorus brachycephalus	10	63.04-81.23	67				1.000	0.328	0.955	0.300	0.090	<0.001
Stolephorus chinensis	9	59.69-70.46	257									
Thryssa chefuensis	10	83.17-96.7	25				0.800	0.720	0.686			
Thryssa dussumieri	15	94.81-120.51	182				0.933	0.475	0.964			
Thryssa hamiltonii	12	98.71-188.16	98				1.000	0.561	0.933			
Thryssa spinidens	6	79.62-121.26	199				1.000	0.583	0.963			

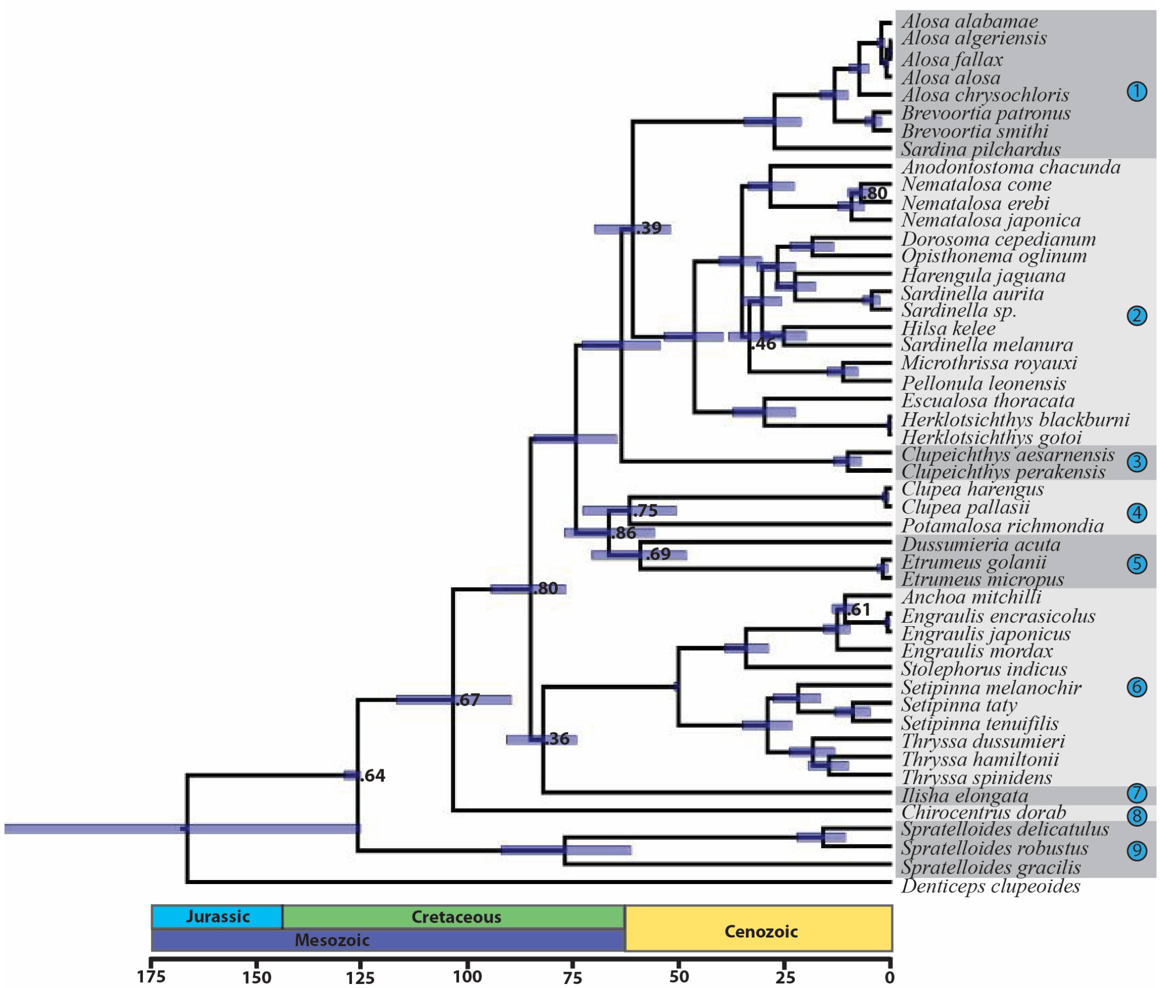


Figure 3.1. Time-calibrated clupeoid phylogeny resulting from concatenated Bayesian analysis of the 6-gene dataset in BEAST v.2.4.5. Nodes are labeled with posterior Bayesian probabilities if support is <0.95. Time, in millions of years, is shown along the x-axis. Node bars show the 95% highest posterior density interval of divergence time estimates. Shaded clupeoid lineages: (1) Alosinae, (2) Dorosomatinae, (3) Ehiravinae, (4) Clupeinae, (5) Dussumieriinae, (6) Engraulidae, (7) Pristigasteridae, (8) Chirocentridae, and (9) Spratelloidinae.

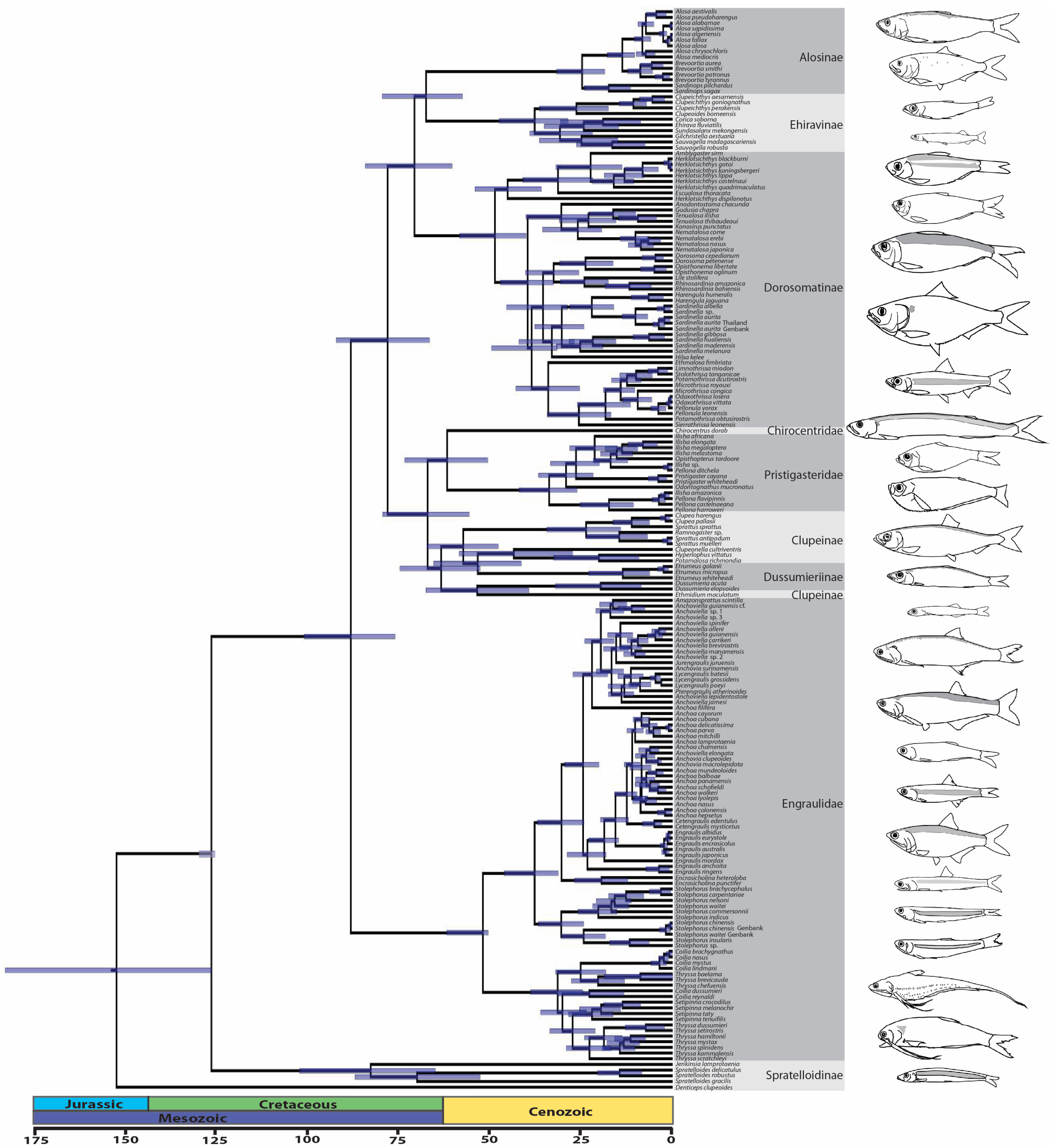


Figure 3.2. Time-calibrated clupeoid phylogeny inferred by concatenated Bayesian analysis of my 4-gene dataset in BEAST 2.4.5. Time, in millions of years, is shown along the x-axis. Node bars show the 95% highest posterior density interval of divergence time estimates. Line drawings of representative clupeoids from top to bottom: *Alosa chrysochloris*, *Brevoortia tyrannus*, *Clupeichthys aesarnensis*, *Sundasalanx mekongensis,*

Herklotsicthys castelnaui, *Escualosa thoracata*, *Sardinella albella*, *Ethmalosa fimbriata*, *Limnothrissa miodon*, *Chriocentrus dorab*, *Ilisha melastoma*, *Opisthopterus tardoore*, *Clupea harengus*, *Dussumieria elopsoides*, *Amazonsprattus scintilla*, *Lycengraulis batesii*, *Pterengraulis atherinoides*, *Anchoa mitchilli*, *Anchoa hepsetus*, *Cetengraulis edentulus*, *Engraulis japonicus*, *Encrasicholina punctifer*, *Stolephorus nelsoni*, *Coilia dussumieri*, *Thryssa setirostris*, and *Spratelloides gracilis*.

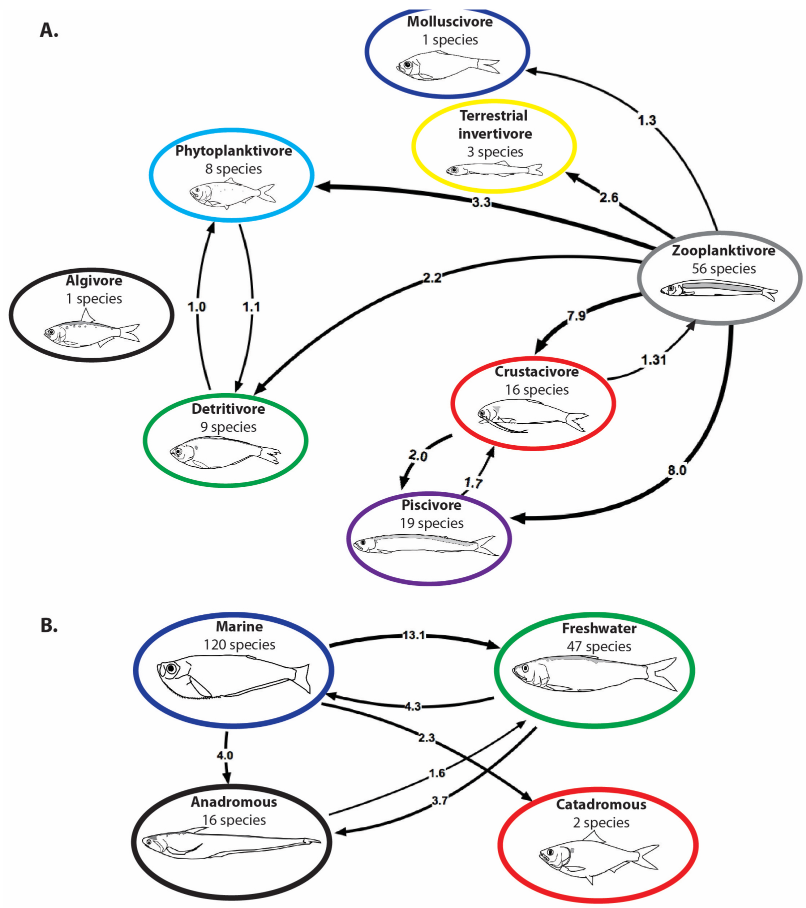


Figure 3.3. Summary of diet (A) and habitat use (B) transition frequencies (average number of transitions) in Clupeoidei estimated using the 4-gene concatenated Bayesian phylogeny with taxa missing habitat and diet character data removed and 1000 stochastic

character mapping simulations. I only show transitions with average frequencies greater than 1.0. A representative clupeoid species is pictured with each character state. Detritivore, phytoplanktivore, and algivore are considered herbivorous trophic guilds.

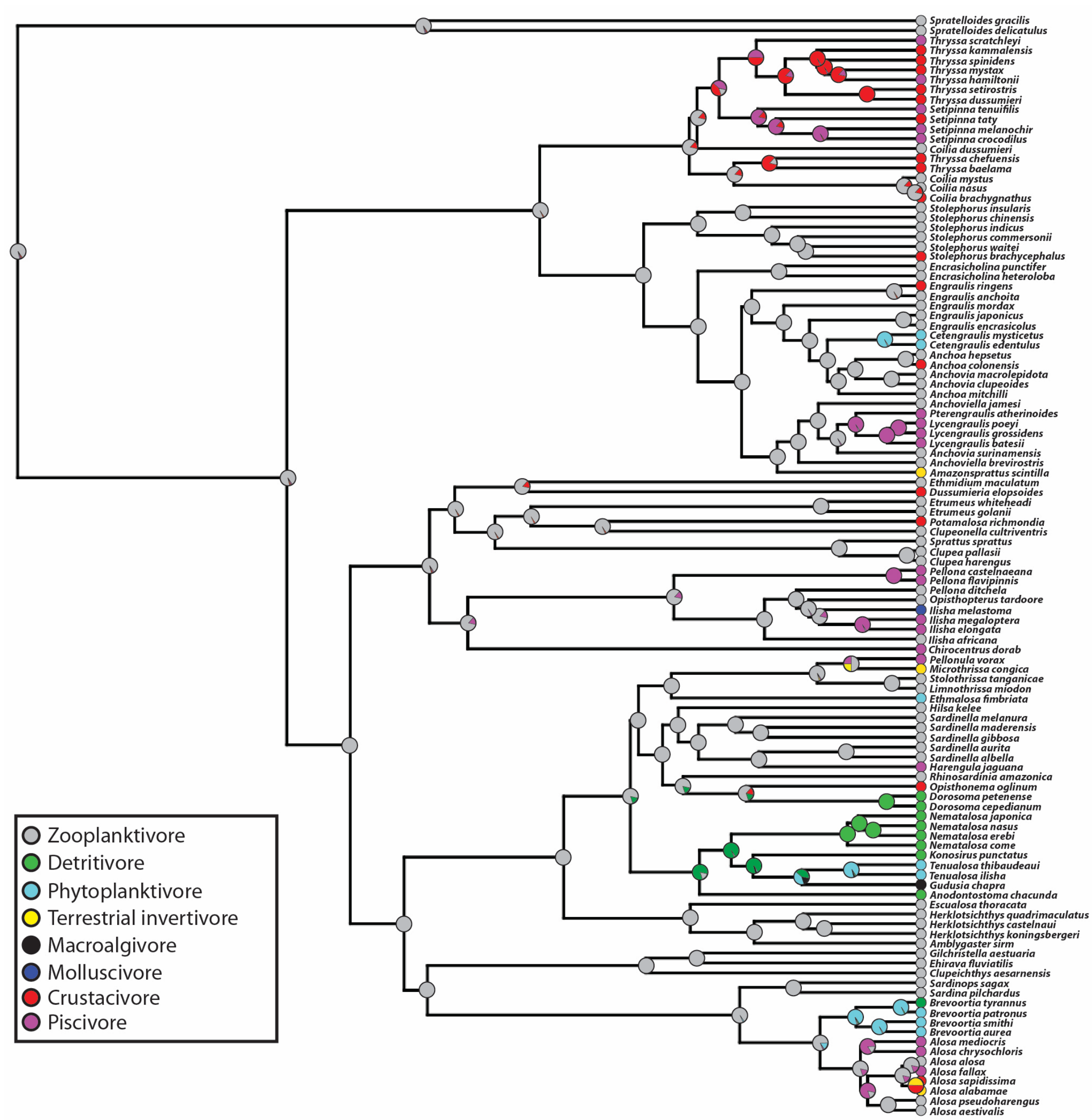


Figure 3.4. Evolutionary history of diet (trophic guilds) in Clupeoidei estimated using the 4-gene concatenated Bayesian phylogeny with taxa trophic guild data removed and 1000 stochastic character mapping simulations. Detritivore, phytoplanktivore, and algivore trophic guilds are considered herbivorous.

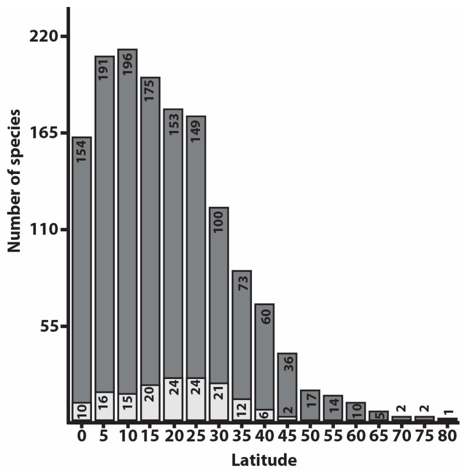


Figure 3.5. Number of clupeoid species (y-axis) at 5^0 latitudinal transects (absolute value of latitude; x-axis). The light gray portion of bars represents the number of herbivorous species and the light (herbivores) and dark (non-herbivores) portions of each bar are labeled with number of species.

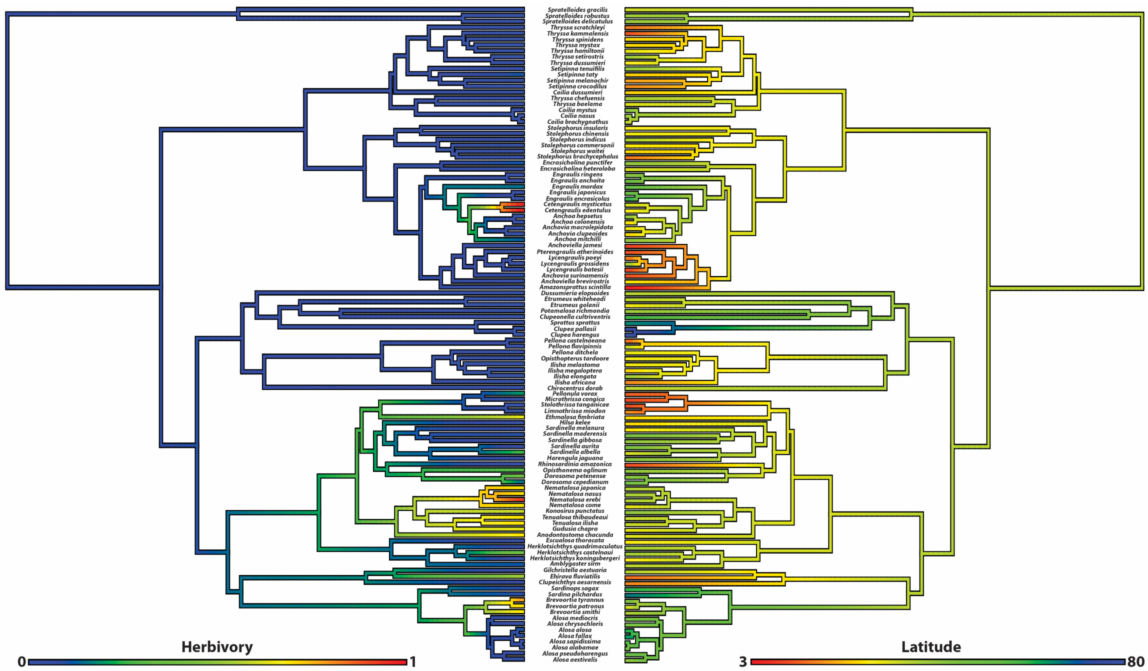


Figure 3.6. Contmap ancestral state reconstructions of continuous characters estimated using my 4-gene concatenated Bayesian clupeoid phylogeny with taxa missing continuous character data removed. The left contmap shows the evolutionary history of the herbivory character (warm colors = highly herbivorous) and the right contmap shows the evolutionary history of the latitude character (cool colors = high latitudes).

CHAPTER 4

Niche breadth, diversification rates, and latitude are decoupled in clupeiform fishes (anchovies, sardines, allies): support for tropical conservatism in the origins of the latitudinal diversity gradient

1. Introduction

The increasing species richness from the poles to the equator, called the latitudinal diversity gradient, is one of the most striking and pervasive spatial patterns of biodiversity. The gradient is global in scale, observed in living and extinct lineages, and exhibited by nearly all groups of organisms regardless of their ecology (Otté & Bohn 1850; Hawkins 2001; O'Brien et al. 2000; Hillebrand 2004a,b; Fuhrman et al. 2008; Buckley et al. 2010; Stomp et al. 2011; Rabosky et al. 2018; Economo et al. 2019). The latitudinal diversity gradient has existed off and on for over 325 million years, seemingly diminishing during warm periods of earth's history and returning during cooler periods (Crame 2001; Leighton 2005; Powell et al. 2012; Mannion et al. 2014; Marcot et al. 2016; Shiono et al. 2018). Despite its pervasiveness, the origins of the latitudinal diversity gradient are poorly understood. This gap in scientific theory limits our understanding of spatial variation in species richness, undermines attempts to predict impacts of changing environments on biodiversity, and hinders sustainable management of natural resources (Brown 2014; Pontarp et al. 2019).

There are numerous hypotheses to explain the processes underlying the formation and maintenance of the latitudinal diversity gradient. These hypotheses can be grouped into three categories: (1) tropical conservatism/time for speciation, (2) species carrying capacity/ecological limits, and (3) diversification rate hypotheses (reviewed by Mittelbach *et al.* 2007; Pontarp *et al.* 2019). These three categories of hypotheses are not mutually exclusive and some share underlying processes (Pontarp et al. 2019). It is clear that climate is a key parameter in any mechanistic model of the latitudinal diversity gradient because climate predicts many of the deviations from this pattern (O'Brien et al. 2000; Morinière et al. 2016). For example, models that included climate variables such as rainfall and temperature better predicted geographic patterns of woody plant species richness than models only including a latitude and longitude variables (O'Brien et al. 2000). However, it remains uncertain which hypothesis or combination of hypotheses explains the latitudinal gradient and what processes interact with climate to shape species richness (Mittelbach *et al.* 2007). Uncertainty remains because rigorously testing competing latitudinal gradient hypotheses requires extensive data, including phylogenies for large groups of organisms (Mittelbach *et al.* 2007; Pontarp *et al.* 2019).

Tropical niche conservatism hypotheses for explaining the diversity gradient posit that the tropics are species rich because tropical climates have had more time to accumulate species than temperate climates, which have shrunk or disappeared entirely during warm periods of Earth's history (Zachos et al. 2001). They also propose that climate niche conservatism limited colonization of temperate environments by tropical lineages (Wiens & Donoghue 2004). Without climate niche conservatism, rapid colonization of temperate areas could rapidly eliminate the latitudinal gradient in scenarios that do not invoke different carrying capacities or diversification rates to explain the diversity gradient. Clades with temperate lineages younger than the re-emergence of temperate environments following Oligocene cooling (~34 Ma) and infrequent transitions to temperate environments are consistent with tropical conservatism hypotheses (Wiens & Donoghue 2004). Several, but not all, recent studies have found stronger support for niche conservatism hypotheses for the latitudinal diversity gradient than competing hypotheses (Miller et al. 2018; Rabosky et al. 2018; Shiono et al. 2018; Economo et al. 2019). There is also evidence that time for diversification and niche conservatism might play a role in generating the inverse latitudinal diversity gradients exhibited by some clades (Rivadeneira et al. 2010; Morinière et al. 2016).

Carrying capacity hypotheses for the diversity gradient propose that certain properties of tropical environments, such as constant, high primary productivity resulting from consistent, high inputs of solar radiation and water, more species to coexist than in temperate regions (Janzen 1967; Mittelbach *et al.* 2007; Hurlbert & Stegen 2014). These hypotheses predict that diversity is approximately at equilibrium across all latitudes and consequently regional net diversification rates are near zero over evolutionary timescales. In this scenario diversification rates might vary over shorter periods to maintain species diversity near carrying capacity. Carrying capacity hypotheses predict that lineages exhibited positive net diversification rates early in their history that subsequently decreased to approximately zero (Mittelbach *et al.* 2007; Hurlbert & Stegen 2014). Most recent studies have not found strong evidence for carrying capacity hypotheses (Marin et al. 2018; Economo et al. 2019). However, there is evidence that carrying capacity might play a role in regulating regional species richness patterns (Coelho et al. 2018; Storch et al. 2018) and diversification rates in some lineages of organisms (Betancur-R et al. 2012; Bloom & Egan 2018).

Diversification rate hypotheses for explaining the latitudinal diversity gradient propose that rapid tropical speciation, low tropical extinction, or both, resulted in a negative correlation between net diversification rate and latitude, thus creating the latitudinal diversity gradient. Many mechanisms have been proposed to produce elevated tropical diversification rates. For example, Jocque et al. (2010) suggested ecological specialization is characteristic of tropical organisms, and this specialization limits dispersal across unfavorable environments, leading to high rates of allopatric speciation. Allen et al. (2006) proposed that high tropical temperatures result in high metabolism, which increases mutation rates. Janzen (1967) hypothesized that high net diversification rates at low latitudes might result from low extinction rates in temporally stable tropical climates. There is no consensus regarding the importance of diversification rates to the diversity gradient, with different studies reporting positive (Rabosky et al. 2018), negative (Pyron & Wiens 2013; Pyron 2014), or no correlation (Rabosky et al. 2015; Tedesco et al. 2017; Miller et al. 2018; Economo et al. 2019) between latitude and diversification rates.

There have been few tests of latitudinal diversity gradient hypotheses using teleost fishes as a study system and these focused on large clades and yielded conflicting results.

Tedesco et al. (2017), using a dataset containing both freshwater and marine fishes, and Rabosky et al. (2018), using a marine fishes dataset, found support for tropical niche conservatism hypotheses. By contrast, Siqueira et al. (2016) reported higher net diversification rates in tropical marine reef fishes relative to extratropical regions, in support of diversification rate hypotheses. These studies tested diversification rate and niche conservatism hypotheses, but did not test the carrying capacity hypothesis. Additional studies that simultaneously test all three types of diversity gradient hypotheses are needed to reveal the forces that generated the latitudinal diversity gradient in fishes. Investigations of specific clades of fishes that incorporate detailed species range and ecology data can lead to a mechanistic understanding of the latitudinal diversity gradient and determine if processes governing species richness patterns vary among different clades of fishes.

I tested the predictions of tropical conservatism, species carrying capacity, and diversification rate hypotheses to gain insight into the origins of the latitudinal diversity gradient in a lineage of teleost fishes, the Clupeiformes (anchovies, herrings, sardines, and relatives). This group contains 394 recognized species, is globally distributed in freshwater and marine habitats, and exhibits a latitudinal diversity gradient (Whitehead et al. 1988; Lavoué et al. 2013; Bloom & Lovejoy 2014; Egan et al. 2018a, Ch3; Egan et al. 2018b, Ch2). This group of fishes originated approximately 150 Ma, which allowed me to examine the timing of transitions to temperate areas and temporal patterns of net diversification (Egan et al. 2018a, Ch3; Bloom & Egan 2018). Additionally, I tested the predictions of a specific diversification rates hypothesis for the latitudinal gradient: the “climate-mediated dispersal-ecological specialization trade-off (CDES trade-off)” hypothesis (Jocque et al. 2010). This model proposes that elevated tropical speciation rates are responsible for the latitudinal diversity gradient. In this model, the seasonality of temperate climates promotes the evolution of generalist species and temporally stable tropical environments promote the evolution of specialists. Generalists are expected to maintain gene flow between populations under a wider range of environmental conditions than specialists, and gene flow between populations can be antagonistic the speciation process (Kisel & Barraclough 2010). Consequently, this model predicts that generalists exhibit slower speciation rates than specialists, resulting in high tropical and low temperate speciation rates, which results in a latitudinal diversity gradient. Although based on compelling arguments, the relationships between environmental variability, the evolution of generalists and specialists, and speciation rates proposed by the CDES trade-off model have yet to be rigously tested.

I used phylogenetic, dietary, and species geographic range data to investigate potential explanations for the origins of the latitudinal diversity gradient in Clupeiformes by testing the following hypotheses: (1) climate niche breadth is phylogenetically conserved, (2) speciation and net diversification rates are negatively correlated with latitude, (3) temperate clupeiform lineages originated after the onset of Oligocene cooling (~34 Ma), (4) niche breadth is positively correlated with latitude, and (5) niche breadth is negatively correlated with speciation and net diversification rates. I did not estimate extinction rates because extinction rate parameter estimates are often unreliable (Davis et al. 2013). As noted above, the three categories of latitudinal diversity gradient hypotheses are not necessarily mutually exclusive and some latitudinal diversity gradient hypotheses share underlying processes (Pontarp et al. 2019). Consequently, the objective of this study was to identify mechanisms that were likely not involved in the origins of the clupeiform latitudinal diversity gradient and identify candidate latitudinal gradient hypotheses deserving additional investigation.

2. Materials and Methods

2.1 Phylogeny

For inferences of trait evolution, estimation of diversification rates, and phylogenetic comparative analyses, I used a time-calibrated clupeiform phylogeny estimated via concatenated Bayesian analyses of one mitochondrial gene (*cytb*) and three nuclear genes (*rag1*, *rag2*, and *slc*). The phylogeny contained 181 clupeiform species, included all major clupeiform lineages, and 67 of 82 genera (Egan et al. 2018a, Ch3; Table 4.1).

2.2 Diet data

I collected prey type and prey size consumption data from scientific articles and by quantifying the gut contents of fish specimens borrowed from museums or collected in Iran, Australia, Taiwan, and Thailand (Table 4.2). Many fishes exhibit ontogenetic shifts in prey type and size consumption (Scharf et al. 2000; Egan et al. 2018b, Ch2). Therefore, I only included diet data from individuals longer than 40% of the maximum reported length for each species in my dataset to standardize interspecific diet comparisons.

I conducted gut content analysis using methods compatible with previous studies measuring clupeiform prey sizes (Egan et al. 2017, Ch1; Egan et al. 2018a, Ch3; Egan et al. 2018b, Ch2) to ensure that published data could be integrated with the novel diet data reported here. I measured the standard length (SL) of each specimen using digital calipers before dissecting gut contents onto a microscope slide with a 1 × 1 mm grid. I only examined prey in the anterior portion of digestive tracts because some prey types digest faster than others, which can bias diet descriptions if heavily digested gut contents are considered (Gannon 1976; Buckland et al. 2017). I quantified prey in the first quarter of digestive tracts in species with no stomachs/gizzards and prey in the digestive tract up to the posterior end of the stomach/gizzard in species with stomachs/gizzards. I excluded individuals if the anterior regions of the digestive tracts were empty or primarily contained highly digested prey. I estimated total gut content volume using the geometric volume equation for a cuboid and measurements of the gut contents obtained by evenly spreading gut contents on a grid slide in a rectangular shape to a depth of 1 mm. I took a representative subsample of the gut contents and identified these prey items to the lowest practical taxonomic level and photographed individual prey items with a microscope-mounted Spot Insight digital camera (Model 14.2 Color Mosaic). I estimated the volumes of individual prey by measuring their width, length, and area using the photographs, ImageJ software (http://www.imagej.nih.gov/ij), and cylinder and ellipsoid equations following Alcaraz et al. (2003), Espinoza and Bertrand (2008), and Egan et al. (2018b, Ch2). In instances when prey were degraded and only prey width was measurable, I estimated prey volume by interpolation based on simple linear regression of prey width versus prey volume from high-quality prey of the same prey type. It was not practical to measure individual detrital particles; however, I observed that detrital particles were nearly always < 100 μm wide. Therefore, when guts contained detritus, I assigned detritus to a 1 μm < 100 μm size bin for calculations and measured the proportions of detrital and non-detrital material in the gut. I expressed prey type consumption for each species as percent volume.

2.3 Prey type trophic guild analysis

To investigate evolutionary and geographic patterns of prey type consumption and facilitate interpolation of prey size niche breadths (see following section) I assigned clupeiform species to trophic guilds. Trophic guilds are groups of species eating similar prey (Root 1967; Garrison & Link 2000). I binned the prey types identified in the literature review and gut content analyses into 19 prey categories for statistical analysis (Table 4.3). These prey categories are similar to those used in previous fish diet studies and describe functional, rather than taxonomic similarity among prey (Nakamura et al. 2003; Hundt et al. 2014; Egan et al. 2017, Ch1; Egan et al. 2018b, Ch2). In this prey type dataset, I included diets expressed as percent number or volume. I excluded diets expressed as frequency of occurrence because this method does not report diets as percentages of prey types summing to 100%, which precluded me from combining these data with numerical and volumetric data to estimate diet dissimilarity. I did not include prey types comprising < 0.001% of a species' diet in analyses. I calculated diet dissimilarity using Bray-Curtis dissimilarity indices (Bray and Curtis 1957; Somerfield 2008), then grouped clupeiforms based upon similarity in prey type consumption using unweighted average linkage hierarchical agglomerative cluster analysis (UPGMA) with the program *R* v3.5.3 (http://www.r-project.org) package *vegan* (Legendre & Legendre, 2012; Oksansen et al. 2016). I identified statistically significant clupeiform groupings (trophic guilds) using a bootstrap randomization approach and the RA4 algorithm (Lawlor 1980) following Jaksić and Medel (1990) and Buchheister and Latour (2015). In addition to a "full" trophic guild scheme that considered all statistically significant predator clusters as trophic guilds, I also used an arbitrary threshold of 75% dissimilarity to demarcate a "conservative" trophic guild scheme. I qualitatively assigned species to trophic guilds for which I was only able to obtain frequency of occurrence or qualitative diet data.

2.4 Niche concepts and quantification

I adhered to the resource-utilization conceptualization of the ecological niche, which defines the ecological niche as a multidimensional volume with axes that describe a species' use of different resources (Schoener 2009). Niche breadth describes the range of resource use along a single niche axis and specialization and generalization are processes describing the evolution of a smaller/narrower or larger/wider niche volume/breadth, respectively (MacArthur & Levins 1967; Schoener 2009; Devictor et al. 2010).

I estimated diet niche breadth in two ways to comprehensively characterize the relationship between diet niche breadth and latitude and diversification rates. First, I used the inverse of Simpson's (1949) diversity index (Pianka 1973) to represent the breadth of prey type consumption.

$$\text{Prey-type niche breadth} = \frac{1}{\sum_{i=1}^{n} P_i^2}$$

P is the proportional use of each prey category *i*. Niche breadth values range from 1 (one prey category used) to *n* (consumption of every prey category). I also measured niche breadth as the range of prey sizes consumed. I did not include prey in prey-size niche breadth calculations that contributed minimally to the overall diet by assigning prey to size bins (<100 μm, 100 μm < 300 μm, 300 μm < 600 μm, etc.) and then excluding prey in bins comprising less than one percent of the diet by volume.

I was unable to quantify prey-size niche breadth for all species in my analysis. Therefore, I interpolated prey-size niche breadths for species for which I was only able to obtain prey type data. I did this by calculating the mean prey-size niche breadths of each trophic guild. I tested for statistically significant differences in prey-size niche breadth between trophic guilds using analysis of variance (ANOVA). Then, I assigned mean prey-size niche breadth values to relevant clupeiform species according to their trophic guild using both the full and conservative trophic guild schemes, yielding two prey-size niche breadth datasets for analysis. I tested for correlation between prey-size and prey-type niche breadth using linear regression.

2.5 Species range data

I collected species range data from the literature (Borsa et al. 2004; Loeb & Alcântara 2013), FishNet2 (www.fishnet2.net) occurrence records, and compiled Ocean Biogeographic Information System (www.iobis.org; Grassle 2000) and Global Biodiversity Information Facility (www.gbif.org; GBIF, 2017) occurrence records accessed via AquaMaps (Kaschner et al. 2016). I used these data to code two characters characterizing the ranges of each species: (1) a continuous character describing the absolute value of the latitude of the furthest point of a species' range from the equator and (2) a discrete character describing the climate zone (tropical, subtropical, or temperate) inhabited by each species, which was determined using FishBase climate zone determinations (based on distributional data and sea surface temperatures) and latitudes encompassed by species' ranges (Table 4.1). Tropical, subtropical, and temperate latitudes were considered to fall approximately within the latitudes of $< 23.5^0$, 23.5^0 to 35^0, and $> 35^0$, respectively.

2.6 Inferring trait evolution

I measured the phylogenetic signal λ (Pagel 1999), a measure of the phylogenetic correlation of species' trait values, of ecological traits (climate zone, prey-size niche breadth, and prey-type niche breadth) assuming a Brownian motion model of trait evolution using the *phylosig R* function in *phytools* (Revell 2012). Values near 1 indicate correlation between species that is close to the expectation under a Brownian model of trait evolution, while values close to 0 indicate little phylogenetic correlation among trait values relative to expectations of Brownian trait evolution.

I estimated the evolutionary history of each discrete ecological trait (climate zone and trophic guild) using Revell's (2012) modification of Bollback's (2006) Bayesian stochastic character mapping method using the *make.simmap phytools* function run for 1000 iterations. I estimated the evolutionary history of continuous characters (maximum latitude, prey-size niche breadth, and prey-type niche breadth) using the *contMap* phytools function. Where necessary, I trimmed trees to match character sampling using the *drop.tip R* function in package *ape* (Paradis & Schliep 2019).

2.7 Testing for correlation between niche breadth, range size, and latitude

I tested for correlation between niche breadth and latitude using phylogenetic ANOVA with the *phylANOVA phytools* function for discrete predictor variables and phylogenetic least squares regression (PGLS) with the *pgls R* function in the *caper* package (Orme et al. 2013) for continuous predictor. I trimmed taxa missing character data from the phylogeny for each analysis and tested for correlations between the following sets of characters: (1) climate zone versus prey-type niche breadth, (2) climate zone versus prey-size niche breadths estimated using the conservative trophic guild scheme, (3) climate zone versus prey-size niche breadths estimated using the full trophic guild scheme, (4) maximum latitude versus prey-type niche breadth, (5) maximum latitude versus prey-size niche breadth estimated using the conservative trophic guild scheme, and (6) maximum latitude versus prey-size niche breadth estimated using the full trophic guild scheme.

2.8 Estimation of macroevolutionary rates

I estimated speciation, extinction, and net diversification rates in Clupeiformes using program BAMM v.2.5.0 (Rabosky 2014). I set priors for analyses using the *setBAMMpriors R* function in *BAMMtools* (Rabosky 2014). I set the prior expectation for shifts to 1, used default Markov Chain Monte Carlo (MCMC) operators, and ran MCMC for $2 \cdot 10^5$ generations. I accounted for incomplete taxon sampling by calculating the proportion of species sampled (sampling fraction) at the genus level if possible and at higher taxonomic levels when necessary (Table 4.3). I checked for convergence of MCMC runs using the log-likelihood trace of MCMC output. I ensured sufficient effective sample sizes of the log-likelihood and number of rate shifts using the *effectiveSize R* function in *coda* (Plummer et al. 2006). To determine which rate shift model was best supported by the data, I computed Bayes factors using *BAMMtools*, which allows for model comparison that is robust to prior selection (Rabosky 2014). I considered Bayes factors greater than 20 to be strong model support following Rabosky et al. (2017). I used the *BAMMtools plotRateThroughTime* function to visualize net diversification rate through time across the entire phylogeny and within three major clupeiform lineages and the *BAMMtools plot.bammdata* function to illustrate model-averaged diversification rates on the phylogeny.

2.9 Testing for correlations between latitude, niche breadth, and speciation rates

I used *STRAPP* (Rabosky & Huang 2016) and *ES-sim* (Harvey & Rabosky 2018) to test for correlations between species traits and diversification rates. I used *STRAPP* for both continuous (maximum latitude, prey-type niche breadth, and prey-size niche breadth) and discrete characters (climate zone) and net diversification rate and speciation rate. I used *ES-sim* to test for correlations between continuous trait data and speciation rates; *ES-sim* does not calculate net diversification rates or accommodate discrete trait data. The *STRAPP* method generates a null distribution of associations between diversification rate and species traits by permuting trait values among *BAMM* speciation rate regimes. This method has a lower type I error rate, but also lower statistical power (limited by the number of rate regimes present in a phylogeny) than alternative methods for identifying correlations between traits and speciation rate, such as *QuaSSE* (FitzJohn 2010; Rabosky & Huang 2016). The *ES-sim* method has more power than *STRAPP* to detect correlations between traits and rates in small phylogenies and phylogenies containing a small number of rate regimes and also has a low type I error rate (Harvey & Rabosky 2018).

3. Results

3.1 Character data

Assembling character data for clupeiforms confirmed the previously reported latitudinal gradient in Clupeformes (Lavoué et al. 2013), with 22, 57, and 315 species occurring in temperate, subtropical, and tropical areas, respectively (Table 4.1). I collected novel diet data for 24 species (Table 4.2).

3.2 Prey type trophic guild analysis

I included 104 species in the prey type cluster analysis. Using a bootstrap ransomization approach, I identified a Bray Curtis dissimilarity index of 0.601 as the threshold for statistically significant differences among clusters. Application of this criterion to cluster analysis results demarcated eight trophic guilds. I call these eight trophic guilds the "full" trophic guild scheme (Figure 4.1). Trophic guild names refer to dominant/distinct prey categories in each trophic guild, but are not indicative of exclusive consumption of a specific prey category and trophic guilds with similar or the same names in other studies (e.g. piscivore) are not necessarily equivalent. Tropical and subtropical areas each contained seven trophic guilds while temperate regions only contained four trophic guilds: tropical (crustacivore, detritivore, molluscivore, phytoplanktivore, piscivore, terrestrial invertivore, zooplanktivore), subtropical (crustacivore, detritivore, algivore, phytoplanktivore, piscivore, terrestrial invertivore, zooplanktivore), and temperate (crustacivore, detritivore, piscivore, zooplanktivore). The prey categories comprising the bulk of the diets in each trophic guild are summarized in Table 4.4.

Using the more conservative Bray Curtis dissimilarity threshold of 0.75, I identified four trophic guilds: omnivore, crustacivore, piscivore, and terrestrial invertivore. In this "conservative" trophic guild scheme the zooplanktivore and crustacivore guilds were combined into a more inclusive crustacivore trophic guild, and detritivore and phytoplanktivore guilds were combined into a more inclusive detritivore trophic guild (Figure 4.1). I assigned 25 additional species to trophic guilds for which only frequency of occurrence or qualitative diet data were available using the results of the trophic guild analyses.

3.3 Niche breadth

I quantified size-based niche breadth for 23 species and interpolated size-based niche breadths for the remaining 98 species included in analyses. Most trophic guilds in the full scheme exhibited differences in prey-size niche breadths, but not all differences were statistically significant (Table 4.5). All trophic guilds in the conservative scheme exhibited statistically significant differences in prey-size niche breadth (Table 4.5). I estimated prey-type niche breadth for 87 species. Prey-type niche breadths were not significantly different between trophic guilds (Table 4.5). Linear regression found no correlation between prey-type and prey-size niche breadth ($p = 0.810$).

3.4 Trait evolution

All ecological traits, except for prey-type niche breadth, exhibited moderate to strong phylogenetic signal: prey-size niche breadth interpolated using full trophic guild scheme ($\lambda = 0.718$), prey-size niche breadth interpolated using conservative trophic guild scheme ($\lambda = 0.654$), prey-type niche breadth ($\lambda = 0.338$), and climate zone ($\lambda = 0.767$). There were 39 total evolutionary transitions in trophic guild. The most common transitions were zooplanktivore to piscivore (8 transitions), zooplanktivore to crustacivore (9 transitions), and zooplanktivore to phytoplanktivore (4 transitions; Figure 4.2). Thirteen of these changes represented trophic specialization and 26 changes represented trophic generalization along the prey size niche axis. The continuous character mapping of prey-type niche breadth also revealed both instances of generalization and specialization (Figure 4.3). Stochastic character mapping analysis identified 14 transitions from tropical to subtropical, 4 transitions from tropical to temperate, 2 transitions from subtropical to tropical, 3 transitions from subtropical to temperate, 2 transitions from temperate to tropical, and 3 transitions from temperate to subtropical areas. These findings are mirrored by the maximum latitude continuous character mapping (Figure 4.4a). All transitions to temperate environments appeared to have occurred more recently than 34 Ma (Figure 4.4a; Figure 4.4b).

3.5 Testing for correlation between niche breadth and range and latitude

Using PGLS, I did not find significant correlations between prey-size or prey-type niche breadth and latitude in any analyses: prey-size niche breadth interpolated using full trophic guild scheme (eight guilds) versus latitude (p = 0.909), prey-size niche breadth interpolated using the conservative trophic guild scheme (four guilds) versus latitude (p = 0.766), and prey-type trophic guild versus latitude (p = 0.815).

3.6 Estimation of macroevolutionary rates

Bayes factors most strongly supported a speciation rate model with 5 regimes: Bayes factor of 120.89 versus 112.89 for a 6-rate regime model, 92.00 for a 4-rate regime model, and 70.56 for a 3-rate regime model. Net diversification rates were positive in Clupeiformes overall and in major clupeiform lineages (Figure 4.4a).

3.7 Latitude and niche breadth versus diversification rates

STRAPP analyses did not find significant correlations between maximum latitude and speciation rate (p = 0.586) or net diversification rate (p = 0.633), climate zone and speciation rate (p = 0.437) or net diversification rate (p = 0.499), prey-size niche breadth and speciation rate (p = 0.564) or net diversification rate (p = 0.580), or prey-type niche breadth and speciation rate (p = 0.531) or net diversification rate (p = 0.637). Similarly, *ES-sim* also did not find significant correlations between maximum latitude and speciation rate (p = 0.890), prey-size niche breadth and speciation rate (p = 0.539), or prey type niche breadth and speciation rate (p = 0.721).

4. Discussion

I used phylogenetic, ecological niche breadth, and species geographic range data to test predictions of three types of latitudinal diversity gradient hypotheses: (1) niche conservatism/time for speciation, (2) diversification rates, and (3) ecological limits. I also tested for niche breadth evolution as a potential mechanism governing diversification rates within clupeiforms. I found no correlations between niche breadth and latitude, niche breadth and diversification rates, or latitude and diversification rates. Climate zone use exhibited strong phylogenetic signal and reconstructions of the evolutionary history of climate zone suggested that temperate clupeiform lineages primarily arose after the start of Oligocene cooling. Taken together, these results support a niche conservatism/time for speciation explanation of the clupeiform latitudinal diversity gradient.

My results identify tropical conservatism/time for speciation hypotheses as the most likely to explain the clupeiform latitudinal diversity gradient. Tropical conservatism hypotheses predict that climate niche is phylogenetically conserved (has strong phylogenetic signal), tropical origins for lineages originating prior to Oligocene cooling, and that temperate lineages arose via dispersal from the tropics after the Oligocene cooling. My findings were consistent with each of these predictions. First, I inferred tropical origins for clupeiforms in agreement with previous clupeiform research (Lavoué et al. 2013; Egan et al. 2018a, Ch3). Second, clupeiform climate use exhibited strong phylogenetic signal. Finally, I inferred seven invasions of temperate latitudes by clupeiforms, all of which appeared to have occurred since Oligocene cooling (Figure 4.4). These findings are congruent with several other recent studies concluding that niche conservatism hypotheses are most likely to explain the latitudinal diversity gradient (Belmaker & Jetz 2015; Marin et al. 2018; Miller et al. 2018; Rabosky et al. 2018; Shiono et al. 2018; Economo et al. 2019), as well as deviations from this pattern (Morinière et al. 2016). However, there is also some evidence suggesting that diversification rate might play a secondary in the diversity gradient in some clades, such as tetrapods (Marin et al. 2018).

I did not find support for diversification rate latitudinal diversity gradient hypotheses. Speciation and net diversification rates were variable in clupeiforms, with *BAMM* identifying five diversification rate regimes. Subsequent statistical tests found no correlations between latitude and speciation or net diversification rate, rather than the negative correlations predicted by diversification rate hypotheses. These findings are consistent with several recent studies concluding that diversification rates were not the primary force generating the latitudinal diversity gradient in a variety of vertebrate and invertebrate taxa (Rabosky et al. 2015; Tedesco et al. 2017; Rabosky et al. 2018; Marin et al. 2018; Miller et al. 2018; Economo et al. 2019). Reports of clades with higher diversification rates in tropical relative to temperate areas are not uncommon, but these clades are often nested within larger clades that do not appear to exhibit the same pattern of a high tropical diversification rate (Pyron & Wiens 2013; Pyron 2014; Siqueira et al. 2016). For example, Pyron & Wiens (2013) and Pyron (2014) report a negative correlation between net diversification rates and latitude in the tetrapod clades Amphibia and Squamata, respectively, but Marin et al. (2018) found little evidence when the entire Tetrapoda lineage was examined. Rabosky et al. (2018) and Miller et al. (2018) reported higher fish diversification rates in species-poor temperate marine regions relative to tropical marine regions, a pattern that I did not observe in clupeiforms. Biased taxon sampling can impact the results of diversification rate analyses (FitzJohn et al. 2009). However, it is unlikely my findings were impacted by biased sampling because I accounted for clade-specific sampling fraction and the phylogeny used in my study was based upon extensive sampling in Africa, the Indo-Pacific region, Europe, and North and South America (Wilson et al. 2008; Bloom & Lovejoy, 2012; Lavoué et al. 2013; Egan et al. 2018a, Ch3).

My findings are also incongruent with carrying capacity diversity gradient hypotheses. These hypotheses predict regional net diversification rates of approximately zero over macroevolutionary timescales and decreases in net diversification rates to near zero in old lineages of organisms, such as clupeiforms (Mittelbach *et al.* 2007; Hurlbert & Stegen 2014). Net diversification rate through time plots revealed that diversification rate has remained positive since the origin of crown clupeiforms approximately 150 Ma and may have even increased slightly during the past 75 to 50 million years (Figure 4.4b). This evidence concurs with recent latitudinal diversity gradient studies also identifying positive net diversification rates in large clades of organisms over evolutionary timescales (Pyron 2014; Belmaker & Jetz 2015; Economo et al. 2019). My findings do not contradict reports of potential ecological limits on species diversity at regional scales and or within small clades (Coelho et al. 2018; Storch et al. 2018). There is evidence that ecological limits have slowed diversification in some taxa (Betancur-R et al. 2012; Bloom & Egan 2018). For example, Bloom & Egan (2018) identified clupeiform lineages exhibiting slow-downs in net diversification rates, possibly resulting from interspecific competition.

I found substantial variation in prey-size and prey-type niche breadth among clupeiforms and demonstrated a lack of correlation between these two niche breadth estimates. There was substantial variation in prey-type and prey-size niche breadth within trophic guilds. Trophic guild was moderately predictive of prey-size niche breadth, but not predictive of prey-type niche breadth. Egan et al. (2018b, Ch2) also report variation in mean prey size consumption and prey-size niche breadth within trophic guilds. It is interesting that prey-type niche breadth varies within and is not predicted by trophic guild because both measurements are based upon the same underlying prey type data. For example, my study quantitatively assigned both *Etrumeus golanii* and *Sardinella albella* to the zooplanktivore trophic guild and both species consumed zooplankton, small crustaceans, and eggs. However, these species exhibited meaningful differences in prey-type niche breadth. *Sardinella albella* consumed relatively similar amounts of each prey type and had a niche breadth of 3.131, while *E. golanii* consumed almost exclusively zooplankton and had a niche breadth of 1.041. These findings highlight the utility of measurements of species resource use that consider niche breadth, in accordance with resource-utilization ecological niche theory, for progress in several areas of biology (e.g. competition, coexistence, phenotypic evolution). These results also demonstrate the increased resolution offered by diet descriptions that measure both prey sizes and types.

I found no support for Jocque et al.'s (2010) hypothesized role of niche breadth evolution in the formation of the latitudinal diversity gradient. I did not identify any correlations between niche breadth and latitude or niche breadth and diversification rates. The small number of previous studies examining relationships between latitude, niche evolution, diversification rates and corollary processes, such as dispersal, have reported mixed results (Dahirel et al. 2015; Gainsbury and Meiri 2017; Tedesco et al. 2017; Martin and Fahrig 2018; Saupe et al. 2019). The temporal variability of high latitudes, relative to low latitudes, is predicted to promote generalization, which allows species to cope with dynamic environmental conditions (Janzen 1967; Jocque et al. 2010). I may not have observed a relationship between niche breadth and latitude because there are alternative mechanisms by which species might cope with temporal environmental variation. For example, temperate fishes might cope with low winter prey availability via decreased winter metabolism and reliance on stored energy acquired during periods of high prey availability (Cunjak & Power 1987; Amundsen & Knudsen 2009). Additionally, niche breadth expansion (generalization) might be most likely in fishes feeding on variable, short-lived primary consumers such as zooplankton or terrestrial insects. There may be limited selective pressure for the evolution of trophic generalism in fishes feeding on larger, longer-lived prey that are at higher trophic levels and have less temporally variable population sizes. Thus, it is possible that the quantity of prey-type and prey-size niche breadth data and coarse resolution of prey-size niche breadth estimates I used in analyses, which resulted from interpolation of prey size niche breadth for some species, precluded me from observing correlations between niche breadth and latitude. Future studies could collect additional diet data, alleviating the need for interpolation, and specifically examine clupeiform species that feed on temporally variable prey, such as zooplankton. Additionally, I only investigated a single aspect of the ecological niche. It is possible that there are associations between high latitudes and generalism along other niche axes.

I inferred instances of both trophic generalization and trophic specialization along prey-type and prey-size niche axes. There is debate regarding the prevalence and significance of the processes of specialization and generalization. For example, specialization has been proposed to be an evolutionary dead end that limits subsequent ecological diversification, and some have argued that generalization is rare in nature and has little relevance to other ecological and evolutionary processes (Futuyma & Moreno 1988; Loxdale et al. 2011; Dennis et al. 2011). I demonstrated that trophic specialization was not a universal dead-end in clupeiforms and that generalization was not particularly rare. In fact, generalization was more common than specialization along the prey-size niche axis (13 instances of specialization and 26 instances of generalization). Other recent studies have found limited evidence of specialization being a dead end and have documented instances of generalism (Kato et al. 2010; Day et al. 2016). Identifying factors that govern niche evolution and relationships between niche size and other ecological and evolutionary processes is challenging given the multidimensional nature of the ecological niche and the large amount of data required to measure niche breadth/size. However, more research investigating factors governing generalization and specialization and the consequences on other processes is warranted given the apparent prevalence of these processes and their hypothesized relevance to numerous biological patterns and processes (Futuyma & Moreno 1988).

The highest diversification rates in clupeiforms were in the temperate and subtropical Alosinae (shads and menhadens) and a largely tropical and almost exclusively South

American clade of anchovies, both lineages that also exhibited high rates of habitat transitions and life history evolution. These lineages contained many evolutionary transitions between freshwater and marine habitats and origins of migratory behavior (Bloom and Lovejoy 2014; Egan et al. 2018a, Ch3). These qualitative observations suggest that evolutionary habitat transitions, migratory behavior, utilization of freshwater habitats, or a combination of these factors may have promoted speciation. Evolutionary habitat transitions have been suggested to facilitate diversification in fishes by allowing lineages to circumvent ecological limits on clade growth, potentially imposed by competition (Betancur-R et al. 2012; Bloom & Egan 2018). Freshwater habitat use has been positively correlated with speciation rate in fishes (Tedesco et al. 2017; Bloom et al. 2013). The impacts of migration on diversification are poorly understood. Tedesco et al. (2017) reported that non-migratory fish lineages exhibited higher diversification rates than migratory lineages, but higher speciation rates and lower extinction rates have been reported in migratory birds (Rolland et al. 2014). Characterizing relationships between habitat transitions, migration, and diversification rates would be a fruitful avenue for additional research.

In this work, I identified tropical conservatism and time for speciation as the most likely explanation for the latitudinal diversity gradient in clupeiforms and found no support for carrying capacity or diversification rate hypotheses. This study adds to a growing body of evidence that tropical conservatism and time for speciation were involved in the formation of the latitudinal diversity gradient. I found no support for trophic niche breadth evolution playing a role in the latitudinal diversity gradient or governing diversification rates. However, diversification rates were variable in clupeiforms and highest in lineages with high frequencies of habitat and life history evolution, suggesting a link between diversification rates and aspects of niche evolution not considered by this study. I found instances of specialization and generalization, highlighting the need for additional research on the causes and consequences of these processes.

Table 4.1. Clupeiform character data. Guilds full = trophic guilds determined using a threashold of 0.601 dissimilarity, guilds cons. = trophic guilds determined using a threashold of 0.750, NB cons. guilds = prey-size niche breadth estimated using the conservative trophic guild scheme, NB full guilds = prey-size niche breadth estimated using the full trophic guild scheme, and Max Lat. = maximum latitude.

Family	Species	Guilds full	Guilds cons.	NB cons. guilds	NB full guilds	Prey-type breadth	Climate zone	Max Lat.	Diet Citations
Chirocentridae	*Chirocentrus dorab*	Pisc	Pisc	10690	10690	1.121	Tropical	35	Chacko 1949; Venkataraman 1960
Clupeidae	*Alosa aestivalis*	Zoop	Crus	1682	993	2.219	Temperate	41	Stone and Daborn, 1987; Winkelman and Van Den Avyle 2002; Buchheister and Latour 2015
Clupeidae	*Alosa alabamae*	Terr	Crus	1682		2.072	Tropical	44	Mickle et al. 2013
Clupeidae	*Alosa algeriensis*	Crus	Crus	1682	2607		Subtropical	41	
Clupeidae	*Alosa alosa*	Zoop	Crus	1682	993	0.972	Tropical	61	Correia et al. 2001; Maitland and Lyle 2005
Clupeidae	*Alosa chrysochloris*	Pisc	Pisc	10690	10690	1.051	Tropical	45	Whitehead et al. 1988
Clupeidae	*Alosa fallax*	Pisc	Pisc	10690	10690	2.047	Tropical	66	Aprahamian 1989; Assis et al. 1992; Maitland and Lyle 2005; Skóra et al. 2012; Nachón et al. 2013
Clupeidae	*Alosa mediocris*	Pisc	Pisc	10690	10690	3.166	Tropical	46	Buchheister and Latour, 2015
Clupeidae	*Alosa pseudoharengus*	Zoop	Crus	1682	993	4.065	Tropical	55	Kohler and Ney, 1980; Stone and Daborn 1987; Buchheister and Latour 2015; Malek et al. 2016
Clupeidae	*Alosa sapidissima*	Crus	Crus	1682	2607	2.214	Tropical	61	Buchheister and Latour 2015; Malek et al. 2016
Clupeidae	*Amblygaster sirm*	Zoop	Crus	1682	993	1.619	Tropical	35	Whitehead et al. 1988
Clupeidae	*Anodontostoma chacunda*	Detr	Omni	209	143	1.024	Tropical	31	Chacko 1949; Venkataraman 1960; Abrantes et al. 2009
Clupeidae	*Brevoortia aurea*	Phyt	Omni	209	275		Subtropical	38	Sanchez 1989; Froese and Pauly 2019
Clupeidae	*Brevoortia patronus*	Phyt	Omni	209	275	1.177	Subtropical	31	Castillo-Rivera et al. 1996; Winemiller et al. 2007
Clupeidae	*Brevoortia smithi*	Phyt	Omni	209	275		Subtropical	37	Whitehead et al. 1988

Clupeidae	*Brevoortia tyrannus*	Detr	Omni	209	143	1.986	Tropical	46	Lewis and Peters 1994
Clupeidae	*Clupea harengus*	Zoop	Crus	1682	993	1.828	Tropical	80	Gorokhova et al. 2004; Malek et al. 2016
Clupeidae	*Clupea pallasii*	Zoop	Crus	1682	993	2.133	Tropical	77	Wailes et al. 1935; Barry et al. 1996
Clupeidae	*Clupeichthys aesarnensis*	Zoop	Crus	1682	993	2.326	Tropical	17	Sirimongkonthaworn and Fernando 1994; Ariyaratne et al. 2008
Clupeidae	*Clupeichthys goniognathus*	Zoop	Crus	1682	993		Tropical	18	Lim et al. 1999
Clupeidae	*Clupeichthys perakensis*	Zoop	Crus	1682	993		Tropical	6	Froese and Pauly 2019
Clupeidae	*Clupeoides borneensis*	Zoop	Crus	1682	993		Tropical	14	Froese and Pauly 2019
Clupeidae	*Clupeonella cultriventris*	Zoop	Crus	1682	993		Tropical	60	Kiyashko et al. 2007
Clupeidae	*Corica soborna*						Tropical	24	
Clupeidae	*Dorosoma cepedianum*	Zoop	Omni	209	143	4.491	Subtropical	49	Kutkuhn 1958; Jude 1973; Mundahl and Wissing 1987
Clupeidae	*Dorosoma petenense*	Detr	Omni	209	143	3.996	Subtropical	42	Haskell 1959; Winkelman and Van Den Avyle 2002
Clupeidae	*Ehirava fluviatilis*	Phyt	Crus	1682	993	2.192	Tropical	14	Mihindukulasooriya and Amarasinghe 2014
Clupeidae	*Escualosa thoracata*	Zoop	Crus	1682	993	1.460	Tropical	27	Hajisamae et al. 2004; Hajisamae and Ibrahim 2008
Clupeidae	*Ethmalosa fimbriata*	Phyt	Omni	209	275	3.562	Tropical	25	Fagade and Olaniyan 1972; Blay and Eyeson 1982
Clupeidae	*Ethmidium maculatum*	Zoop	Crus	1682	993		Subtropical	37	Froese and Pauly 2019
Clupeidae	*Gilchristella aestuaria*	Zoop	Crus	1682	993	2.205	Tropical	36	Blaber 1979; Bennett and Branch 1990
Clupeidae	*Gudusia chapra*	Algi					Tropical	30	Mondal and Kaviraj 2010; Phukan et al. 2012
Clupeidae	*Harengula humeralis*						Tropical	34	
Clupeidae	*Harengula jaguana*	Pisc	Pisc	10690	10690	2.972	Tropical	43	Vega-Cendejas et al. 1994
Clupeidae	*Herklotsichthys blackburni*						Tropical	21	
Clupeidae	*Herklotsichthys castelnaui*	Zoop	Crus	1682	993	1.963	Subtropical	39	Abrantes et al. 2009
Clupeidae	*Herklotsichthys dispilonotus*	Zoop	Crus	1682	993		Tropical	20	Hajisamae & Ibrahim 2008
Clupeidae	*Herklotsichthys gotoi*						Tropical	19	
Clupeidae	*Herklotsichthys koningsbergeri*	Zoop	Crus	1682	993		Tropical	27	Abrantes et al. 2009
Clupeidae	*Herklotsichthys lippa*						Tropical	24	
Clupeidae	*Herklotsichthys quadrimaculatus*	Zoop	Crus	1682	993	2.230	Tropical	39	Milton et al. 1994

Clupeidae	*Hilsa kelee*	Zoop	Crus	1682	993	1.000	Tropical	25	Blaber 1979
Clupeidae	*Hyperlophus vittatus*	Crus	Crus	1682	2607		Tropical	40	Hossain et al. 2017
Clupeidae	*Konosirus punctatus*	Detr	Omni		143	2.448	Subtropical	42	Kanou et al. 2004; Inoue et al. 2005
Clupeidae	*Lile stolifera*	Zoop	Crus	1682	993		Tropical	33	Froese and Pauly 2019
Clupeidae	*Limnothrissa miodon*	Zoop	Crus	1682	993	4.375	Subtropical	18	De Longh et al. 1983
Clupeidae	*Microthrissa congica*	Terr	Crus	1682		1.871	Tropical	10	Kimbembi-ma-Ibaka and Nzuki 2001
Clupeidae	*Microthrissa royauxi*						Tropical	8	
Clupeidae	*Nematalosa come*	Detr	Omni	209	143	1.034	Tropical	30	Nanjo et al. 2008; Abrantes et al. 2009
Clupeidae	*Nematalosa erebi*	Detr	Omni	209	143	1.109	Subtropical	37	Pusey et al. 1995; Medeiros and Arthington 2008
Clupeidae	*Nematalosa japonica*	Detr	Omni	209	143		Tropical	37	Froese and Pauly 2019
Clupeidae	*Nematalosa nasus*	Zoop	Crus	1682	993		Tropical	38	Froese and Pauly 2019
Clupeidae	*Odaxothrissa ansorgii*						Tropical	16	
Clupeidae	*Odaxothrissa losera*						Tropical	14	
Clupeidae	*Opisthonema libertate*	Phyt	Omni	209	275		Tropical	28	Froese and Pauly 2019
Clupeidae	*Opisthonema oglinum*	Crus	Crus	1682	2607	2.939	Tropical	41	Vega-Cendejas et al. 1994
Clupeidae	*Pellonula leonensis*	Terr	Crus	1682			Tropical	17	Ikusemiju et al. 1983
Clupeidae	*Pellonula vorax*	Pisc	Pisc	10690	10690	4.796	Tropical	13	Offem et al. 2009
Clupeidae	*Potamalosa richmondia*	Crus	Crus	1682	2607		Tropical	39	Froese and Pauly 2019
Clupeidae	*Potamothrissa acutirostris*						Tropical	7	
Clupeidae	*Potamothrissa obtusirostris*	Zoop	Crus	1682	993		Tropical	8	Froese and Pauly 2019
Clupeidae	*Rhinosardinia amazonica*	Zoop	Crus	1682	993		Tropical	10	Froese and Pauly 2019
Clupeidae	*Rhinosardinia bahiensis*					1.124	Tropical	20	
Clupeidae	*Sardina pilchardus*	Zoop	Crus	1682	993	2.916	Subtropical	68	Garrido et al. 2008; Morote et al. 2010; Nikolioudakis et al. 2012; Costalago et al. 2012; Costalago et al. 2014; Costalago et al. 2015
Clupeidae	*Sardinella albella*	Zoop	Crus	1682	993	3.131	Tropical	31	Venkataraman 1960; Horinouchi et al. 2012
Clupeidae	*Sardinella aurita*	Zoop	Crus	1682	993	2.650	Subtropical	47	Tsikliras et al., 2005; Lomiri et al., 2008
Clupeidae	*Sardinella gibbosa*	Zoop	Crus	1682	993	2.790	Tropical	41	Chacko 1949; Nyunja et al. 2002; Mavuti et al. 2004; Abrantes et al. 2009; Shahraki et

									al. 2014
Clupeidae	*Sardinella hualiensis*						Tropical	29	
Clupeidae	*Sardinella lemuru*	Zoop	Crus	1682	993	1.000	Tropical	38	Horinouchi et al. 2012; Metillo et al. 2018
Clupeidae	*Sardinella maderensis*	Zoop	Crus	1682	993	1.610	Tropical	46	Fagade and Olaniyan 1972; Faye et al. 2012
Clupeidae	*Sardinella melanura*	Zoop	Crus	1682	993	2.329	Tropical	26	Kuthalingam 1961
Clupeidae	*Sardinops sagax*	Zoop	Crus	1682	993	1.913	Subtropical	61	Burchmore et al. 1984; Van de Lingen 2002; Mketsu 2008; Espinoza et al. 2009
Clupeidae	*Sauvagella madagascariensis*						Tropical	26	
Clupeidae	*Sauvagella robusta*						Tropical	15	
Clupeidae	*Sierrathrissa leonensis*	Zoop	Crus	1682	993		Tropical	18	Whitehead et al. 1988
Clupeidae	*Spratelloides delicatulus*	Zoop	Crus	1682	993	1.162	Tropical	40	Milton et al. 1990; Nakamura et al. 2003; Mavuti et al. 2004; Gajdzik et al. 2014
Clupeidae	*Spratelloides gracilis*	Zoop	Crus	1682	993	1.000	Tropical	33	Nakane et al. 2011
Clupeidae	*Sprattus antipodum*						Tropical	48	
Clupeidae	*Sprattus muelleri*						Tropical	51	
Clupeidae	*Sprattus sprattus*	Zoop	Crus	1682	993	1.192	Tropical	66	Moore and Moore 1976; Köster and Möllmann 2000; Gorokhova et al. 2004
Clupeidae	*Stolothrissa tanganicae*	Zoop	Crus	1682	993		Tropical	10	Froese and Pauly 2019
Clupeidae	*Sundasalanx mekongensis*						Tropical	17	
Clupeidae	*Tenualosa ilisha*	Phyt	Omni	209	275	5.493	Tropical	34	De and Datta 1990; Dutta et al. 2014
Clupeidae	*Tenualosa thibaudeaui*	Phyt	Omni	209	275		Tropical	20	Froese and Pauly 2019
Clupeidae	*Thrattidion noctivagus*	Terr	Crus	1682			Tropical	6	Whitehead et al. 1988
Dussumieriidae	*Dussumieria acuta*						Tropical	31	
Dussumieriidae	*Dussumieria elopsoides*	Crus	Crus	1682	2607	1.897	Tropical	36	Chacko 1949; Venkataraman 1960
Dussumieriidae	*Etrumeus golanii*	Zoop	Crus	1682	993	1.041	Tropical	18	Tanaka et al. 2006
Dussumieriidae	*Etrumeus micropus*						Subtropical	35	
Dussumieriidae	*Etrumeus whiteheadi*	Zoop	Crus	1682	993		Subtropical	35	Froese and Pauly 2019
Engraulidae	*Amazonsprattus scintilla*	Terr	Crus	1682			Tropical	3	Whitehead et al. 1988
Engraulidae	*Anchoa cayorum*						Tropical	28	
Engraulidae	*Anchoa chamensis*						Tropical	10	
Engraulidae	*Anchoa colonensis*	Crus	Crus	1682	2607	2.378	Tropical	23	

Engraulidae	*Anchoa cubana*						Tropical	36	
Engraulidae	*Anchoa delicatissima*						Subtropical	34	
Engraulidae	*Anchoa filifera*						Tropical	27	
Engraulidae	*Anchoa hepsetus*	Zoop	Crus	1682	993	1.476	Subtropical	44	Carr and Adams 1973
Engraulidae	*Anchoa lamprotaenia*						Tropical	28	
Engraulidae	*Anchoa lyolepis*						Tropical	38	
Engraulidae	*Anchoa mitchilli*	Zoop	Crus	1682	993	2.424	Subtropical	42	Carr and Adams 1973; Odum and Heald 1972; Livingston 1982
Engraulidae	*Anchoa mundeoloides*						Subtropical	32	
Engraulidae	*Anchoa nasus*						Tropical	31	
Engraulidae	*Anchoa panamensis*						Tropical	10	
Engraulidae	*Anchoa parva*						Tropical	23	
Engraulidae	*Anchoa scofieldi*						Tropical	25	
Engraulidae	*Anchoa spinifer*						Tropical	26	
Engraulidae	*Anchoa walkeri*						Tropical	31	
Engraulidae	*Anchovia clupeoides*	Zoop	Crus	1682	993		Tropical	25	Whitehead et al. 1988
Engraulidae	*Anchovia macrolepidota*	Zoop	Crus	1682	993		Tropical	30	Whitehead et al. 1988
Engraulidae	*Anchovia surinamensis*	Zoop	Crus	1682	993	3.082	Tropical	11	Mérona et al. 2001; Mérona et al. 2008
Engraulidae	*Anchoviella alleni*						Tropical	8	
Engraulidae	*Anchoviella balboae*						Tropical	10	
Engraulidae	*Anchoviella brevirostris*	Zoop	Crus	1682	993		Tropical	27	Wakabara et al. 1996
Engraulidae	*Anchoviella carrikeri*						Tropical	15	
Engraulidae	*Anchoviella elongata*						Tropical	19	
Engraulidae	*Anchoviella guianensis*						Tropical	9	
Engraulidae	*Anchoviella jamesi*	Zoop	Crus	1682	993		Tropical	9	Röpke et al. 2013
Engraulidae	*Anchoviella lepidentostole*						Tropical	27	Froese and Pauly 2019
Engraulidae	*Anchoviella manamensis*						Tropical	10	
Engraulidae	*Cetengraulis edentulus*	Phyt	Omni	209	275	2.087	Tropical	28	Gay et al. 2002; Krumme et al. 2008
Engraulidae	*Cetengraulis mysticetus*	Phyt	Omni	209	275	1.050	Tropical	32	Bayliff 1963
Engraulidae	*Coilia brachygnathus*	Crus	Crus	1682	2607		Subtropical	32	Zhang et al. 2013
Engraulidae	*Coilia dussumieri*	Zoop	Crus	1682	993	2.086	Tropical	24	Rao 1967
Engraulidae	*Coilia lindmani*						Tropical	14	
Engraulidae	*Coilia mystus*	Zoop	Crus	1682	993		Tropical	42	Cheng and Fang 1956
Engraulidae	*Coilia nasus*	Zoop	Crus	1682	993	1.000	Subtropical	42	Islam and Tanaka 2006
Engraulidae	*Coilia reynaldi*	Zoop	Crus	1682	993		Tropical	26	Froese and Pauly 2019
Engraulidae	*Encrasicholina heteroloba*	Zoop	Crus	1682	993	2.704	Tropical	32	Venkataraman 1960; Rao 1967; Milton et al. 1990; Nair 1998; Abrantes et al.

									2009
Engraulidae	*Encrasicholina punctifer*	Zoop	Crus	1682	993	2.248	Tropical	42	Nair 1998; Salarpour et al. 2008
Engraulidae	*Engraulis albidus*						Subtropical	43	
Engraulidae	*Engraulis anchoita*	Zoop	Crus	1682	993	1.020	Tropical	50	Capitanio et al. 2005
Engraulidae	*Engraulis australis*						Subtropical	47	
Engraulidae	*Engraulis encrasicolus*	Zoop	Crus	1682	993	1.975	Subtropical	62	Plounevez and Champalbert 1999; Mketsu 2008; Morote et al. 2010; Borme et al. 2009; Costalago et al. 2012
Engraulidae	*Engraulis eurystole*	Zoop	Crus	1682	993		Subtropical	45	
Engraulidae	*Engraulis japonicus*	Zoop	Crus	1682	993	1.958	Subtropical	49	Inoue et al. 2005; Tanaka et al. 2006
Engraulidae	*Engraulis mordax*	Zoop	Crus	1682	993	1.478	Tropical	51	Koslow 1981; Whitehead et al. 1988; Barry et al. 1996
Engraulidae	*Engraulis ringens*	Crus	Crus	1682	2607	1.854	Subtropical	43	Arrizaga et al. 1993; Espinoza and Bertrand 2008
Engraulidae	*Jurengraulis juruensis*						Tropical	14	
Engraulidae	*Lycengraulis batesii*	Pisc	Pisc	10690	10690	2.017	Tropical	9	Mérona et al. 2001; Mérona et al. 2008; Röpke et al. 2013
Engraulidae	*Lycengraulis grossidens*	Pisc	Pisc	10690	10690		Tropical	41	Froese and Pauly 2019
Engraulidae	*Lycengraulis limnichthys*						Tropical	9	
Engraulidae	*Lycengraulis poeyi*	Pisc	Pisc	10690	10690		Tropical	14	Froese and Pauly 2019
Engraulidae	*Pterengraulis atherinoides*	Pisc	Pisc	10690	10690	2.058	Tropical	11	Mérona et al. 2001; Krumme et al. 2005
Engraulidae	*Setipinna crocodilus*	Pisc	Pisc	10690	10690		Tropical	17	Froese and Pauly 2019
Engraulidae	*Setipinna melanochir*	Pisc	Pisc	10690	10690		Tropical	19	Froese and Pauly 2019
Engraulidae	*Setipinna taty*	Crus	Crus	1682	2607	1.954	Tropical	24	Rao 1967; Hong 1990; Chaudhuri et al. 2014
Engraulidae	*Setipinna tenuifilis*	Pisc	Pisc	10690	10690	1.084	Tropical	42	Froese and Pauly 2019
Engraulidae	*Stolephorus brachycephalus*	Crus	Crus	1682	2607	1.090	Tropical	15	Egan et al. 2018a; Egan et al. 2018b
Engraulidae	*Stolephorus carpentariae*	Zoop	Crus	1682	993		Tropical	32	
Engraulidae	*Stolephorus chinensis*	Zoop	Crus	1682	993	1.723	Tropical	29	
Engraulidae	*Stolephorus commersonnii*	Zoop	Crus	1682	993	1.289	Tropical	27	Venkataraman 1960; Blaber 1979; Hayase et al. 1999; Hajisamae and Ibrahim 2008

Engraulidae	*Stolephorus indicus*	Zoop	Crus	1682	993	1.709	Tropical	37	Chacko 1949; De Troch et al. 1998; Hajisamae et al. 2003; Hajisamae and Ibrahim 2008; Horinouchi et al. 2012
Engraulidae	*Stolephorus insularis*	Zoop	Crus	1682	993	2.500	Tropical	28	Rao 1967; Hayase et al. 1999; Egan et al. 2017
Engraulidae	*Stolephorus waitei*	Zoop	Crus	1682	993	2.414	Tropical	25	Nair 1998
Engraulidae	*Thryssa baelama*	Crus	Crus	1682	2607	1.000	Tropical	31	Marichamy 1972
Engraulidae	*Thryssa brevicauda*	Crus	Crus	1682	2607		Tropical	13	
Engraulidae	*Thryssa chefuensis*	Crus	Crus	1682	2607	1.714	Tropical	39	Egan et al. 2018a; Egan et al. 2018b
Engraulidae	*Thryssa dussumieri*	Crus	Crus	1682	2607	1.002	Tropical	27	Chacko 1949; Egan et al. 2018a
Engraulidae	*Thryssa hamiltonii*	Pisc	Pisc	10690	10690	1.002	Tropical	31	Bapat and Bal 1950; Rao 1967; Brewer et al. 1995; Salini et al. 1998; Hajisamae et al. 2003; Baker and Sheaves 2005; Deshmukh 2007; Hajisamae and Ibrahim 2008; Taher 2010; Chew et al. 2012; Zagars et al. 2013; Egan et al. 2017; Egan et al. 2018a; Egan et al. 2018b
Engraulidae	*Thryssa kammalensis*	Crus	Crus	1682	2607		Tropical	11	Hajisamae and Ibrahim 2008
Engraulidae	*Thryssa mystax*	Crus	Crus	1682	2607		Tropical	25	Froese and Pauly 2019
Engraulidae	*Thryssa setirostris*	Crus	Crus	1682	2607	1.973	Tropical	40	Froese and Pauly 2019
Engraulidae	*Thryssa spinidens*	Crus	Crus	1682	2607	1.053	Tropical	25	
Pristigasteridae	*Ilisha africana*	Zoop	Crus	1682	993	2.672	Tropical	17	Fagade and Olaniyan 1973; Marcus 1986
Pristigasteridae	*Ilisha amazonica*						Tropical	12	
Pristigasteridae	*Ilisha elongata*	Pisc	Pisc	10690	10690	1.681	Tropical	39	Rao 1967; Blaber et al. 1998
Pristigasteridae	*Ilisha megaloptera*	Pisc	Pisc	10690	10690	1.472	Tropical	24	Blaber et al. 1998
Pristigasteridae	*Ilisha melastoma*	Moll				1.420	Tropical	29	Blaber et al. 1998; Shahraki et al. 2014
Pristigasteridae	*Odontognathus mucronatus*						Tropical	26	
Pristigasteridae	*Opisthopterus tardoore*	Zoop	Crus	1682	993	2.489	Tropical	29	Venkataraman 1960
Pristigasteridae	*Pellona castelnaeana*	Pisc	Pisc	10690	10690	1.221	Tropical	13	Mérona et al. 2001; González and Vispo 2003; Pouilly et al. 2004
Pristigasteridae	*Pellona ditchela*	Crus	Crus	1682	993	2.230	Tropical	30	Mavuti et al. 2004

Pristigasteridae	*Pellona flavipinnis*	Pisc	Pisc	10690	10690	2.648	Tropical	35	González and Vispo 2003; Pouilly et al. 2003; Moreira-Hara et al. 2009
Pristigasteridae	*Pellona harroweri*						Tropical	30	
Pristigasteridae	*Pristigaster cayana*						Tropical	2	
Pristigasteridae	*Pristigaster whiteheadi*						Tropical	3	
Clupeidae	*Jenkinsia lamprotaenia*	Zoop	Crus	1682	993		Subtropical	34	Froese and Pauly 2019
Denticipitidae	*Denticeps clupeoides*	Zoop	Crus	1682	993		Tropical	7	Froese and Pauly 2019

Table 4.2. Diet data generated by this study reported as the proportional volume of each prey type in the diet. N = number of fish specimens analyzed containing identifiable prey.

Species	n	Diet (% volume)
Alosa braschnikowi	15	Fish (100)
Alosa chrysochloris	11	Fish (97.5), Insecta terrestrial (0.2), Insecta aquatic (1.2)
Anodontostoma chacunda	3	Detritus (98.8), Foraminifera (0.2)
Cetengraulis edentulus	3	Detritus (99.9), phytoplankton (<0.1)
Cetengraulis mysticetus	2	Detritus (1.0), phytoplankton (99.0)
Chirocentrus dorab	93	Fish (94.3), zquid (5.5), Crustacea (0.2)
Encrasicholina heteroloba	7	Crustacea (36.2), zooplankton (63.6)
Nematalosa come	3	Detritus (98.4), zooplankton (1.2)
Nematalosa erebi	4	Detritus (94.9), zooplankton (4.6), algae (0.3), plant (0.3)
Papuengraulis micropinna	19	Crustacea (100.0)
Pellona ditchella	30	Cephlaopoda (39.2), Crustacea (53.9), fish (6.3), zooplankton (0.6)
Sardinella albella	24	Crustacea (32.3), egg (1.6), phytoplankton (26.9), zooplankton (37.7)
Sardinella brachysoma	17	Crustacea (34.1), phytoplankton (1.5), zooplankton (51.8)
Setipinna tenuifilis	30	Crustacea (96.0), fish (3.2), zooplankton (0.8)
Stolephorus andhraensis	12	Phytoplankton (2.9), zooplankton (97.1)
Stolephorus brachycephalus	7	Crustacea (97.5), fish (2.5)
Stolephorus carpentariae	34	Annelida (4.0), Crustacea (16.7), Nemertia (0.2), phytoplankton (0.3), terrestrial Invertebrata (0.2), zooplankton (77.0)
Stolephorus chinensis	5	Crustacea (71.0), fish (27.6), zooplankton (1.3)
Stolephorus commersonii	5	Crustacea (4.4), fish (0.3), Mollusca (4.4), zooplankton (87.9)
Thryssa aestuaria	5	Crustacea (71.0), zooplankton (27.6)
Thryssa brevicauda	3	Zooplankton (100)
Thryssa hamiltonii	58	Crustacea (100.0)
Thryssa setirostris	39	Crustacea (55.8), fish (44.2)

Thryssa spinidens	6	Crustacea (97.4), zooplankton (2.8)

Table 4.3. Prey types comprising each prey category.

Prey category	Prey category composition
Algae (Alga)	Filamentous algae
Annelida (Anne)	Annelida, Nematoda, Polychaeta
Cephlapoda (Ceph)	Cephlapoda, squid
Crustacea (Crus)	Acetes, Alpheidae, Amphipoda, Anomura, Apseudidae, Arthropoda, Brachyura, Caprellidae, Caridea, Collembola, Crustacea, Cumacea, Decapoda, Decapoda megalopa, Entomostracans, Euphausidae, Gammeridea, Hyperiidae, Isopoda, Lucifer, Malacostraca, Meiofauna, Mysida, Paguridae, Pycnogonida, shrimp, Stomatopoda, Tanaidacea, Thalassinidae, unidentified crustacea nekton
Detritus (Detr)	Detritus
Egg	Invertebrate eggs, fish eggs
Enteropneusta (Ente)	Enteropneusta
Eugenophyta (Eugl)	Eugenophyta
Fish	Fish
Foraminifera (Fora)	Foraminifera
Mollucsa (Moll)	Benthic gastropoda, benthic mollusca
Nemertea (Neme)	Nemertea
Phytoplankton (Phyt)	Centric diatom, Dinoflagellata, pennate diatom, single-celled algae
Plant (Plan)	Aquatic and terrestrial macrophytes, pollen
Protozoa (Prot)	Protozoa
Rotifera (Roti)	Rotifera
Insecta terrestrial (Terr)	Terrestrial Insecta
Insecta aquatic (Insa)	Aquatic Insecta
Zooplankton (Zoop)	Bivalva veliger, Cheatognatha, Cirripedia cypris, Cladocera, Copepoda, Crustacea nauplii, Decapoda zoea, Gastropoda veliger, Larvacea, Ostracoda, Trematoda

Table 4.4. Three most important categories comprising the majority of the diet in each trophic guild (proportion of diet). Prey category acronyms are defined in Table 4.3.

Trophic guild	Important prey categories
Algivore	Alga (0.556), Crus (0.126), Prot (0.074)
Crustacivore	Crus (0.8215), Zoop (0.130), Fish (0.033)
Detritivore	Detr (0.706), Zoop (0.1442), Algae (0.023)
Molluscivore	Moll (0.830), Fish (0.112), Crus (0.050)
Piscivore	Fish (0.664), Crus (0.196), Terr (0.058)
Phytoplanktivore	Phyt (0.607), Zoop (0.3416), Detr (0.1763)
Terrestrial invertivore	Terr (0.711), Detr (0.036), Fish (0.004)
Zooplanktivore	Zoop (0.653), Crus (0.151), Phyt (0.022)

Table 4.5. Ranges of prey-size and prey-type niche breadth estimates by trophic guild using the trophic guilds in the full scheme and conservative scheme. Results of ANOVAs testing for differences in prey-size and prey-type niche breadth between trophic guilds.

Trophic guild	Prey-size niche breadth		Prey-type niche breadth		Pairwise comparison of prey-size niche versus guild	p-value
	Mean	Range	Mean	Range		
Full guild scheme						
Crustacivore	3066	894-7743	1.52946	1.0 to 2.939	Detritivore-Crustacivore	0.9207897
Detritivore	143	90-249	1.84714	1.034 to 3.996	Phytoplanktivore-Crustacivore	0.9357766
Phytoplanktivore	275	90-569	2.51457	1.05 to 5.493	Piscivore-Crustacivore	0.0005385
Piscivore	11300	5108-23260	2.05341	1.051 to 4.796	Zooplanktivore-Crustacivore	0.9559339
Zooplanktivore	1299	451-2808	1.9485	1.0 to 4.375	Phytoplanktivore-Detritivore	0.9999994
					Piscivore-Detritivore	0.0023154
					Zooplanktivore-Detritivore	0.9919665
					Piscivore-Phytoplanktivore	0.0026223
					Zooplanktivore-Phytoplanktivore	0.9950148
					Zooplanktivore-Piscivore	0.0000559
Conservative guild scheme						
Crustacivore	2197	451-7743			Omnivore-Crustacivore	0.486
Omnivore	209	90-569			Piscivore-Crustacivore	0.004
Piscivore	11300	5108-23260			Piscivore-Omnivore	0.002

Table 4.6. Results (p-values) of phylogenetic ANOVAs testing for differences in prey-type niche breadth (Prey-type), prey-size niche breadth estimated using the conservative trophic guild scheme (Prey-size cons.), and prey-size niche breadth estimated using the full trophic guild scheme (Prey-size full) between climate zones.

Climate comparison	Prey-type	Prey-size cons.	Prey-size full
Tropical/subtropical	0.750	0.228	0.231
Tropical/temperate	1.000	0.954	0.977
Subtropical/temperate	1.000	0.440	0.466

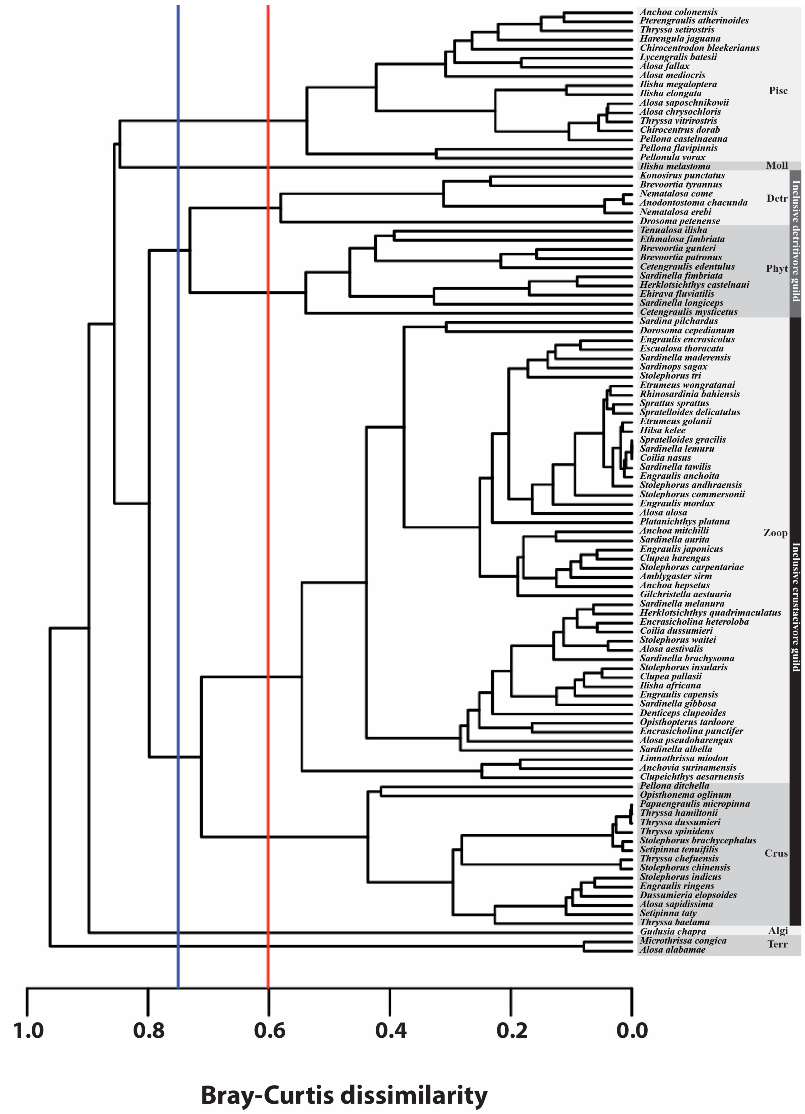


Figure 4.1. Dendrogram resulting from hierarchical agglomerative cluster analysis based upon Bray-Curtis dissimilarity of clupeiform prey type consumption. The red line indicates the dissimilarity value (0.61) identified by bootstrapping as the threshold for statistically significant differences in diet used to designate the trophic guilds in the “full” guild scheme. The blue shows the arbitrary dissimilarity (0.75) used to designate the guilds included in the “conservative” scheme. Pisc = piscivore, Moll = molluscivore, Detr = detritivore, Phyt = phytoplanktivore, Zoop = zooplanktivore, Crus = crustacivore, Algi = algivore, and Terr = terrestrial invertivore.

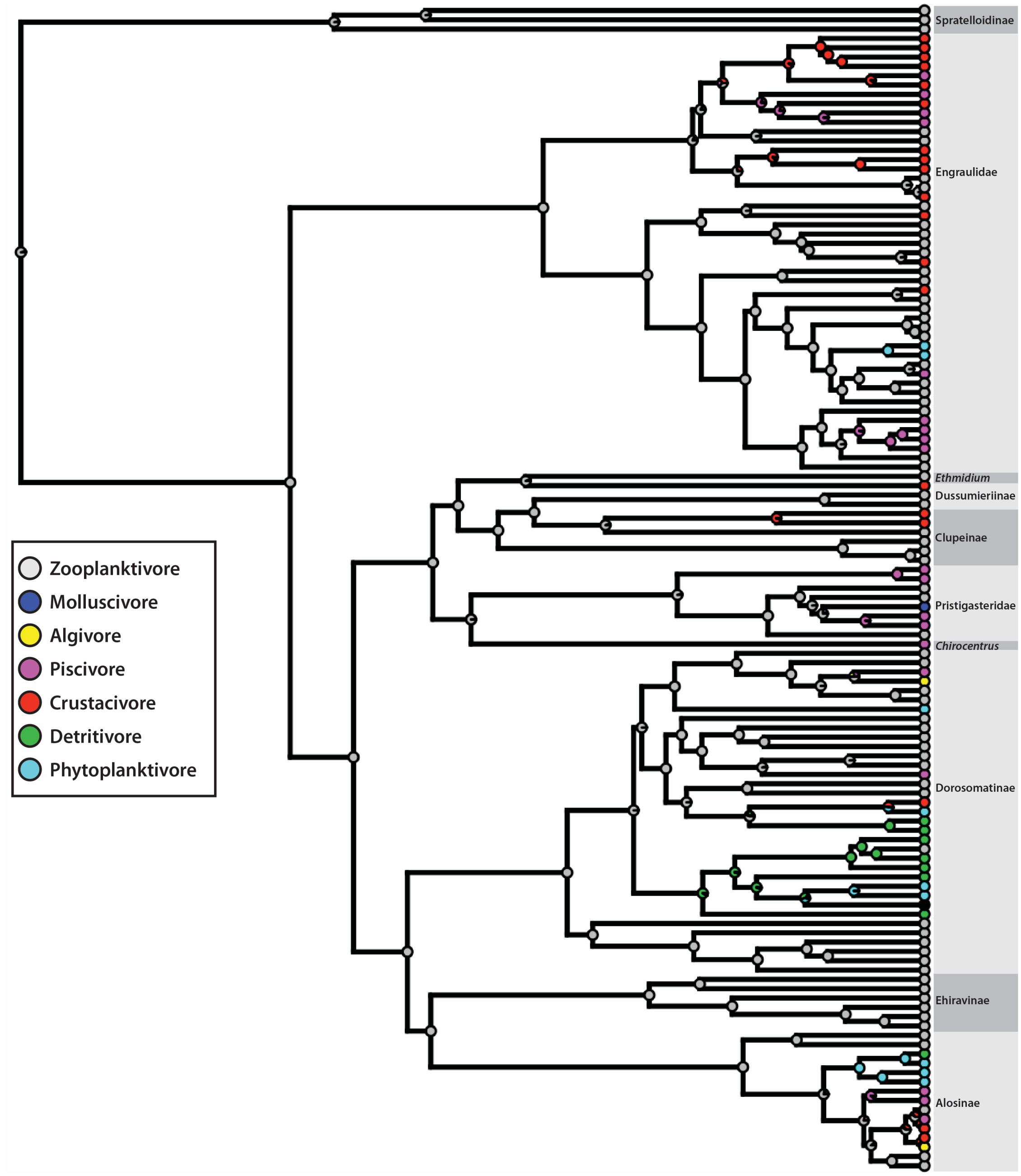


Figure 4.2. Evolutionary history of diet (trophic guilds) in clupeiforms estimated with 1000 stochastic character mapping simulations.

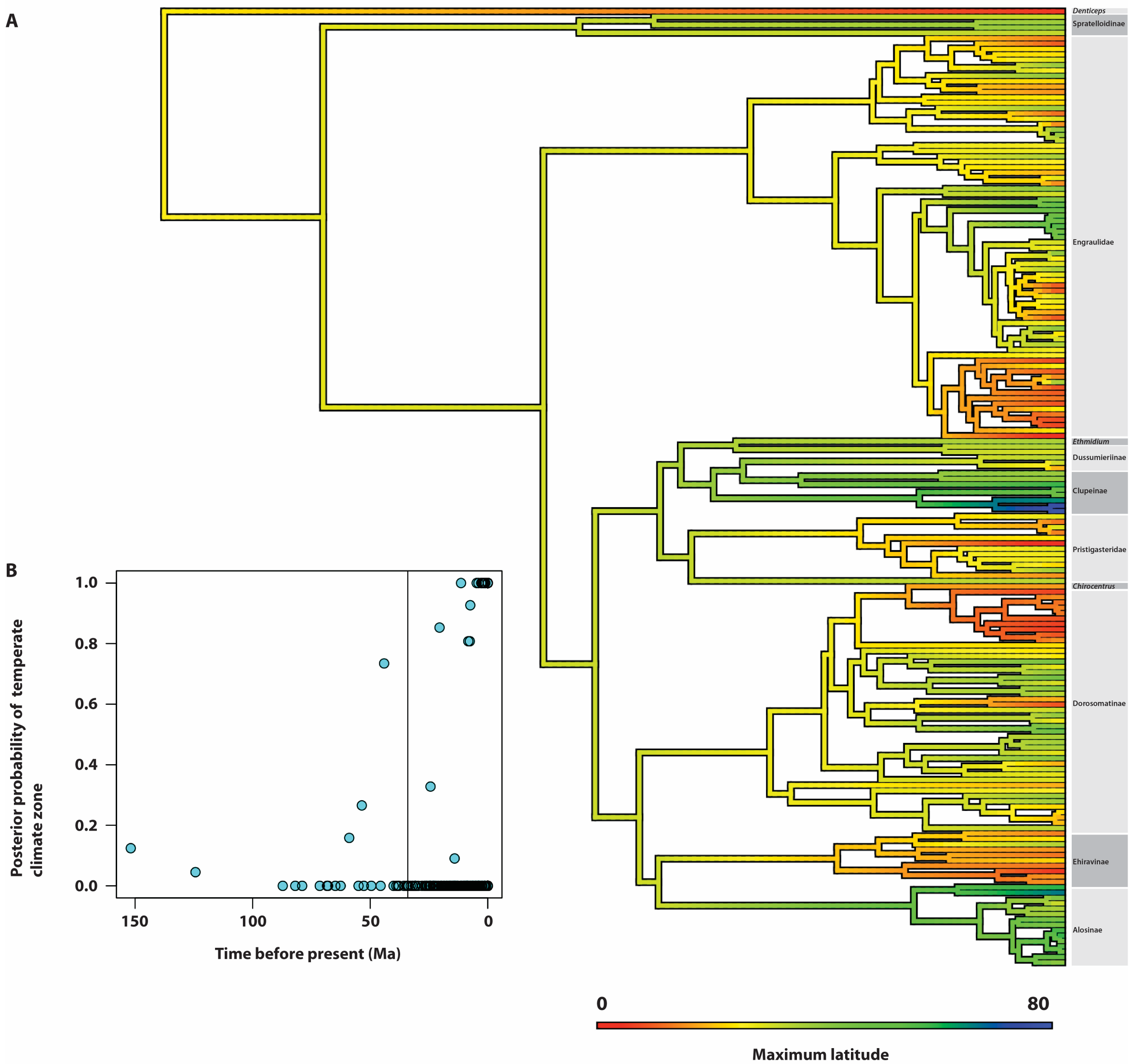


Figure 4.3. (a) Continuous character map (contmap) illustrating the evolution of maximum latitude in clupeiforms and (b) scatterplot of the posterior probability of nodes in the clupeiform phylogeny having a temperate character state (y-axis) versus node age (x-axis).

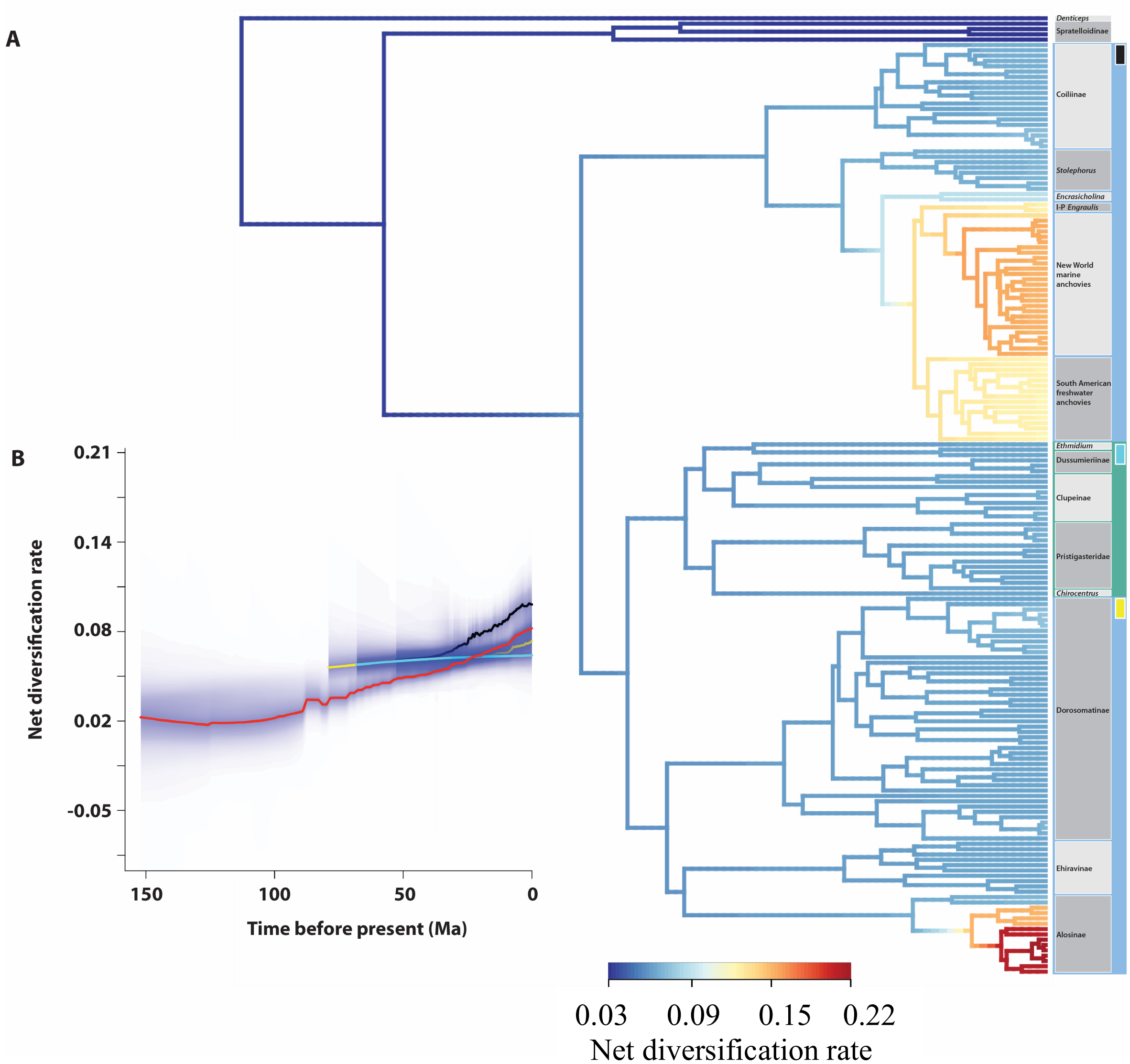


Figure 4.4. (a) Mean net diversification rates in clupeiforms. (b) Net diversification rates through time in all clupeiforms (red) and selected clupeiform lineages (yellow, cyan, and black). Colored boxes following tip labels in figure 4a correspond to the colors illustrating net diversification rates in figure 4b.

Bibliography

Abrantes, K., M. Sheaves. 2009. Food web structure in a near-pristine mangrove area of the Australian wet tropics. Estuarine, Coastal and Shelf Science 82: 597-607.

Alcaraz, M., E. Saiz, A. Calbet, I. Trepat, E. Broglio. 2003. Estimating zooplankton biomass through image analysis. Marine Biology 143: 307-315.

Allen, A.P., J.F. Gillooly, V.M. Savage, J.H. Brown. 2006. Kineticeffects of temperature on rates of genetic divergence and speciation. Proceedings of the National Academy of Sciences 103(24): 9130-9135.

Amundsen, P.A., R. Knudsen. 2009. Winter ecology of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in a subarctic lake, Norway. Aquatic Ecology 43(3): 765-775.

Aprahamian, M.W. 1989. The diet of juvenile and adult twaite shad *Alosa fallax fallax* (Lacépède) from the rivers of Severn and Wye (Britain). Hydrobiologia 179: 173-182.

Ariyaratne, M.G., P.B. Amarasinghe, N.C. Lopez, M. Kakkaeo, J. Vijverberg. 2008. Selective feeding of small zooplanktivorous pelagic fish species in tropical Asian reservoirs (Sri Lanka, Thailand) and Lake Taal (Philippines). IN: Schiemer, F., Simon, D., Amarasinghe, U., Moreau, J., (Eds.) Aquatic Ecosystems and Development: Comparative Asian Perspectives. Backhuys Publishers, pp.: 235-248. Publication 4116 NIOO-KNAW.

Arrizaga, A., M. Fuentealba, C. Espinoza, J. Chong, Y.C. Oyarzun. 1993. Trophic habits of two pelagic fish species *Strangomera bentinkcki* (Norman, 1936) and *Engraulis ringens* Jenyns 1842 in the littoral of the Biobío Region, Chile. Boletín de la Sociedad de Biologia de Concepción 64: 27-35.

Assis, C.A., P.R. Almeida, F. Moreira, J.L. Costa, M.J. Costa. 1992. Diet of the twaite shad *Alosa fallax* (Lacépède) (Clupeidae) in the River Tagus Estuary, Portugal. Journal of Fish Biology 41: 1049-1050.

Ayón, P., G. Swartzman, P. Espinoza, A. Bertrand. 2011. Long-term changes in zooplankton size distribution in the Peruvian Humboldt Current System: conditions favoring sardine or anchovy. Marine Ecoloy Progress Series 422: 211-222.

Bachok, Z., M.I. Mansor, R.M. Noordin. 2004. Diet composition and food habits of demersal and pelagic marine fishes from Terengganu waters, east coast of peninsular Malaysia. NAGA Worldfish Center Quarterly 27: 41-47.

Baker, R., M. Sheaves. 2005. Redefining the piscivore assemblage of shallow estuarine nursery habitats. Marine Ecology Progress Series 291: 197-213.

Baker, R., A. Buckland, M. Sheaves. 2014. Fish gut content analysis: robust measures of diet composition. Fish and Fisheries 15: 170-177.

Bapat, S.V., D.V. Bal. 1950. The food of some young clupeids. Proceedings of the Indian Academy of Sciences B 32: 39-58.

Barry, J.P., M.M. Yoklavich, G.M. Cailliet, D.A. Ambrose, B.S. Antrim. 1996. Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974-1980. Estuaries 19(1): 115-138.

Bayliff, W.H. 1963. The food and feeding habits of the Anchoveta, *Cetengraulis mysticetus*, in the Gulf of Panama. Inter-American Tropical Tuna Commission Bulletin 7(6): 397-459.

Behrens, M.D., K.D. Lafferty. 2007. Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. Canadian Journal of Fisheries and Aquatic Sciences 64: 867-873.

Belmaker, J., W. Jetz. 2015 Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. Ecology Letters 18: 563-571.

Bennett, B.A., G.M. Branch. 1990. Relationships between production and consumption of prey species by resident fish in the Bot, a cool temperate South African estuary. Estuarine, Coastal and Shelf Science 31: 139-155.

Bergamino, L., D. Lercari, O. Defeo. 2011. Food web structure of sandy beaches: Temporal and spatial variation using stable isotope analysis. Estuarine, Coastal and Shelf Science 91: 536-543.

Betancur-R R, G. Ortí, A.M. Stein, A.P. Marceniuk, A.R. Pyron. 2012. Apparent signal of competition limiting diversification after ecological transitions from marine to freshwater habitats. Ecology Letters 15(8): 822-830.

Blaber, S.J.M., A.K. Whitfield. 1977. The feeding ecology of juvenile mullet (Mugilidae) in south-east African estuaries. Biological Journal of the Linnean Society 9: 277-284.

Blaber, S.J.M. 1979. The biology of filter feeding teleosts in Lake St. Lucia, Zululand. Journal of Fish Biology 15: 37-59.

Blaber, S.J.M., D.P. Cyrus. 1983. The biology of Carangidae (Teleostei) in Natal estuaries. Journal of Fish Biology 22: 173-188.

Blaber, S.J.M., J. Staunton-Smith, D.A. Milton, G. Fry, T. Van der Velde, J. Pang, P. Wong, O. Boon-Teck. 1998. The biology and life-history strategies of *Ilisha* (Teleostei: Pristigasteridae) in the coastal waters and estuaries of Sarawak. Estuarine, Coastal and Shelf Science 47: 499-511.

Blay, J., K.N. Eyeson. 1982. Feeding activity and food habits of the shad, *Ethmalosa fimbriata* (Bowditch), in the coastal waters of Cape Coast, Ghana. Journal of Fish Biology 21: 403-410.

Bloom, D.D., N.R. Lovejoy. 2012. Molecular phylogenetics reveals a pattern of biome conservatism in New World anchovies (family Engraulidae). Journal of Evolutionary Biology 25: 701-715.

Bloom, D.D., J.T. Weir, K.R. Piller, N.R. Lovejoy. 2013. Do freshwater fishes diversify faster than marine fishes? A test using state-dependent diversification analyses and molecular phylogenetics of New World silversides (Atherinopsidae). Evolution 67(7): 2040-2057.

Bloom, D.D., N.R. Lovejoy. 2014. The evolutionary origins of diadromy inferred from a time-calibrated phylogeny for Clupeiformes (herring and allies). Proceedings of the Royal Society B. 281: 20132081.

Bloom, D.D., J.P. Egan. 2018. Systematics of Clupeiformes and testing for ecological limits on species richness in a trans-marine/freshwater clade. Neotropical Ichthyology 16(3).

Bollback, J.P. 2006. Stochastic character mapping of discrete traits on phylogenies. BMC Bioinformatics 7: 88.
Borme, D., V. Tirelli, S.B. Brandt, S.F. Umani, E. Arneri. 2009. Diet of *Engraulis encrasicolus* in the northern Adriatic Sea (Mediterranean): ontogenetic changes and feeding selectivity. Marine Ecology Progress Series 392: 193-209.
Borsa P., A. Collet, J.-D. Durand. 2004. Nuclear-DNA markers confirm the presence of two anchovy species in the Mediterranean. Biologie des populations 327: 1113-1123.
Bouckaert, R., J. Heled, D. Kuhnert, T. Vaughan, C.H. Wu, D. Xie, M.A. Suchard, A. Rambaut, A.J. Drummond. 2014. BEAST 2: a software platform for bayesian evolutionary analysis. Plos Computational Biology e10.
Bray, R.J., J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27: 325-349.
Brett, J.R., D.A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. Journal of the Fisheries Board of Canada 27(10): 1767-1779.
Brewer, D.T., S.J.M. Blaber, J.P. Salini, M.J. Farmer. 1995. Feeding ecology of predatory fishes from Groote Eylandt in the Gulf of Carpentaria, Australia, with special reference to predation on penaeid prawns. Estuarine, Coastal and Shelf Science 40: 577-600.
Brown, J.H. 2014. Why are there so many species in the tropics? Journal of Biogeography 41: 8-22.
Brosset, P., B. Le Bmyg, D. Costalago, D. Bănaru, E. Van Beveren, J.-H. Bmydeix, J.-M. Fromentin, F. Ménard, C. Saraux. 2016. Linking small pelagic dietary shifts and ecosystem changes in the Gulf of Lions. Marine Ecology Progress Series 554: 157-171.
Buchheister, A., R.J. Latour. 2015. Diets and trophic-guild structure of a diverse fish assemblage in Chesapeake Bay, U.S.A. Journal of Fish Biology 86: 967-992.
Buckland, A., R. Baker, N. Loneragan, M. Sheaves. 2017. Standardising fish stomach content analysis: the importance of prey condition. Fisheries Research 196: 126-140.
Buckley, L.B., T.J. Davies, D.D. Ackerly, N.J. Kraft, S.P. Harrison, B.L. Anacker, H.V. Cornell, E.I. Damschen, J.A. Grytnes, B.A. Hawkins, C.M. McCain. 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. Proceedings of the Royal Society B 277(1691): 2131-2138.
Burchmore, J.J., D.A. Pollard, J.D. Bell. 1984. Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* Seagrass habitat in Port Hacking, New South Wales. Aquatic Botany 18: 71-87.
Burin, G., W.D. Kissling, P.R. Guimarães Jr., Ç.H. Şekercioğlu, T.B. Quental. 2016. Omnivory in birds is a macroevolutionary sink. Nature Communications 7: 11250.
Capitanio, F.L., M. Pájaro, G.B. Esnal. 2005. Appendicularians: an important food supply for the Argentine anchovy *Engraulis anchoita* in coastal waters. Journal of Applied Ichthyology 21: 414-419.
Carpenter, K.E., V. Niem. eds. 2001. FAO species identification guide for fishery purposes. The living marine resmyces of the Istern Central Pacific. Rome: FAO.

Carr, W.E.S., C.A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Transactions of the American Fisheries Society 102(3): 511-540.

Case, T.J. 1983. Niche overlap and the assembly of island lizard communities. OIKOS 41: 427-433.

Casini M., J. Hjelm, J.-C. Molinero, J. Lövgren, M. Cardinale, V. Bartolino, A. Belgrano, G. Kornilovs. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. PNAS 106(1): 197-202.

Castillo-Rivera, M., A. Kobelkowsky, V. Zamayoa. 1996. Food resource partitioning and trophic morphology of *Brevoortia gunteri* and *B. patronus*. Journal of Fish Biology 49: 1102-1111.

Chacko, P.I. 1949. Food and feeding habits of the fishes of the Gulf of Manaar. Proceedings: Plant Sciences 29(3): 83-97.

Chakrabarty, P., J.S. Sparks, H.-C. Ho. 2010. Taxonomic review of the ponyfishes (Perciformes: Leiognathidae) of Taiwan. Marine Biodiversity 40: 107-121.

Chaudhuri, A., S. Mukherjee, S. Sen, S. Chakrabarty, S. Homechaudhuri. 2012. A comparison of spatial and temporal pattern of fish diversity of Matla River and adjacent mudflats in Sunderban Bioshere Reserve, India. The Clarion 1(1): 46-55.

Cheng, C., Z.C. Fang. 1956 Studies on the food of Coilia mystus (L.) Journal of Xiamen University (Natural Science) 1.

Chew, L. L., V.C. Chong, K. Tanaka, A. Sasekumar. 2012. Phytoplankton fuel the energy flow from zooplankton to small nekton in turbid mangrove waters. Marine Ecology Progress Series 469: 7-24.

Chubaty, A.M., B.O. Ma, R.W. Stein, D.R. Gillespie, L.M. Henry, C. Phelan, E. Palsson, F.W. Simon, B.D. Roitberg. 2014. On the evolution of omnivory in a community context. Ecology and Evolution 4: 251-265.

Clarke, K.R., P.J. Somerfield, R.N. Gorley. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366: 56-69.

Clements, K.D., D. Raubenheimer, J.H. Choat. 2009. Nutritional ecology of marine herbivorous fishes: ten years on. Functional Ecology 23: 79-92.

Coates, D. 1993. Fish ecology and management of the Sepik-Ramu, New Guinea, a large contemporary tropical river basin. Environmental Biology of Fishes 38: 345-368.

Coelho, M.T.P., C. Dambros, D.F. Rosauer, E.B. Pereira, T.F. Rangel. 2018. Effects of neutrality and productivity on mammal richness and evolutionary history in Australia. Ecography 42(3): 478-487.

Colton, D.E., W.S. Alevizon. 1983. Feeding ecology of bonefish in Bahamian waters. Transactions of the American Fisheries Society 112: 178-184.

Conway, D.V.P., S.H. Coombs, C. Smith. 1998. Feeding of anchovy *Engraulis encrasicolus* larvae in the northIstern Adriatic Sea in response to changing hydrobiological conditions Marine Ecology Progress Series 175: 35-49.

Correia, M.J., J.L. Costa, C. Teixeira, P.R. Almeida, I. Domingos, M.J. Costa. 2001. Feeding habits and condition of two landlocked populations of allis shad (*Alosa alosa*) in Portugal. Bulletin Francais de la Pêche et de la Pisciculture 362/363: 823-835.

Costalago, D., J. Navarro, I. Álvarez-Calleja, I. Palomera. 2012. Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. Marine Ecology Progress Series 460: 169-181.

Costalago, D., I. Palomera. 2014. Feeding of European pilchard (*Sardina pilchardus*) in the northIstern Mediterranean: from late larvae to adults. Scientia Marina 78(1): 41-54.

Costalago, D., S. Garrido, I. Palomera. 2015. Comparison of the feeding apparatus and diet of European sardines *Sardina pilchardus* of Atlantic and Mediterranean waters: ecological implications. Journal of Fish Biology 86: 1348-1362.

Crabtree, R.E., C. Stevens, D. Snodgrass, F.J. Stengard. 1998. Feeding habits of bonefish, *Albula vulpes*, from the waters of the Florida Keys. Fishery Bulletin, US 96: 754-766.

Crame, J.A. 2001. Taxonomic diversity gradients through geological time. Diversity and Distributions 7: 175-189.

Crowder, D.W., I. Snyder. 2010. Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. Biological Invasions 12(9): 2857-2876.

Cunjak, R.A., A. Curry, G. Power. 1987. Seasonal energy budget of brook trout in streams: implications of a possible deficit in early winter. Transactions of the American Fisheries Society 116(6): 817-828.

Cury, P., A. Bakun, R.J.M Crawford, A. Jarre, R.A. Quiñones, L.J. Shannon, H.M. Verheye. 2000. Small pelagics in upIlling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES Journal of Marine Science 57: 603-618.

Czekanowski, J. 1909. Zur differential diagnose der neandertalgruppe. Korrespondenzblatt der deutschen Gesellschaft fur Anthropologie, Enthnologie und Urgeschichte 40: 44-47.

Dahirel, M., E. Olivier, A. Guiller, M.C. Martin, L. Madec, A. Ansart. 2015. Movement propensity and ability correlate with ecological specialization in European land snails: comparative analysis of a dispersal syndrome. Journal of Animal Ecology, 84(1): 228-238.

Daskalov G.M., A.N. Grishin, S. Rodionov, V. Mihneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. PNAS 104(25): 10518-10523.

Davis, A.M., P.J. Unmack, B.J. Pusey, J.B. Johnson, R.G. Pearson. 2012. Marine-freshwater transitions are associated with the evolution of dietary diversification in terapontid grunters (Teleostei: Terapontidae). Journal of Evolutionary Biology 25(6): 1163-1179.

Davis, M.P., P.E. Midford, W. Maddison. 2013. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. BMC Evolutionary Biology 13: 38.

Day, R.D., D.P. German, J.M. Manjakasy, I. Farr, M.J. Hansen, I.R. Tibbetts. 2011. Enzymatic digestion in stomachless fishes: how a simple gut accommodates both herbivory and carnivory. Journal of Comparative Physiology B. 181(5): 603-613.

Day, E.H., X. Hua, L. Bromham. 2016. Is specialization an evolutionary dead end? Testing for differences in speciation, extinction and trait transition rates across

diverse phylogenies of specialists and generalists. Journal of Evolutionary Biology 29(6): 1257-1267.
Deegan, L.A., R.H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. Marine Ecology Progress Series 147: 31-47.
De, D.K., N.C. Datta. 1990. Studies on certain aspects of the morpho-histology of Indian shad Hilsa, *Tenualosa ilisha* (Hamilton) in relation to food and feeding habits. Indian Journal of Fisheries 37(3): 189-198.
De Longh, H.H., P.C. Spliethoff, V.G. Frank. 1983. Feeding habits of the clupeid *Limnothrissa miodon* (Boulenger), in Lake Kivu. Hydrobiologia 102: 113-122.
De Troch, M., J. Mees, E. Wakwabi. 1998. Diets of abundant fishes from beach seine catches in seagrass beds of a tropical bay (Gazi Bay, Kenya). Belgian Journal of Zoology 128(2): 135-154.
Dennis, R.L.H., L. Dapporto, S. Fattorini, L.M. Cook. 2001. The generalism-specialsim debate: the role of generalists in the life and death of species. Biological Journal of the Linnean Society 104: 725-737.
Deshmukh, V. D. 2007. Predators of non–penaeid prawns of Mumbai coast. Journal of the Bombay Natural History Society 104: 266-274.
Devictor, V., J. Clavel, R. Julliard, S. Lavergne, D. Mouillot, W. Thuiller, P. Venail, S. Villeger, N. Mouquet. 2010. Defining and measuring ecological specialization. Journal of Applied Ecology 47(1): 15-25.
Di Dario, F. 2009. Chirocentrids as engrauloids: evidence from suspensorium, branchial arches, and infraorbital bones (Clupeomorpha, Teleostei). Zoological Journal of the Linnean Society 156(2): 363-383.
Donoghue, M.J., E.J. Edwards. 2014. Biome shifts and niche evolution in plants. Annual Review of Ecology, Evolution, and Systematics 45: 547-572.
Duda, T.F., S.R. Palumbi. 2004. Gene expression and feeding ecology: evolution of piscivory in the venomous gastropod genus *Conus*. Proceedings of the Royal Society of London. Series B: Biological Sciences 271(1544): 1165-1174.
Dutta, S., S. Maity, S.B. Bhattacharyya, J.K. Sundaray, S. Hazra. 2014. Diet composition and intensity of feeding of *Tenualosa ilisha* (Hamilton, 1822) occurring in the northern Bay of Bengal, India. Proceedings of the Zoological Society 67(1): 33-37.
Economo, E.P., J.-P. Huang, G. Fischer, E.M. Sarnat, N. Narula, M. Janda, B. Guénard, J.T. Longino, L.L. Knowles. 2019. Evolution of the latitudinal diversity gradient in the hyperdiverse and genus *Pheidole*. Global Ecology and Biogeography 28: 456-470.
Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32(5): 1792-1797.
Egan, J.P., U.-S. Chew, C.-H. Kuo, V. Villarroel-Diaz, P.J. Hundt, N.G. Iwinski, M.P. Hammer, A.M. Simons. 2017. Diets and trophic guilds of small fishes from coastal marine habitats in Istern Taiwan. Journal of Fish Biology 91(1): 331-345.
Egan, J.P., D.D. Bloom, C.-H. Kuo, M.P. Hammer, P. Tongnunui, S.P. Iglésias, M. Sheaves, C. Grudpan, A.M. Simons. 2018a. Phylogenetic analysis of trophic niche evolution reveals a latitudinal herbivory gradient in Clupeoidei (herrings, anchovies, and allies). Molecular Phylogenetics and Evolution 124: 151-161.

Egan, J.P., S. Gibbs, A.M. Simons. 2018. Trophic niches through ontogeny in 12 species of Indo-Pacific marine Clupeoidei (herrings, sardines, and anchovies) Marine Biology 165: 153.

Elliott, M., A.K. Whitfield, I.C. Potter, S.J.M. Blaber, D.P. Cyrus, F.G. Nordlie, T.D. Harrison. 2007. The guild approach to categorizing estuarine fish assemblages: a global review. Fish and Fisheries 8: 241-268.

Elliott, J.P., D.R. Bellwood. 2003. Alimentary tract morphology and diet in three coral reef fish families. Journal of Fish Biology 63: 1598-1609.

Espinoza, P., A. Bertrand. 2008. Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system. Progress in Oceanography 79: 215-227.

Fagade, S.O., C.I.O. Olaniyan. 1972. The biology of the west African shad *Ethmalosa fimbriata* (Bowdich) in the Lagos Lagoon, Nigeria. Journal of Fish Biology 4: 519-533.

Fatema, K., W.M.W. Omar, M.M. Isa. 2015. Variation of food items in the stomach contents of two mullets, *Chelon subviridis* and *Valamugil buchanani* from Merbok Estuary, Kedah, Malaysia. Bangladesh Journal of Zoology 43: 213-220.

Faye, D., F.L. Loc'h, O.T. Thiaw, L.T. de Moraïs. 2012. Mechanisms of food partitioning and ecomorphological correlates in ten fish species from a tropical estuarine marine protected area (Bamboung, Senegal, West Africa). African Journal of Agricultural Research 7(3): 443-455.

FitzJohn, R.G., W.P. Maddison, S.P. Otto. 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. Systematic Biology 58(6): 595-611.

FitzJohn, R.G. 2010. Quantitative traits and diversification. Systematic Biology 59: 619-633.

Floeter, S.R., C.E.L. Ferreira, A. Dominici-Arosemena, I.R. Zalmon. 2004. Latitudinal gradients in Atlantic reef fish communities: trophic struture and spatial use patterns. Journal of Fish Biolgy 64: 1680-1699.

Floeter, S.R., M.D. Behrens, C.E.L. Ferreira, M.J. Paddack, M.H. Horn. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. Marine Biology 147: 1435-1447.

Frederiksen, M., M. Edwards, A.J. Richardson, N.C. Halliday, S. Wanless. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. Journal of Animal Ecology 75: 1259-1268.

Friedman, S.T., S.A. Price, A.S. Hoey, P.C. Wainwright. 2016. Ecomorphological convergence in planktivorous surgeonfishes. Journal Evolutionary Biology 29: 965-978.

Fuhrman, J.A., J.A. Steele, I. Hewson, M.S. Schwalbach, M.V. Brown, J.L. Green, J.H. Brown. 2008. A latitudinal diversity gradient in planktonic marine bacteria. PNAS 105(22): 7774-7778.

Futuyma, D.J., G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology, Evolution, and Systematics. 19: 207-233.

Froján, C.R.S.B., M.A. Kendall, G.L.J. Paterson, L.E. Hawkins, S. Nimsantijaroen, C. Aryuthaka. 2006. Patterns of polychaete diversity in selected tropical intertidal habitats. Scientia Marina 70: 239-248.

Froese, R., D. Pauly. Editors. 2019. Fishbase. World Wide Web electronic publication. www.fishbase.org.
Gaines, S.D., J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. Annual Review of Ecology, Evolution, and Systematics 13: 111-138.
Gainsbury, A., S. Meiri S. 2017. The latitudinal diversity gradient and interspecific competition: no global relationship between lizard dietary niche breadth and species richness. Global Ecology and Biogeography 26: 563-572.
Gajdzik, L., A. Vanreusel, N. Koedam, J. Reubens, A.W.N. Muthumbi. 2014. The mangrove forests as nursery habitats for the ichthyofauna of Mida Creek (Kenya, East Africa). Journal of the Marine Biological Association of the United Kingdom 94(5): 865-877.
Gannon, J.E. 1976. The effects of differential digestion rates of zooplankton by alewife, *Alosa pseudoharengus*, on determinations of selective feeding. Transactions of the American Fisheries Society 105: 89-95.
Garrido, S., R. Ben-Hamadou, P.B. Oliveira, M.E. Cunha, M.A Chícharo, C.D. van der Lingen. 2008. Diet and feeding intensity of sardine *Sardina pilchardus*: correlation with satellite-derived chlorophyll data. Marine Ecology Progress Series 354: 245-256.
Garrison, L.P., J.S. Link. 2000. Dietary guild structure of the fish community in the northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202: 231-240.
Gay, D., C. Bassani, S. Sergipense. 2002. Diel variation and selectivity in the diet of *Cetengraulis edentulus* (Cuvier 1828) (Engraulidae-Clupeiformes) in the Itaipu Lagoon, Niterói, Rio de Janeiro. Atlântica, Rio Grande 24(2): 59-68.
GBIF.org, 2017. GBIF Home Page. Available from: http://gbif.org.
Goldman-Huertas, B., R.F. Mitchell, R.T. Lapoint, C.P. Faucher, J.G. Hildebrand, N.K. Whiteman. 2015. Evolution of herbivory in Drosophilidae linked to loss of behaviors, antennal responses, odorant receptors, and ancestral diet. PNAS 112(10): 3026-3031.
González, N., C. Vispo. 2003. Aspects of the diets and feeding ecologies of fish from nine floodplain lakes of the lower Caura, Venezuelan Guayana. Scientia Guaianae 12: 329-366.
González-Bergonzoni, I., M. Meerhoff, T.A. Davidson, F. Teixeira-de Mello, A. Baattrup-Pedersen, E. Jeppesen. 2012. Meta-analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. Ecosystems 15: 492-503.
Gorokhova, E., T. Fagerberg, S. Hansson. 2004. Predation by herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) on *Cercopgis pengoi* in a western Baltic Sea bay. ICES Journal of Marine Science 61: 959-965.
Grassle, J.F. 2000. The Ocean Biogeographic Information System (OBIS): an on-line, worldwide atlas for accessing, modelling and mapping marine biological data in a multidimensional geographic context. Oceanography 13: 5-7.
Gravel, D., T. Poisot, C. Albouy, L. Velez, D. Mouillot. 2013 Inferring food web structure from predator-prey body size relationships. Methods in Ecology and Evolution 4: 1083-1090.

Hadfield, J.D. 2010. MCMC methods for multi-purpose generalized linear mixed models: the MCMCglmm R Package. Journal of Statistical Software 33(2): 1-22.
Hajisamae, S., L.M. Chou, S. Ibrahim. 2003. Feeding habits and trophic organization of the fish community in shallow waters of an impacted tropical habitat. Estuarine, Coastal and Shelf Science 58: 89-98.
Hajisamae, S., L.M. Chou, S. Ibrahim. 2004. Feeding habits and trophic relationships of fishes utilizing an impacted coastal habitat, Singapore. Hydrobiologia 520: 61-71.
Hajisamae, S., S. Ibrahim. 2008. Seasonal and spatial variations of fish trophic guilds in a shallow, semi-enclosed tropical estuarine bay. Environmental Biology of Fishes 82: 251-264.
Harvey, M.G., D.L. Rabosky. 2018. Continuous traits and speciation rates: alternatives to state-dependent diversification models. Methods in Ecology and Evolution 9: 984-993.
Haskell, W.L. 1959. Diet of the Mississippi threadfin shad, *Dorosoma petenense*, in Arizona. Copeia 4: 298-302.
Hata, H., H. Motomura. 2017. Validity of *Encrasicholina pseudoheteroloba* (Hardenberg 1933) and redescription of *Encrasicholina heteroloba* (Rüppell 1837), a senior synonym of *Encrasicholina devisi* (Whitly 1940) (Clupeiformes: Engraulidae). Ichthyological Research 64(1): 18-28.
Hawkins, B.A. 2001 Ecology's oldest pattern? Trends in Ecology and Evolution 16(8): 470.
Hayase, S., T. Ichikawa, K. Tanaka. 1999. Preliminary report on stable isotope ratio analysis for samples from Matang Mangrove brackish water ecosystems. Japan Agricultural Research Quarterly 33: 215-221.
Heck, K.L. Jr., T.J.B. Carruthers, C.M. Duarte, A.R. Hughes, G. Kendrick, R.J. Orth, S.W. Williams. 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. Ecosystems 11(7): 1198-1210.
Heithaus, E.R., P.A. Heithaus, M.R. Heithaus, D. Burkholder, C.A. Layman. 2011. Trophic dynamics in a relatively pristine subtropical fringing mangrove community. Marine Ecology Progress Series 428: 49-61.
Henrique, P., C. Pereira, B. Barros, R. Zemoi, B.P. Ferreira. 2014. Ontogenetic diet changes and food partitioning of *Haemulon* spp. coral reef fishes, with a review of the genus diet. Reviews in Fish Biology and Fisheries 25(1): 245-260.
Hillebrand, H. 2004a. Strength, slope and variability of marine latitudinal gradients. Marine Ecology Progress Series 273: 251-267.
Hillebrand, H. 2004b. On the generality of the latitudinal diversity gradient. The American Naturalist 163: 192-211.
Hong, G.U. 1990. Feeding habits and food composition of half-fin anchovy *Setipinna taty* (C et V) in the Bohai Sea. Chinese Journal of Oceanology and Limnology 8(3): 280-288.
Horinouchi, M., P. Tongnunui, K. Furumitsu, Y. Nakamura, K. Kanou, A. Yamaguchi, K. Okamoto, M. Sano. 2012. Food habits of small fishes in seagrass habitats in Trang, southern Thailand. Fisheries Science 78(3): 577-587.
Horn, M.H., R.N. Gibson. 1990. Effects of temperature on the food processing of three species of seaweed-eating fishes from European coastal waters. Journal of Fish Biology 37(2): 237-247.

Hossain, M.A., D.A. Hemraj, Q. Ye, S.C. Leterme, J.G. Qin. 2017. Diet overlap and resource partitioning among three forage fish species in Coorong, the largest inverse estuary in Australia. Environmental Biology of Fishes 100: 639-654.

Hothorn, T., A. Zeileis, R.W. Farebrother, C. Cummins, M. Giovanni, D. Mitchell. 2017. Package “lmtest”. <https://cran.r-project.org/package=lmtest>

Hubbs, C.L., K.F. Lagler. 1941. *Guide to the fishes of the great lakes and tributary waters*. Bloomfield Hills, MI: Cranbrook Press.

Hundt, P.J., Y. Nakamura, K. Yamaoka. 2014. Diet of combtooth blennies (Blenniidae) in Kochi and Okinawa, Japan. Ichthyological Research 61: 76-82.

Hurlbert, A.H., J.C. Stegen. 2014. When should species richness be energy limited, and how would we know? Ecology Letters 17(4): 401-413.

Hyslop, E.J. 1980. Stomach contents analysis – a review of methods and their application. Journal of Fish Biology 17: 411-429.

Ibañez, C., J. Belliard, R.M. Hughes, P. Irz, A. Kamdem-Toham, N. Lammyoux, P.A. Tedesco, T. Oberdorff. 2009. Convergence of temperate and tropical stream fish assemblages. Ecography 32(4): 658-670.

Ikusemiju, K., A.A. Oki, M. Graham-Douglas. 1983. On the biology of an estuarine population of the clupeid *Pellona afzeliusi* (Johnels) in Lagos Lagoon, Nigeria. Hydrobiologia 102: 55-59.

Inoue, T., Y. Suda, M. Sano. 2005. Food habits of fishes in the surf zone of a sandy beach at Sanrimatsubara, Fukuoka Prefecture, Japan. Ichthyological Research 52: 9-14.

Islam, S., M. Tanaka. 2006. Spatial variability in nursery functions along a temperate estuarine gradient: role of detrital versus algal trophic pathways. Canadian Journal of Fisheries and Aquatic Sciences 63: 1848-1864.

Jaksić, F.M., R.G. Medel. 1990. Objective recognition of guilds: testing for statistically significant species clusters. Oecologia 82: 87-92.

Janzen, D.H. 1967. Why mountain passes are higher in the tropics. The American Naturalist 101(919): 233-249.

Jensen, H., K.K. Kahilainen, P.-A. Amundsen, K.Ø. Gjelland, A. Tuomaala, T. Malinen, T. Bøhn. 2008. Predation by brown trout (*Salmo trutta*) along a diversifying prey community gradient. Canadian Journal of Fisheries and Aquatic Sciences 65: 1831-1841.

Jocque, M., R. Field, L. Brendonck, L.D. Meester. 2010. Climate control of dispersal-ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? Global Ecology and Biogeography 19(2): 244-252.

Jude, D.J. 1973. Food and feeding habits of gizzard shad in Pool 19, Mississippi River. Transactions of the American Fisheries Society 102(2): 378-383.

Kalko, E.K.V., H.-U. Schnitzler, I. Kaipf, A.D. Grinnell. 1998. Echolocation and foraging behavior of the lesser bulldog bat, *Noctilio albiventris*: Preadaptations for piscivory? Behavioral Ecology and Sociobiology. 42(5): 305-319.

Kanou, K., M. Sano, H. Kohno. 2004. Food habits of fishes on unvegetated tidal mudflats in Tokyo Bay, central Japan. Fisheries Science 70: 978-987.

Kaschner, K., K. Kesner-Reyes, C. Garilao, J. Rius-Barile, T. Rees, R. Froese. 2016. Aquamaps: predicted range maps for aquatic species. World wide web electronic publication, www.aquamaps.org, version 08/2016.

Kato, T., A. Bonet, H. Yoshitake, J. Romero-Nápoles, U. Jinbo, M. Ito, M. Shimada.

2010. Evolution of host utilization patterns in the seed beetle genus Mimosestes Bridwell (Coleoptera: Chrysomelidae: Bruchinae). Molecular phylogenetics and Evolution 55(3): 816-32.

Kimbembi-ma-ibaka, A., B. Nzuki. 2001. Régime alimentaire de *Microthrissa congica* Regan 1917 (Pisces, Clupeidae) du basin du Congo. Tropicultura 19(2): 53-55.

Kisel, Y., T.G. Barraclough. 2010. Speciation has a spatial scale that depends on levels of gene flow. The American Naturalist 173(3): 316-334.

Kitching, R.L. 1987. Spatial and temporal variation in food webs in water-filled treeholes. Oikos 48: 280-288.

Kiyashko, V.I., N.A. Khalko, V.I. Lazareva 2007. On the diurnal rhythm and feeding electivity in kilka (*Clupeonella cultriventris*) in Rybinsk Reservoir. Journal of Ichthyology 47(4): 310-319.

Koenker, R., P.T. Ng, A. Zeileis, P. Grosjean, B.D. Ripley. 2018. Package "quantreg"

Kohler, C.C., J.J. Ney. 1980. Piscivority in a land-locked alewife (*Alosa pseudoharengus*) population. Canadian Journal of Fisheries and Aquatic Sciences 37: 1314-1317.

Koslow, J.A. 1981. Feeding selectivity of schools of northern anchovy, *Engraulis mordax* in the southern California bight. Fishery Bulletin 79(1): 131-142.

Köster, F.W., C. Möllmann. 2000. Egg cannibalism in Baltic spat *Sprattus sprattus*. Marine Ecology Progress Series 196: 269-277.

Krebs, J.M., R.G. Turingan. 2003. Intraspecific variation in gape-prey size relationships and feeding success during early ontogeny in red drum, *Sciaenops ocellatus.* Environmental Biology of Fishes 66: 75-84.

Krück, N.C., C.A. Chargulaf, U. Saint-Paul, I.R. Tibbetts. 2009. Early post–settlement habitat and diet shifts and the nursery function of tidepools during *Sillago* spp. Recruitment in Moreton Bay, Australia. Marine Ecology Progress Series 384: 207-219.

Krumme, U., H. Keuthen, M. Barletta, W. Villwock, U. Saint-Paul. 2005. Contribution to the feeding ecology of the predatory wingfin anchovy *Pterengraulis atherinoides* (L.) in north Brazilian mangrove creeks. Journal of Applied Ichthyology 21: 469-477.

Krumme, U., H. Keuthen, M. Barletta, U. Saint-Paul, W. Villwock. 2008. Resuspended intertidal microphytobenthos as major diet component of planktivorous Atlantic Anchoveta *Cetengraulis edentulus* (Engraulidae) from equatorial mangrove creeks. Ecotropica 14: 121-128.

Kuthalingam, M.D.K. 1961. Observations on the feeding habits of some sardines together with the key to the identification of the young ones of the genus *Sardinella*. Records of the Indian Museum 59(4): 455-469.

Kutkuhn, J.H. 1958. Utilization of plankton by juvenile gizzard shad in a shallow prairie lake. Transactions of the American Fisheries Society 87(1): 80-103.

Lakshmi, S.A. 2010. Interrelationship between the alimentary tract, food and feeding habits of plueronectiform fishes of southeast coast of India. Journal of Experimental Sciences 1: 1-7.

Lanfear, R., B. Calcott, S.Y.W. Ho, S. Guindon. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analysis. Molecular Biology and Evolution 41(6): 983-991.

Lavoué, S., M. Miya, P. Musikasinthorn, W.-J. Chen, M. Nishida. 2013. Mitogenomic evidence for an indo-west pacific origin of the Clupeoidei (Teleostei: Clupeiformes). PLoS one 8(2): e56485.

Lavoué, S., P. Konstantinidis, W.-J. Chen. 2014. Progress in Clupeiformes systematics. In: Ganias, K. editor. Biology and ecology of anchovies and sardines. Enfield, New Hampshire: Science Publishers pp. 3-42.

Lavoué, S., M.E. Arnegard, D.L. Rabosky, P.B. McIntyre, D. Arcila, R.P. Vari, M. Nishida. 2017a. Trophic evolution in African citharinoid fishes (Teleostei: Characiformes) and the origin of infraordinal pterygophagy. Molecular Phylogenetics and Evolution 113: 23-32.

Lavoué, S., J.A.M. Bertrand, H.-Y. Wang, W.-J. Chen, H.-C. Ho, H. Motomura, H. Hata, T. Sado, M. Miya. 2017b. Molecular systematics of the anchovy genus *Encrasicholina* in the Northwest Pacific. PLoS one. 12(7): e0181329.

Lavoué, S., J.A.M. Bertrand, W.J. Chen, H.C. Ho, H. Motomura, T. Sado, M. Miya. 2017c. Phylogenetic position of the rainbow sardine Dussumieria (Dussumieriidae) and its bearing on the early evolution of the Clupeoidei. Gene 623: 41-47.

Lavoué, S., H.-C. Ho. 2017. *Pseudosetipinna* Peng & Zhao is a junior synonym of *Setipinna* Swainson and *Pseudosetipinna haizhouensis* Peng & Zhao is a junior synonym of *Setipinna tenuifilis* (Valenciennes) (Teleostei: Clupeoidei: Engraulidae). Zootaxa 4294(3): 342-348.

Lawlor, L.R. 1980. Structure and stability in natural and randomly constructed competitive communities. American Naturalist 116: 394-408.

Legendre, P., L. Legendre. 2012. Numerical Ecology, 3rd English ed. Amsterdam: Elsevier Science BV.

Leighton, L.R. 2005. The latitudinal diversity gradient through deep time: testing the "Age of the Tropics" hypothesis using Carboniferous productidine brachiopods. Evolutionary Ecology 19: 563-581.

Lewis, V.P., D.S. Peters. 1994. Diet of juvenile and adult Atlantic menhaden in estuarine and coastal habitats. Transactions of the American Fisheries Society 123(5): 803-810.

Li, C., G. Ortí, G. Zhang, G. Lu. 2007. A practical approach to phylogenomics: the phylogeny of ray-finned fish (Actinopterygii) as a case study. BMC Evolutionary Biology 7.

Li, C., G. Ortí, J. Zhao. 2010. The phylogenetic placement of sinipercid fishes ("Perciformes") revealed by 11 nuclear loci. Molecular Phylogenetics and Evolution 56: 1096-1104.

Lim, P., S. Lek, S.T. Touch, S.-O. Mao, B. Chhouk. 1999. Diversity and spatial distribution of freshwater fish in Great Lake and Tonle Sap River (Cambodia, Southeast Asia). Aquatic Living Resources 12(6): 379-386.

Lin, H.-J., W.-Y. Kao, Y.-T. Wang. 2007. Analyses of stomach contents and stable isotopes reveal food smyces of estuarine detritivorous fish in tropical/subtropical Taiwan. Estuarine, Coastal and Shelf Science 73: 527-537.

Linzmaier, S.M., L.A. Twardochleb, J.D. Olden, T. Mehner, R. Arlinghaus. 2018. Size-dependent foraging niches of European Perch *Perca fluviatilis* (Linnaeus, 1758)

and North American Yellow Perch *Perca flavescens* (Mitchill, 1814). Environmental Biology of Fishes 101: 23-37.
Livingston, R.J. 1982. Trophic organization of fishes in a coastal seagrass system. Marine Ecology Progress Series 7: 1-12.
Lobato, F.L., D.R. Barneche, A.C. Siqueira, A.M.R. Liedke, A. Lindner, M.R. Pie, D.R. Bellwood, S.R. Floeter 2014. Diet and diversification in the evolution of coral reef fishes. PLoS one. 9(7): e102094.
Loeb, M.V., A.V. Alcântara. 2013. A new species of *Lycengraulis* Günther, 1868 (Clupeiformes: Engraulinae) from the Amazon basin, Brazil, with comments on *Lycengraulis batesii* (Günther, 1868). Zootaxa 3693(2): 200-206.
Lomiri, S., U. Scacco, E. Mostarda, F. Andaloro. 2008. Size-related and temporal variation in the diet of the round sardinella, *Sardinella aurita* (Valenciennes, 1847), in the central Mediterranean Sea. Journal of Applied Ichthyology 24: 539-545.
López, J.A., W.-J. Chen, G. Ortí. 2004. Esociform phylogeny. Copeia 2004(3): 449-464.
Loxdale, H.D., G. Lushai, J.A. Harvey. 2011. The evolutionary improbability of 'generalism' in nature, with special reference to insects. Biological Journal of the Linnean Society. 103(1): 1-8.
MacArthur, R.H., R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. The American Naturalist 101(921): 377-385.
Macpherson, E. 1981. Resource partitioning in a Mediterranean demersal fish community. Marine Ecology Progress Series 4: 183-193.
Maitland, P.S., A.A. Lyle. 2005. Ecology of Allis shad *Alosa alosa* and twaite shad *Alosa fallax* in the Solway Firth, Scotland. Hydrobiologia 534: 205-221.
Majluf, P., S. De la Puente, V. Christensen. 2017. The little fish that can feed the world. Fish and Fisheries 18(4): 772-777.
Major, P.F. 1973. Scale feeding behavior of the leatherjacket, *Scomberoides lysan* and two species of the genus *Oligoplites* (Pisces: Carangidae). *Copeia* 1973: 151-154.
Malabarba, M.C., F.D. Dario. 2017. A new predatory herring-like fish (Teleostei: Clupeiformes) from the early Cretaceous of Brazil, and implications for relationships in the Clupeoidei. Zoological Journl of the Linnean Society 180(1): 175-194.
Malek, A.J., J.S. Collie, D.L. Taylor. 2016. Trophic structure of a coastal fish community determined with diet and stable isotope analysis. Journal of Fish Biology 89: 1513-1536.
Mannion, P.D., P. Upchurch, R.B.J. Benson, A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. Trends in Ecology and Evolution 29(1): 42-50.
Marcot, J.D., D.L. Fox, S.R. Niebuhr. 2016. Late Cenozoic onset of the latitudinal diversity gradient of North American mammals. PNAS 113(26): 7189-7194.
Marcus, O. 1986. Food and feeding habits of *Ilisha africana* (Bloch) (Pisces: Clupeidae) off the Lagos coast, Nigeria. Journal of Fish Biology 29: 671-683.
Marichamy, R. 1972. Food and feeding habits of the short-jaw anchovy, *Thrissina baelama* (Forskal), of the Andaman Sea. Indian Journal of Fisheries 19(1&2): 54-59.
Marin, J., G. Rapacciuolo, G.C. Costa, C.H. Graham, T.M. Brooks, B.E. Young, V.C.

Radeloff, J.E. Behm, M.R. Helmus, S.B. Hedges. 2018. Evolutionary time drives global tetrapod diversity. Proceedings of the Royal Society B 285(172): 20172378.

Marramà, G., G. Carnevale. 2016. An Eocene anchovy from Monte Bolca, Italy; The earliest known record for the family Engraulidae. Geological Magazine 153(1): 84-94.

Martin, T.J., S.J.M. Blaber. 1983. The feeding ecology of Ambassidae (Osteichthyes: Perciformes) in Natal estuaries. South African Journal of Zoology 18: 353-362.

Martin, A.E., L. Fahrig. 2018. Habitat specialist birds disperse farther and are more migratory than habitat generalist birds. Ecology 99(9): 2058-2066.

Mavuti, K.M., J.A. Nyunja, E.O. Wakwabi. 2004. Trophic ecology of some common juvenile fish species in Mtwapa Creek, Kenya. Western Indian Ocean Journal of Marine Science 3(2): 179-187.

Medeiros, E.S.F., A.H. Arthington. 2008. The importance of zooplankton in the diets of three native fish species in floodplain waterholes of a dryland river, the Macintyre River, Australia. Hydrobiologia 614: 19-31.

Mérona, B. de, G.M. dos Santos, R.G. de Almeida. 2001. Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. Environmental Biology of Fishes 60: 375-392.

Mérona, B. de, B. Hugueny, F.L. Tejerina-Garro, E. Gautheret. 2008. Diet-morphology relationship in a fish assemblage from a medium-sized river of French Guiana: the effect of species taxonomic proximity. Aquatic Living Resources 21(2): 171-184.

Metillo, E.B., W.L. Campos, C.L. Villanoy, K.-I. Hayashizaki, T. Tsunoda, S. Nishida. 2018. Ontogenetic feeding shift and size-based zooplanktivory in *Sardinella lemuru* (Pisces, Clupeidae) during an upwelling in southeastern Sulu Sea, The Philippines. Fisheries Management and Ecology 25: 441-445.

Mickle, P.F., J.F. Schaefer, D.A. Yee, S.B. Adams. 2013. Diet of juvenile Alabama shad (*Alosa alabamae*) in two northern Gulf of Mexico drainages. Southeastern Naturalist 12(1): 233-237.

Mihalitsis, M., D.R. Bellwood. 2017. A morphological and functional basis for maximum prey size in piscivorous fishes. PloS one 12(9): e0184679.

Mihindukulasooriya, I.D., U.S. Amarasinghe. 2014. Food and feeding of *Ehirava fluviatilis* (Osteichthyes, Clupeidae) in Rajanganaya Reservoir, Sri Lanka. Sri Lanka Journal of Aquatic Science 19: 31-39.

Milton, D.A., S.J.M. Blaber, N.J.F. Rawlinson. 1990. Diet and prey selection of six species of tuna baitfish in three coral reef lagoons in the Solomon Islands. Journal of Fish Biology 37: 205-224.

Milton, D.A., S.J.M. Blaber, N.J.F. Rawlinson. 1994. Diet, prey selection and their energetic relationship to reproduction in the tropical herring *Herklotsichthys quadrimaculatus* in Kiribati, central Pacific. Marine Ecology Progress Series 103: 239-250.

Miller, R.R. 1982. First fossil record (Plio-Pleistocene) of threadfin shad, *Dorosoma petenense*, from the Gatuna Formation of southeastern New Mexico. Journal of Paleontology 56(2): 423-425.

Miller, M.A., W. Pfeiffer, T. Schwartz. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing

Environments Workshop (GCE), 14 November 2010, New Orleans, LA, 1-8.
Miller, C.M., J.T. Hayashi, D. Song, J.J. Wiens. 2018. Explaining the ocean's richest biodiversity hotspot and global patterns of fish diversity. Proceedings of the Royal Society B: Biological Sciences 285: 20181314.
Milton, D.A., S.J.M. Blaber, N.J.F. Rawlinson. 1990. Diet and prey selection of six species of tuna baitfish in three coral reef lagoons in the Solomon Islands. Journal of Fish Biology 37: 205-224.
Mittelbach, G.G., D.W. Schemske, H.V. Cornell, A.P. Allen, J.M. Brown, M.B. Bush, S.P. Harrison, A.H. Hurlbert, N. Knowlton, H.A. Lessios, C.M. McCain, A.R. McCune, L.A. McDade, M.A. McPeek, T.J. Near, T.D. Price, R.E. Ricklefs, K. Roy, D.F. Sax, D. Schluter, J.M. Sobel, M. Turelli. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10(4): 315-331.
Mketsu, Q.K. 2008. Comparative dietary analysis of four small pelagic fish species from presumed mixed shoals off South Africa's east coast. Master's Thesis University of Cape Town.
Mondal, D.K., A. Kaviraj. 2010. Feeding and reproductive biology and Indian shad *Gudusia chapra* in two floodplain lakes of India. Electronic Journal of Biology 6(4): 98-102.
Montoya, J.M., R.V. Solé. 2003. Topological properties of food webs: from real data to community assembly models. Oikos 102: 614-622.
Moore, J.W., I.A. Moore. 1976. The basis of food selection in some estuarine fishes. Eels, *Anguilla Anguilla* (L.), whiting, *Merlangius merlangus* (L.), spat, *Sprattus sprattus* (L.) and stickleback, *Gasterosteus aculeatus* L. Journal of Fish Biology 9: 375-390.
Moreira-Hara, S.S., J.A.S. Zuanon, S.A. Amadio. 2009. Feeding of *Pellona flavipinnis* (Clupeiformes, Pristigasteridae) in a central Amazonian floodplain. Iheringia Série Zoologia 99(2): 153-157.
Morinière, J., M.H. Van Dam, O. Hawlitschek, J. Bergsten, M.C. Michat, L. Hendrich, I. Ribera, E.F. Toussaint, M. Balke. 2016. Phylogenetic niche conservatism explains an inverse latitudinal diversity gradient in freshwater arthropods. Scientific reports 6: 26340.
Morote, E., M.P. Olivar, F. Villate, I. Uriarte. 2010. A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest Mediterranean: influence of prey availability and ontogeny. ICES Journal of Marine Science 67(5): 897-908.
Mundahl, N.D., T.E. Wissing. 1987. Nutritional importance of detritivory in the growth and condition of gizzard shad in an Ohio reservoir. Environmental Biology of Fishes 20(20): 129-142.
Munk, P. 1997. Prey size spectra and prey availability of larval and small juvenile cod. Journal of Fish Biology 51: 340-351.
Munroe, T.A., M. Nizinski. 1999. Engraulidae. Anchovies. In: Carpenter KE, Niem VH (eds.) FAO species identification guide for fishery purposes. The living marine resmyces of the WCP. Vol. 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae). FAO, Rome pp 1698-1706.

Munroe, T.A., T. Wongratana, M.S. Nizinski. 1999. Clupeidae. Herrings (also, sardines, shads, sprats, pilchards and menhadens). p. 1775-1784. In K.E. Carpenter and V.H. Niem (eds.) FAO species identification guide for fishery purposes. The living marine resmyces of the WCP. Vol. 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae). FAO, Rome.

Nachón, D.J., J. Sánchez-Hernández, R. Vieira-Lanero, F. Cobo. 2013. Feeding of twaite shad, *Alosa fallax* (Lacépède, 1803), during the upstream spawning migration in the River Ulla (NW Spain). Marine and Freshwater Research 64: 233-236.

Nair, K.V. 1998. Studies on the fishery, biology and population dynamics of anchovies of the Kerala coast. Dissertation, Mahatma Gandhi University.

Nakamura, Y., M. Horinouchi, T. Nakai, M. Sano. 2003. Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. Ichthyological Research 50: 15-22.

Nakane, Y., Y. Suda, M. Sano. 2011. Food habits of fishes on an exposed sandy beach at Fukiagehama, south-west Kyushu Island, Japan. Helgoland Marine Research 65: 123-131.

Nanjo, K., H. Kohno, M. Sano. 2008. Food habits of fishes in the mangrove estuary of Urauchi River, Iriomote Island, southern Japan. Fisheries Science 74: 1024-1033.

Near, T.J., R.I. Eytan, A. Dornburg, K.L. Kuhn, J.A. Moore, M.P. Davis, P.C. Wainwright, M. Friedman, W.L. Smith. 2012. Resolution of ray-finned fish phylogeny and timing of diversification. PNAS 109(34): 13698-13703.

Nelson, J., C. Stallings, W. Landing, J. Chanton. 2013. Biomass transfer subsidizes nitrogen to offshore food webs. Ecosystems 16: 1130-1138.

Nikolioudakis, N., S. Isari, P. Pitta, S. Somarakis. 2012. Diet of sardine *Sardina pilchardus*: an “end-to-end” field study. Marine Ecology Progress Series 453: 173-188.

Nyunja, J.A., K.M. Mavuti, E.O. Wakwabi. 2002. Trophic ecology of *Sardinella gibbosa* (Pisces: Clupeidae) and *Atherinomorous lacunosus* (Pisces: Atherinidae) in Mtwapa Creek and Wasini Channel, Kenya. Western Indian Ocean Journal of Marine Science 1(2): 181-189.

O'brien, E.M., R. Field, R.J. Whittaker. 2000. Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. Oikos 89(3): 588-600.

Odum, W.E., E.J. Heald. 1972. Trophic analyses of an estuarine mangrove community. Bulletin of Marine Science 22(3): 671-738.

Offem, B.O., Y.A. Samsons, I.T. Omoniyi. 2009. Trophic ecology of commercially important fishes in the Cross River, Nigeria. The Journal of Animal and Plant Sciences 19(1): 37-44.

Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O’Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, H. Wagner. 2016. vegan: Community Ecology Package. *R package version 2.4-0.* Available at https://CRAN.R-project.org/package=vegan.

Olden, J.D., N.L. Poff, K.R. Bestgen. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. Ecological Monographs 76(1): 25-40.

Orme, D., R. Freckleon, G. Thomas, T. Petzoldt. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. *R package version* 5.2: 1-36.

Otté, E.C., H.B. Bohn translators (1850) Views of Nature: or contemplations on the sublime phenomena of creation; with Scientific Illustrations*,* 3rd edn (Alexander von Humboldt), Henry G. Bohn.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401: 877-884.

Paradis, E., K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526-528.

Paszkowski, C.A., W.M. Tonn, I.J. Holopainen. 1989. An experimental study of body size and food size relations in crucian carp, *Carassius carassius*. Experimental Biology of Fishes 24: 275-286.

Pearre, S. 1986. Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. Marine Ecology Progress Series 27: 299-314.

Pekár, S., J.A. Coddington, T.A. Blackledge. 2011. Evolution of stenophagy in spiders (Araneae): evidence based on the comparative analysis of spider diets. Evolution 63(3): 776-806.

Pepin, P., R.W. Penney. 1997. Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? Journal of Fish Biology 51(Supplement A): 84-100.

Phukan, B., S. Baishya, P. Sharma, A. Rajbongshi, A. Rahman. 2012. Food and feeding habits of *Gudusia chapra* (Hamilton, 1822) from Silinga Beel of lower reaches of Subansiri River in Assam, N-E India. Environment and Ecology 30(3): 578-580.

Pianka, E.R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53-74.

Plounevez, S., G. Champalbert. 1999. Feeding behavior and trophic environment of *Engraulis encrasicolus* (L.) in the Bay of Biscay. Estuarine, Coastal and Shelf Science 49: 177-191.

Plummer, M., N. Best, K. Cowles, K. Vines. 2006. CODA: convergence diagnosis and output analysis for MCMC. R News 6(1): 7-11.

Polis, G.A. 1984. Age structure component of niche width and intraspecific resmyce partitioning: can age groups function as ecological species? The American Naturalist 123(4): 541-564.

Pontarp, M., L. Bunnefeld, J.S. Cabral, R.S. Etienne, S.A. Fritz, R. Gillespie, C.H. Graham, O. Hagen, F. Hartig, S. Huang, R. Jansson, O. Maliet, T. Münkemüller, L. Pellissier, T.F. Rangel, D. Storch, T. Wiegand, A.H. Hurlbert. 2019. The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. Trends in Ecology and Evolution 34(3): 211-223.

Pouilly, M., F. Lino, J.-G. Bretenoux, C. Rosales. 2003. Dietary-morphological relationships in a fish assemblage of the Bolivian Amazonian floodplain. Journal of Fish Biology 62: 113-1158.

Pouilly, M., T. Yunoki, C. Rosales, L. Torres. 2004. Trophic structure of fish assemblages from Mamoré River floodplain lakes (Bolivia). Ecology of Freshwater Fish 13: 245-257.

Powell, M.G., V.P. Beresford, B.A. Colaianne. 2012. The latitudinal position of peak marine diversity in living and fossil biotas. Journal of Biogeography 39(9): 1687-1694.

Price, S.A., S.S.B. Hopkins, K.K. Smith, V.L. Roth. 2012. Tempo of trophic evolution and its impact on mammalian diversification. PNAS 109(18): 7008-7012.

Pusey, B.J., M.G. Read, A.H. Arthington. 1995. The feeding ecology of freshwater fishes in two rivers of the Australian wet tropics. Environmental Biology of Fishes 43: 85-103.

Pyron, R.A., J.J. Weins. 2013. Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. Proceedings of the Royal Society B: Biological Sciences 280(1770): 20131622.

Pyron, R.A. 2014. Biogeographic analysis reveals ancint continental vicariance and recent oceanic dispersal in amphibians. Systematic Biology 63(5): 779-797.

R Development Core Team (2016). R: A language and environment for statistical computing. Version 3.3.1, Vienna, Austria. Available at: http://www.R-project.org.

Rabosky, D.L. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. PloS ONE 9: e89543.

Rabosky, D.L., P.O. Title, H. Huang. 2015. Minimal effects of latitude on present-day speciation rates in New World birds. Proceedings of the Royal Society B: Biological Sciences. 282(1809): 20142889.

Rabosky, D.L., H. Huang. 2016. A robust semi-parametric test for detecting trait-dependent diversification. Systematic Biology 65: 181-193.

Rabosky, D.L., J.S. Mitchell, J. Chang. 2017. Is BAMM flawed? Theoretical and practical concerns in the analysis of multi-rate diversification models. Systematic Biology 66(4): 477-498.

Rabosky, D.L., J. Chang, P.O. Title, P.F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T.J. Near, M. Coll, M.E. Alfaro. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559(7714): 392.

Rainboth, W.J. 1996. Fishes of the Cambodian Mekong. FAO species identification field guide for fishery purposes. Rome: FAO.

Raje, S.G. 1993. Some aspects of biology of *Alepes djedaba* (Forskål) from Veraval, Gujarat. Indian Journal of Fisheries 40: 189-192.

Ralston, S.L., M.H. Horn. 1986. High tide movements of the temperate-zone herbivorous fish *Cebidichthys violaceus* (Girard) as determined by ultrasonic telemetry. Journal or Experimental Marine Biology and Ecology 98: 35-50.

Rambaut, A., M.A. Suchard, D. Xie, A.J. Drummond. 2014. Traver v1.6 http://tree.bio.ed.ac.uk/software/tracer/

Rao, K.S. 1967. Food and feeding habits of fishes from trawl catches in the Bay of Bengal with observations on diurnal variation in the nature of the feed. Indian Journal of Fisheries 11(1): 277-314.

Rao, Y.P., D.N.K. Veni, I.R. Sirisha. 2015. Biology of orange fin pony fish, *Photopectoralis bindus* (Valenciennes, 1935), off Visakhapatnam, east coast of India. International Journal of Environmental Sciences 5: 1159-1171.

Revell, L.J. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3: 217-223.

Rivadeneira, M.M., M. Thiel, E.R. González, P.A. Haye. 2011. An inverse latitudinal gradient of diversity of peracarid crustaceans along the Pacific Coast of South America: out of the deep south. Global Ecology and Biogeography 20(3): 437-448.

Rolland, J., F. Jiguet, K.A. Jønsson, F.L. Condamine, H. Morlon. 2014. Settling down of seasonal migrants promotes bird diversification. Proceedings of the Royal Society B: Biological Sciences, 281(1784): p.20140473.

Root, R.B. 1967. The niche exploitation pattern of the Blue-Gray Gnatcatcher. Ecological Monographs 37: 317-350.

Röpke, C.P., E. Ferreira, J. Zuanon. 2013. Seasonal changes in the use of feeding resources by fish in stands of aquatic macrophytes in an Amazonian floodplain, Brazil. Environmental Biology of Fishes 97(4): 401-414.

Sabatés, A., E. Saiz. 2000. Itra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. Marine Ecology Progress Series 201: 261-271.

Salarpmy, A., D. Mohammad, S. Behzadi, F. Seraji. 2008. Reproduction and feeding of buccaneer anchovy (*Encrasicholina punctifer*) from coastal waters of Qeshm Island, the Persian Gulf. Iranian Scientific Fisheries Journal 17(1): 45-54.

Salarpour, A., D. Mohammad, S. Behzadi, F. Seraji. 2008. Reproduction and feeding of buccaneer anchovy (*Encrasicholina punctifer*) from coastal waters of Qeshm Island, the Persian Gulf. Iranian Scientific Fisheries Journal 17(1): 45-54.

Salini, J.P., D.T. Brewer, S.J.M. Blaber. 1998. Dietary studies on the predatory fishes of the Norman River Estuary, with particular reference to penaeid prawns. Estuarine, Costal and Shelf Science 46: 837-847.

Sanchez, M.F. 1989. Morphological characteristics of digestive tract and trophic spectrum of saraca (*Breevoortia aurea*, Clupeiformes, Pisces). Physis-A 47(112): 21-33.

Sanchez, J.L., J.C. Trexler. 2016. The adaptive evolution of herbivory in freshwater systems. Ecosphere 7: e01414.

Santini, F., M.R. May, G. Carnevale, B.R. Moore. 2015. Bayesian inference of divergence times and feeding evolution in grey mullets (Mugilidae). bioRxiv: 019075.

Sarkar, S.K., A. Bhattacharya, S. Giri, B. Bhattacharya, D. Sarkar, D.C. Nayak, A.K. Chattopadhaya. 2005. Spatiotemporal variation in benthic polychaetes (Annelida) and relationships with environmental variables in a tropical estuary. Wetlands Ecology and Management 13: 55-67.

Saupe, E.E., C.E. Myers, A.T. Peterson, J. Soberón, J. Singarayer, P. Valdes, H. Qiao. 2019. Non-random latitudinal gradients in range size and niche breadth predicted by spatial patterns of climate. Global Ecology and Biogeography 28(7): 928-942.

Scharf, F.S., F. Juanes, M. Sutherland. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. Ecology 79(2): 448-460.

Scharf, F.S., F. Juanes, R.A. Rountree. 2000. Predator size - prey size relationships of marine fish predators: interspecific variation and the effects of ontogeny and body size on trophic niche breadth. Marine Ecology Progress Series 208: 229-248.

Scharf, F.S., K.K. Schlight. 2000. Feeding habits of red drum (Scianops ocellatus) in Galveston Bay, Texas; seasonal diet variation and predator-prey size relationships. Estuaries 23(1): 128-139.

Schmitz, E.H., C.D. Baker. 1969. Digestive anatomy of the gizzard shad, *Dorosoma cepedianum* and the threadfin shad *D. petenense*. Transactions of the American Microscopical Society 88(4): 525-546.

Schneider, C.A., W.S. Rasband, K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9: 671-675.

Schoener, T.W. 2009. Ecological Niche. In: Levin SA (ed) The Princeton Guide to Ecology, Princeton University Press, New Jersey, pp 3-13.

Seah, Y.G., S. Abdullah, C.C. Zaidi, A.G. Mazlan. 2009. Systematic accounts and some aspects of feeding and reproductive biology of ponyfishes (Perciformes: Leiognathidae). Sains Malaysiana 38: 47-56.

Seah, Y.G., A.G. Mazlan, S. Abdullah, C.C. Zaidi, G. Usup, C.A.R. Mohamed. 2011. Feeding guild of the dominant trawl species in the southeastern waters of peninsular Malaysia. Journal of Biological Sciences 11: 221-225.

Shahraki, M., B. Fry, U. Krumme, T. Rixen. 2014. Microphytobenthos sustain fish food webs in intertidal arid habitats: a comparison between mangrove-lined and un-vegetated creeks in the Persian Gulf. Estuarine, Costal and Shelf Science 149: 203-212.

Shakman, E., R. Kinzelbach. 2006. The halfbeak fish, *Hemiramphus far* (Forskal, 1775), in the coastal waters of Libya. Zoology in the Middle East 39: 111-112.

Shannon, L.J., J.G. Field, C.L. Moloney. 2004. Simulating anchovy-sardine regime shifts in the southern Benguela ecosystem. Ecological Modeling 172: 269-281.

Sheaves, M., R. Baker, K.G. Abrantes, R.M. Connolly. 2016. Fish biomass in tropical estuaries: substantial variation in food web structure, sources of nutrition and ecosystem-supporting processes. Estuaries and Coasts 40(2): 580-593.

Shiono, T., B. Kusumoto, M. Yasuhara, Y. Kubota. 2018. Roles of clime niche conservatism and range dynamics in woody plant diversity patterns through the Cenozoic. Global Ecology and Biogeography 27(7): 865-874.

Simberloff, D., T. Dayan. 1991. The guild concept and the structure of ecological communities. Annual Review of Ecology and Systematics 22: 115-143.

Simon, T., J.-C. Joyeux, H.T. Pinheiro. 2013. Fish assemblages on shipwrecks and natural rocky reefs strongly differ in trophic structure. Marine Environmental Research 90: 55-65.

Simpson, E.H. 1949. Measurement of diversity. Nature 163: 688.

Siqueira, A.C., L.G.R. Oliveira-Santos, P.F. Cowman, S.R. Floeter, A. Algar. 2016. Evolutionary processes underlying latitudinal differences in reef fish diversity. Global Ecology and Biogeography 25: 1466-1476.

Sirimongkonthaworn, R., C.H. Fernando. 1994. Biology of *Clupeichthys aesarnensis* (Clupeidae) in Ubolratana Reservoir, Thailand, with special reference to food and feeding habits. Internationale Revue der Gesamten Hydrobiologie und Hydrographie 79(1): 95-112.

Sivakami, S. 1990. Observations on some aspects of biology of *Alepes djedaba* (Forskål) from Cochin. Journal of the Marine Biological Association of India 32: 107-118.

Skóra, M.E., M.R. Sapota, K.E. Skóra, A. Pawelec. 2012. Diet of the twiate shad *Alosa fallax* (Lacépède, 1803) (Clupeidae) in the Gulf of Gdansk, the Baltic Sea. Oceanological and Hydrobiological Studies 41(3): 24-32.

Slatyer, R.A., M. Hirst, J.R. Sexton. 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecology Letters 16(8): 1104-1114.

Smoot, J.C., R.H. Findlay. 2010. Caloric needs of detritivorous gizzard shad *Dorosoma cepedianum* are met with sediment bacterial and algal biomass. Aquatic Biology 8(2): 105-114.

Somerfield, P.J. 2008. Identification of the Bray-Curtis similarity index: comment on Yoshioka 2008. Marine Ecology Progress Series 372: 303-306.

Specziár, A., E.T. Rezsu. 2009. Feeding guilds and food resource partitioning in a lake fish assemblage: an ontogenetic approach. Journal of Fish Biology 75: 247-267.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312-1313.

Stern, N., J. Douek, M. Goren, B. Rinkevich. 2017. With no gap in mind: a shallow genealogy within the world's most widespread small pelagic fish. Ecography 40: 1-13.

Stomp, M., J. Huisman, G.G. Mittelbach, E. Litchman, C.A. Klausmeier. 2011. Large-scale biodiversity patterns in freshwater phytoplankton. Ecology 92(11): 2096-2107.

Stone, H.H., G.R. Daborn. 1987. Diet of alewives, *Alosa pseudoharengus* and blueback herring, *A. aestivalis* (Pisces: Clupeidae) in Minas Basin, Nova Scotia, a turbid, macrotidal estuary. Environmental Biology of Fishes 19(1): 55-67.

Storch, D., E. Bohdalková, J. Okie. 2018. The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. Ecology letters: 21(6): 920-937.

Taher, M.M. 2010. Specialization, trophic breadth and diet overlap of thirteen small marine fish species from Shatt Al-Basrah Canal, Southern Iraq. Marsh Bulletin 5(2): 118-130.

Tampi, P.R.S. 1958. On the food of *Chanos chanos* (Forskål). Indian Journal of Fisheries 5: 107-117.

Tanaka, H., I. Aoki, S. Ohshimo. 2006. Feeding habits and gill raker morphology of three planktivorous pelagic fish species off the coast of northern and western Kyushu in summer. Journaal of Fish Biology 68: 1041-1061.

Tedesco, P.A., E. Paradis, C. Lévêque, B. Hugueny. 2017. Explaining global-scale diversification patterns in actinopterygian fishes. Journal of Biogeography 44: 773-783.

Tsikliras, A.C., M. Torre, K.I. Stergiou. 2005. Feeding habits and trophic level of round sardinella (*Sardinella aurita*) in the northeastern Mediterranean (Aegean Sea, Greece). Journal of Biological Research 3: 67-75.

Van der Lingen, C.D. 2002. Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. South African Journal of Marine Science 24(1): 301-316.

Vander Zanden, M.J., W.W. Fetzer. 2007. Global patterns of aquatic food chain length. Oikos 116: 1378-1388.

Vega-Cendejas, M.E., M. Hernandez, F. Arreguin-Sanchez. 1994. Trophic interrelations in a beach seine fishery from the northwestern coast of the Yucatan Peninsula, Mexico. Journal of Fish Biology 44: 647-659.

Venkataraman, G. 1960. Studies on the food and feeding relationships of the inshore fishes off Calicut on the Malabar coast. Indian Journal of Fisheries 7(2): 275-306.

Wailes, G.H. 1935. Food of *Clupea pallasii* in Southern British Columbia waters. Journal of the Biological Board of Canada 1(6): 477-486.

Wakabara, Y., M.N. Flynn, A.S. Tararam. 1996. Ingestion and selection of suprabenthic crustaceans by small-sized fishes in a lower saltmarsh system. Revista Brasileira de Oceanografia 44(2): 89-103.

Weinberger, C.S., J.M. Posada. 2005. Analysis on the diet of bonefish, *Albula vulpes*, in Los Roques Archipelago National Park, Venezuela. Contributions in Maine Science 37: 30-45.

Werle, E., C. Schneider, M. Renner, M. Völker, W. Fiehn. 1994. Convenient single-step, one tube purification of PCR products for direct sequencing. Nucleic Acids Research 22: 4354-4355.

Werner, E.E. 1997. Species packing and niche complementarity in three sunfishes. The American Naturalist 111: 553-578.

Whitaker, D., C. Christman. 2015. Clustsig: Significant cluster analysis. *R Package Version 1.1.* Available at https://CRAN.R-project.org/package=clustsig.

Whitehead, P.J.P., G.J. Nelson, T. Wongratana. 1988. FAO Species Catalogue, Vol. 7. Clupeoid Fishes of the World (Suborder Clupeoidei). UNDP FAP, Rome.

Wiens, J.J., M.J. Donoghue. 2004. Historical biogeography, ecology and species richness. TRENDS in Ecology and Evolution 19(12): 639-644.

Wilson, J., M. Sheaves. 2001. Short-term temporal variations in taxonomic composition and trophic structure of a tropical estuarine fish assemblage. Marine Biology 139: 787-796.

Wilson, S.K., D.R. Bellwood, J.H. Choat, M.J. Furnas. 2003. Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanography and Marine Biology: an Annual Review 41: 279-309.

Wilson, A.B., G.G. Teugels, A. Meyer. 2008. Marine incursion: the freshwater herring of Lake Tanganyika are the product of a marine invasion into West Africa. PLoS One 3(4): e1979.

Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60: 331-367.

Winemiller, K.O., S. Akin, S.C. Zeug. 2007. Production sources and food web structure of a temperate tidal estuary: integration of dietary and stable isotope data. Marine Ecology Progress Series 343: 63-76.

Winkelman, D.L., M.J. Van Den Avyle. 2002. A comparison of diets of blueback herring (*Alosa aestivalis*) and threadfin shad (*Dorosoma petenense*) in a large southeastern U.S. reservoir. Journal of Freshwater Ecology 17(2): 209-221.

Xia, X., Z. Xie, M. Salemi, L. Chen, Y. Wang. 2003. An index of substitution saturation and its application. Molecular Phylogenetics and Evolution 26(1): 1-7.

Xia, X. 2017. DAMBE6: New tools for microbial genomics, phylogenetics, and molecular evolution. Journal of Heredity 108(4): 431-437.

Yang, Z., S. Kumar, M. Nei. 1995. A new method of inference of ancestral nucleotide and amino acid sequences. Genetics 141: 1641-1650.

Yamahira, K., T. Kikuchi, S. Nojima. 1996. Age specific food utilization and spatial distribution of the puffer, *Takifugu niphobles*, over an intertidal sand flat. Environmental Biology of Fishes 45: 311-318.

Yang, K.Y., S.Y. Lee, G.A. Williams. 2003. Selective feeding by the mudskipper (*Boleophthalmus pectinirostris*) on the microalgal assemblage of a tropical mudflat. Marine Biology 143: 245-256.

Yang, Z. 2006. Computational Molecular Evolution. Oxford University Press, Oxford.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 686-693.

Zagars, M., K. Ikejima, A. Kasai, N. Arai, P. Tongnunui. 2013. Trophic characteristics of a mangrove fish community in southIst Thailand: Important mangrove contribution and intraspecies feeding variability. Estuarine, Coastal, and Shelf Science 119: 145-152.

Zhang, H., G. Wu, H. Zhang, P. Xie, J. Xu, Q. Zhou. 2013. Role of body size and temporal hydrology in the dietary shifts of shortjaw tapertail anchovy *Coilia brachygnathus* (Actinopterygii, Engraulidae) in a large floodplain lake. Hydrobiologia 703: 247-256.