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Ontogenetic and Long-Term Diet Shifts of a Generalist Juvenile Predatory Fish in an Urban Estuary Undergoing Dramatic Changes in Habitat Availability

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Abstract

Vegetated areas such as seagrass beds provide food and essential habitat for many fish and invertebrate species. In particular, many economically important fishes depend on seagrass beds as nursery grounds. In recent decades, there has been a rapid decline in seagrass coverage due to the development of coastal areas worldwide, altering these ecosystems and their community structure. Within Tampa Bay (Florida's largest estuary), seagrass coverage and water quality underwent a decline followed by a recovery over the past three decades; these changes may have altered the community structure of seagrass-associated fauna. We examined the diets of juvenile Spotted Seatrout Cynoscion nebulosus, a common estuarine predator, to assess whether documented changes in water quality and habitat were reflected in their trophodynamics. Stomach contents of Spotted Seatrout from Tampa Bay were sampled during three different studies conducted in 1981–1982, 1991–1992, and 2005–2013. We analyzed data from these studies to compare the diet across size-classes and time periods. Using canonical analysis of principal coordinates, we discerned significant differences in diet composition among size-classes and among time periods. Ontogenetic shifts in diet during all three time periods were consistent with those previously reported, highlighting the plasticity of a generalist piscivore in a recovering seagrass ecosystem. Subtle shifts in diet were detected among the three time periods, suggesting that changes in seagrass coverage contributed to altered trophodynamics in this estuarine system. Our efforts highlight the utility of using a generalist piscivore's diet as a tool for monitoring and quantifying faunal shifts in an ecosystem.

Vegetated aquatic habitats (e.g., seagrass beds) are important environments for fishes and macroinvertebrates (e.g., Beck et al. 2001; Geiger et al. 2010; Greening et al. 2011). Seagrass habitats in particular provide food and shelter and serve as nursery grounds for many economically important species (Beck et al. 2001; Matheson et al. 2010); they also stabilize sediments and play a key role in the cycling of nutrients (Johansson 2002; Greening and Janicki 2006;

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Greening et al. 2011). Because seagrasses have high light requirements, they are often restricted to water depths of 2 m or less within estuarine systems and are especially susceptible to reductions in water quality and clarity (Greening et al. 2011). Worldwide, the rapid development of coastal areas has led to the eutrophication of many marine ecosystems, ultimately generating a decline in seagrass coverage during recent decades (Lewis et al. 1999; Greening and Janicki 2006; Orth et al. 2006; Waycott et al. 2009; Greening et al. 2011; Burghart et al. 2013).

Increased loads of nitrogen and phosphorus, often from sources such as sewage and fertilizers, can cause an increase in both the number and magnitude of phytoplankton blooms, preventing light penetration to the depths required for photosynthesis by seagrasses and other benthic primary producers (McClelland and Valiela 1998; Lewis et al. 1999; Orth et al. 2006). Alterations in nutrient regimes toward a eutrophic system also allow fast-growing macroalgae to outcompete slow-growing seagrasses, which in turn can influence the faunal assemblages associated with these habitats (Duarte 1995; Duffy 2006; Greening and Janicki 2006; Craig and Bosman 2013; Stallings et al. 2015). Although nutrient input fuels the production of phytoplankton-a primary food source for zooplankton, which are important as food for animals at higher trophic levels-an excess of nutrients can result in hypoxia and can cause reductions in benthic meiofaunal biomass (Livingston 1984; Capriulo et al. 2002; Tewfik et al. 2005). The loss of macrophytes and the eventual loss of seagrass detritus alter food webs and can be detrimental to an ecosystem (McClelland and Valiela 1998; Capriulo et al. 2002; Tewfik et al. 2005). Complex food webs connect many components of these systems, often in unexpected ways, and ultimately derive energy from either benthic (i.e., seagrasses, epiphytes, microalgae, and detritus) or planktonic (i.e., phytoplankton) sources (Livingston 1984; France 1995). An understanding of the pathways on which the food web is based gives further insight into the biological balance of the ecosystem (Livingston 1984; Mason and Zengel 1996); thus, it is important for research and management to expand beyond the single-species approach (Paine 1966; Polis and Strong 1996; Arkema et al. 2006).

In Tampa Bay, the largest estuary in Florida (Lewis and Estevez 1988), seagrass coverage declined from an estimated 15,380 ha in the 1950s to approximately 8,000 ha in the early 1980s (a reduction of ~50%), largely due to increased nutrient inputs from a fast-growing human population and expanding industrial development in the region (Johansson 1991; Avery et al. 2010; Greening et al. 2011). Regulations that were designed to reduce nutrient inputs from land-based activities were implemented in the late 1970s and early 1980s. As a result, water quality and clarity improved greatly, leading to an increased expansion of seagrass coverage by the mid-1980s (Lewis et al. 1999; Johansson 2002; Greening et al. 2011). Seagrass coverage

throughout Tampa Bay in 2012 was estimated at 14,019 ha, which is almost equal to the coverage that was measured prior to rapid urbanization during the mid-20th century (Tampa Bay Estuary Program 2013), although recovery has been faster in certain regions than in others (Greening et al. 2011).

The predatory Spotted Seatrout Cynoscion nebulosus is a popular target of sport and commercial fisheries and occurs along the southeastern coastal waters of the United States from Massachusetts through the coastal Gulf of Mexico and south to Mexico's Yucatan Peninsula (Mercer 1984; Hettler 1989; Wenner and Archambault 1996). These estuarine-dependent fish are often associated with vegetated areas, such as shallow seagrass beds and saltmarsh habitats, and they spend their entire life cycle in bays and lagoons (Iverson and Tabb 1962; Peebles and Tolley 1988; Hettler 1989; Baltz et al. 1993). Spotted Seatrout are common in Tampa Bay, utilizing seagrass beds as a foraging and refuge habitat (McMichael and Peters 1989; Flaherty et al. 2009; Murphy et al. 2009; Hall-Scharf and Stallings 2014; Flaherty-Walia et al. 2015). Juvenile Spotted Seatrout in particular are more abundant in the freshwater-influenced, Halodule-dominated seagrass beds of Tampa Bay and generally occur in seagrass beds with greater than 50% overall coverage and varying salinities; however, spawning activity and environmental gradients (e.g., salinity) may also function as important drivers of distribution (McMichael and Peters 1989; Flaherty-Walia et al. 2015). Previous diet studies on Spotted Seatrout have shown that this generalist predator feeds on a wide diversity of prey species (benthic and planktonic) and-like many piscivoresundergoes ontogenetic shifts in diet (Mercer 1984; McMichael and Peters 1989; Wenner and Archambault 1996; Hall-Scharf and Stallings 2014). Therefore, the Spotted Seatrout's generalist predatory behavior makes this species a good case example for the use of diet analysis to monitor faunal shifts in an ecosystem.

Improvements in water quality and associated increases in seagrass coverage within Tampa Bay over the past 30 years may have affected the abundance and structure of faunal communities, which could be reflected in the diets of juvenile Spotted Seatrout. To address this question, we compared data from three diet studies conducted between 1981 and 2013 (i.e., a period of 32 years), and we examined whether diet composition changed over ontogeny or among time periods.

METHODS

Collection and processing of diet samples in 2005–2013.— For the present study, Spotted Seatrout were collected from 2005 to 2013 as part of monthly stratified random monitoring efforts in Tampa Bay (Figure 1); collections were obtained by using a 21.3-m seine and a 6.1-m otter trawl (for additional details, see Greenwood et al. 2006). Up to five Spotted



FIGURE 1. Map of the study area in Tampa Bay, Florida, where juvenile Spotted Seatrout were sampled for use in diet analyses.

Seatrout per haul were culled for stomach content analysis; after stomachs were removed, they were placed in a 10% solution of formalin for at least 48 h. For individuals smaller than 100 mm SL, the entire fish was placed in 10% formalin, and the peritoneal cavity was punctured to facilitate preservation. Stomachs and fish (<100 mm) were rinsed with freshwater and stored in a 50% solution of isopropanol until processing. Only stomach contents from the esophagus to the pylorus were used in the analysis. Freshwater was used to flush the contents from the gut lining and into a gridded Petri dish; the contents were identified to the lowest possible taxonomic level with the aid of dissecting and compound microscopes. Each prey type was enumerated based upon identifiable structures (e.g., eyes and chelae) and was measured volumetrically by using several methods (i.e., the graduated cylinder method, ellipsoid method, cylinder method, and squash-plate technique; McComish 1967; Hellawell and Abel 1971; Hyslop 1980). The volumetric method used was selected based on the size, condition, and composition of the sample.

Quantitative comparisons with previous diet studies.—To test for potential decadal shifts in the diets of Spotted Seatrout, data from the present study (2005–2013) were compared with data from two previous Tampa Bay studies conducted by (1) McMichael and Peters (1989), who collected juvenile Spotted Seatrout in 1981 and 1982; and (2) Peebles and Hopkins (1993), who sampled juveniles during 1991 and 1992. The collection and processing procedures used in the two studies were similar to those of the present study, but there were some minor differences in field and laboratory methods, as described below.

Collections from Peebles and Hopkins (1993) and from the present (2005-2013) study were part of the same field program, with similar gear types and monthly stratified random sampling; however, Peebles and Hopkins (1993) also included data from fixed sampling locations that were chosen to be representative of the greater Tampa Bay sampling universe. Collections by McMichael and Peters (1989) were obtained with plankton nets and bag seines at fixed sampling locations, but all three studies overlapped in space across similar habitats (i.e., shallow, vegetated and nonvegetated sites throughout Tampa Bay; salinities ranging from 0% to 35%; sampling in all seasons). Laboratory methods were largely the same across studies. Computer-based worksheets with standardized taxonomic menus that electronically calculated the volumes of prey based on prey dimensions and volumetric methods were used by Peebles and Hopkins (1993) and in the present study. Additionally, four methods were used to determine prey volumes (i.e., graduated cylinder method, cylindrical method, ellipsoid method, and squash-plate techniques) during the Peebles and Hopkins (1993) study and our study, while only the graduated cylinder and squash-plate techniques were used by McMichael and Peters (1989). Volume of prey was the reported metric in all three diet studies.

Raw, individual-specific diet data as well as site-specific data, such as location and water quality information, were unavailable from McMichael and Peters (1989) or Peebles and Hopkins (1993), so our analyses were conducted by using data pooled across locations, seasons, and sites within each study. Because we were interested in examining whether ontogenetic diet shifts occurred across the sizes of Spotted Seatrout analyzed in the three studies, the data were separated into an ordinal series of sizeclasses. McMichael and Peters (1989) summarized diet data in 15-mm increments, whereas Peebles and Hopkins (1993) summarized data in 10-mm increments. To facilitate comparability among studies, we used 15-mm increments based on the ontogenetic shifts observed by McMichael and Peters (1989) and because this maximized the overlap in size data across the three studies (Table 1). Furthermore, despite citing notable changes in the diets of juvenile Spotted Seatrout, other studies have used various size-class ranges, and many of those studies did not report

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TABLE 1. Summary of the size-class intervals (mm SL) assigned to facilitate comparisons of the Spotted Seatrout diet among studies conducted in Tampa Bay, Florida, during three separate decades: 1981–1982 (McMichael and Peters 1989); 1991–1992 (Peebles and Hopkins 1993); and 2005–2013 (present study).

Size-class	1981–1982	1991–1992	2005-2013
1	15–30	10–30	15-30
2	30–45	30-40	30–45
3	45-60	40-60	45-60
4	60-75	60-70	60-75
5	75–120	70–130	75–120

comparable prey details that could be used as a model for our breakdown of size-classes (Moody 1950; Rutherford et al. 1982; Mercer 1984; Mason and Zengel 1996; Llanso et al. 1998). This required us to combine three size-classes from the McMichael and Peters (1989) study: data from the 75–90-mm, 90–105-mm, and 105–120-mm size-classes were aggregated into 75-120 mm for size-class 5. We also combined size-classes from the Peebles and Hopkins (1993) study: data from the 10-20-mm and 20-30-mm size-classes were pooled into 10-30 mm for size-class 1; and data for 40-50 mm and 50-60 mm were aggregated into 40-60 mm for size-class 3. We then calculated weighted averages (based on the sample of nonempty stomachs) of prey volume for each size-class by using the reported summary data from McMichael and Peters (1989) and Peebles and Hopkins (1993), and we averaged the raw data from the present (2005-2013) study. Although Spotted Seatrout can reach SLs of 450 mm or greater (Iverson and Tabb 1962; Murphy et al. 2009), data for fish smaller than 8 mm or fish in the 8-15-mm size-class sampled by McMichael and Peters (1989) were excluded from the comparison due to the lack of corresponding data from Peebles and Hopkins (1993) or from our study. Likewise, data for fish larger than 120 mm sampled in our study were excluded from the comparison due to the lack of comparable data from the McMichael and Peters (1989) and Peebles and Hopkins (1993) studies. The outcome of these weighted data summaries was a matrix of percent volume for each prey taxon consumed by Spotted Seatrout of each size-class during each study period. When the taxonomic resolution of prey data differed between studies, the data were pooled to the lowest common taxonomic resolution. This involved combining all species of Mysidacea, Copepoda, Mollusca, Amphipoda, and Tanaidacea to the order, suborder, or subclass level. Decapod shrimps, decapod crabs, and fishes were mainly aggregated to the family level (Tables 2, 3). Data from 1,669 stomachs were used in our comparisons of sizeclasses and study periods: 609 stomachs from the McMichael and Peters (1989) study; 668 stomachs from

the Peebles and Hopkins (1993) study; and 392 stomachs from the present study (Table 2).

Analytical methods.-To examine diet patterns across size-classes and studies, a Bray-Curtis resemblance metric (Bray and Curtis 1957) was constructed on square-roottransformed data. We then conducted constrained ordinations by using canonical analysis of principal coordinates (CAP; Anderson and Willis 2003; Anderson et al. 2008). The CAP used a leave-one-out method (similar to jackknife permutation; Anderson and Willis 2003) to maximize differences among size-classes and among studies. The number of principal coordinate axes (m) that explained the greatest amount of original variability was chosen automatically by this method and maximized the leave-one-out allocation success with a minimal leave-one-out residual sum of squares (Anderson and Willis 2003; Anderson et al. 2008). A permutation test was run, and vectors based on Spearman's rank correlations (coefficient r_S) were superimposed to determine which prey items were responsible for observed differences in diet composition across size-classes and across studies. Anderson et al. (2008) suggested an r_S value of at least 0.2 for the superimposed vectors, but we used a more conservative value ($r_s > 0.55$) to restrict output to the primary drivers of differences in diet composition. Stacked bar graphs were created (PRIMER-E Ltd., Plymouth, UK) by using percent volume of prey for each size-class and each study period to visually display the differences in diet composition.

Generalized linear models were employed to determine whether the proportion of empty stomachs differed among studies (1) for all size-classes combined within each study and (2) for each size-class. Generalized linear models were conducted by using the binomial link function in R software (R Development Core Team 2015) followed by Tukey's pairwise comparisons performed with the R package "multcomp" (Hothorn et al. 2008).

RESULTS

The CAP indicated a significant difference in dietary composition across size-classes of Spotted Seatrout (trace statistic [tr] = 2.44, P = 0.019; 999 permutations). The optimal model, as determined by the leave-one-out reclassification method, had an *m*-value of 6, explained 95% of the variation, and resulted in a misclassification rate of 33%. Clear shifts were apparent (1) between size-classes 1 and 2 for the McMichael and Peters (1989) study and the present (2005–2013) study; (2) between size-classes 2 and 3 for the present study; (3) between size-classes 3 and 4 for the Peebles and Hopkins (1993) study and our study; and (4) between size-classes 4 and 5 for the Peebles and Hopkins (1993) study. Although the 33% misclassification rate was in the acceptable range, this rate may have been a result of

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TABLE 2. Summary of the diets consumed by juvenile Spotted Seatrout in Tampa Bay, reported as percent volume of prey (rounded to the nearest tenth) determined during three decades: 1981–1982 (80s; McMichael and Peters 1989); 1991–1992 (90s; Peebles and Hopkins 1993); and 2005–2013 (00s; present study). Common taxonomy based on combined prey taxa was used in comparisons

among predator size-classes (defin	ed in Table	1) and amon	ig studies.												
		Size-class	1	Si	ze-class 2		Siz	ze-class 3		Si	ze-class	4	Si	ze-class	5
Study	80s	90s	00s	80s	90s	00s	80s	90s	00s	80s	90s	00s	80s	90s	00s
Number of stomachs containing food	85	268	182	257	127	63	142	176	32	68	32	34	57	65	81
Number of empty stomachs	14	6	9	20	8	٢	14	б	7	Ś	4	1	8	1	4
Mollusca	0.3	I	I	0.1	I	8	0.1	I	I	I	I	I	I	I	0.1
Copepoda	9.9	6.8	20.8	0.1	I	2.0	I	I	1.0	I	I	I	Ι	I	I
Amphipoda	2.0	1.8	4.9	0.5	I	9.1	0.3	I	4.9	0.1	I	2.5	0.2	1.0	5.3
Mysidacea	38.1	26.7	35.1	17.5	9.0	24.7	9.6	6.2	22.8	1.8	Ι	7.0	1.8	1.0	6.7
Decapoda															
Alpheidae	Ι	Ι	0.2	Ι	Ι	3.0	Ι	I	Ι	Ι	I	Ι	I	2.1	1.1
Callianassoidea	I	I	а	I	I	I	I	I	I	I	I	I	I	I	I
Caridea	Ι	Ι	0.7	I	I	I	I	I	I	0.5	I	0.2	I	I	1.1
Hippolytidae	12.4	Ι	3.4	14.9		9.3	24.3	I	3.6	1.7	I	14.6	0.2	I	7.9
Palaemonidae	I	I	I	2.2	7.0	7.2	3.6	3.2	3.9	2.9	2.1	12.2	5.6	2.1	7.1
Penaeidae	I	5.5	1.3	I	1.0	Ι	I	1.5	Ι	1.8	9.5	7.0	5.0	8.2	9.1
Processidae	I	2.4	I	I	3.0	2.9	I	2.6	8.2	I	1.1	0.2	Ι	I	0.9
Sergestoidea	I	0.2	I	I	I	Ι	I	I	Ι	I	I	I	Ι	Ι	I
Upogebiidae	Ι	Ι	I	I	Ι	Ι	Ι	I	I	Ι	I	Ι	Ι	Ι	0.8
Shrimp, unidentified	12.4	15.8	0.9	27.9	15.0	2.6	19.2	24.0	11.0	14.2	3.2	7.5	51.3	15.5	5.7
Albuneidae	Ι	Ι	ab	Ι	Ι	Ι	I	I	Ι	I	I	Ι	Ι	Ι	I
Panopeidae	Ι	Ι	I	Ι	Ι	I	I	I	Í	I	Ι	Í	Ι	Ι	0.2
Pinnotheridae	Ι	I	I	I	I	Ι	I	I	I	I	I	I	Ι	I	0.1
Porcellanidae	Ι	Ι	0.1^{b}	Ι	Ι	Ι	I	I	Ι	I	I	Ι	Ι	Ι	I
Xanthidae	Ι	I	ab	I	I	Ι	I	I	I	I	I	I	Ι	I	I
Crab, unidentified	$0.4^{\rm b}$	I	0.5^{b}	I	I	Ι	0.4	I	0.4	I	I	I	Ι	I	I
Decapod, unidentified	2.6	Ι	0.2	0.6	Ι	2.1	2.6	Ι	Ι	0.3	Ι	5	0.3	Ι	Ι
Osteichthyes Atherinopsidae	I	I	I	a	I	I	I	I	3.6	I	I	I	I	I	2.6

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TABLE 2. Continued.															
		Size-class	1	Si	ze-class 2		Siz	e-class 3		Si	ze-class	4	Si	ze-class	5
Study	80s	90s	00s	80s	90s	00s	80s	90s	00s	80s	90s	00s	80s	90s	00s
Clupeidae	I	I	I	I	I	1.6	I	I	I	I	I	Ι	Ι	I	1.1
Cyprinodontiformes	Ι	I	1.6	Ι	Ι	3.3	19.7	Ι	3.6	Ι	Ι	Ι	I	9.3	3.9
Engraulidae	I	12.8	3.8	I	5.0	4.0	I	11.5	7.1	I	20.0	16.0	4.4	14.4	8.9
Gerreidae	I	Ι	0.6	I	I	Ι	0.4	I	3.6	I	Ι	I	I	7.2	2.4
Gobiidae	I	5.5	1.3	I	28.0	6.7	I	4.1	4.3	9.0	8.4	6.2	I	5.2	6.6
Sciaenidae	I	I	0.6	0.3	2.0	I	I	2.1	I	I	17.9	1.3	I	10.3	3.5
Syngnathidae	Ι	I	1.1	I	1.0	I	I	I	I	I	I	I	I	I	0.3
Fish, unidentified	24.1	20.4	19.0	35.8	28.0	17.2	22.7	42.3	17.6	67.7	37.9	25.5	31.3	22.7	23.9
Miscellaneous															
Arthropoda	I	I	1.3	I	I	I	I	I	1.8	I	I	I	I	I	0.1
Crustacea, unidentified	I	1.0	0.1	I	1.0	4.0	I	2.6	Ι	Ι	Ι	I	I	Ι	a
Cumacea	I	Ι	Ι	I	I	Ι	I	I	Ι	I	Ι	a	I	Ι	I
Eggs	0.5	I	I	Ι	Ι	Ι	I	Ι	2.8	I	Ι	I	I	Ι	I
Isopoda	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	I	I	I	0.7
Ostracoda	I	Ι	a	a a	I	5	I	I	a	I	Ι	a	I	Ι	I
Tanaidacea	0.5	1.6	0.1	0.1	Ι	0.1	в	Ι	Ι	0.1	Ι	Ι	8	1.0	8
Annelida	I	I	2.1	I	I	I	I	I	I	I	I	I	I	I	a

^aDenotes that a prey volume was measured, but the rounded value was below the minimum for presentation in the table.

^bDenotes the zoea or megalopa stage of development.

placing divisions between size-classes at points where a natural break may not have existed. The CAP reclassified size-class 3 from the Peebles and Hopkins (1993) study to size-class 2; size-classes 3 and 4 from McMichael and Peters (1989) to size-class 5; size-class 5 from McMichael and Peters (1989) to size-class 4; and size-class 5 from the present study to size-class 4. Axis 1 distinguished size-class 1 from size-classes 2-5 (Appendix Table A.1; Figure 2). Correlation vectors ($r_S > 0.55$) indicated that copepods, mysids, tanaids, crabs, ghost shrimps, and annelids were all of greater dietary importance for size-class 1 than for larger Spotted Seatrout (Figure 2). Copepods were observed only in the stomach contents of size-class 1 across all three studies (Figure 3). Axis 2 distinguished size-classes 2 and 3 from size-classes 4 and 5. The separation along axis 2 appeared to have been driven by high abundances of processid shrimps observed in the diets for size-classes 2 and 3 versus the high abundances of fish and palaemonid shrimps in the diets for size-classes 4 and 5. The percent volume of mysids in the diet was high for smaller size-classes and decreased progressively for larger size-classes. In addition, the percent volume of fishes (Figure 4) and shrimps (Figure 5) increased progressively in larger size-classes (Figure 3).

The CAP indicated that there was a significant difference in diet composition among the three studies (tr = 1.67, P =0.001; 999 permutations). An m-value of 5 was determined by using the leave-one-out method, explaining 90% of the total variation and resulting in a 13% misclassification rate. Size-class 5 from Peebles and Hopkins (1993) was reclassified to our 2005-2013 diet data set; size-class 4 from our study was reclassified to the Peebles and Hopkins (1993) data set. Axis 1 distinguished the McMichael and Peters (1989) data from the Peebles and Hopkins (1993) data and our data (Appendix Table A.2; Figure 6). Unidentifiable fish, unidentifiable shrimp, mollusks, and hippolytid shrimps in the diet drove the separation between the McMichael and Peters (1989) data set and the Peebles and Hopkins (1993) and present data sets (Figure 6). Axis 2 distinguished the Peebles and Hopkins (1993) data from our data. This separation was attributable to greater relative abundances of engraulid fishes, sciaenid fishes, and processid shrimps in the Peebles and Hopkins (1993) diet data and the greater abundances of clupeid fishes, amphipods, atherinopsid fishes, hippolytid shrimps, and mollusks in the present data. Percent volume of unidentifiable fish and unidentifiable shrimp decreased between 1981-1982 and 2005-2013 (Figure 3). Overall, the McMichael and Peters (1989) data indicated a higher percent volume of shrimp (identifiable and unidentifiable combined) in the diets of Spotted Seatrout, and the Peebles and Hopkins (1993) data indicated that more fish (identifiable and unidentifiable combined) were present in the diets. Copepods and amphipods were both more abundant and ubiquitous across Spotted Seatrout size-classes in our data than in the McMichael and Peters (1989) or Peebles and Hopkins (1993) data; during 1981– 1982 and 1991–1992, these groups were observed only in the diets of the smallest size-classes (Figure 3).

There were proportionately more empty stomachs among fish sampled during the McMichael and Peters (1989) study (proportion empty = 0.096) compared with the Peebles and Hopkins (1993) study (proportion empty = 0.039; z = 3.89, P < 0.001) and the present study (proportion empty = 0.055; z = 2.35, P = 0.049). The proportion of empty stomachs did not differ between the 1991-1992 and 2005-2013 data sets (z = 1.21, P = 0.447). These interdecadal patterns were largely driven by a higher proportion of empty stomachs in 1981-1982 for the smallest size-class (1981-1982 versus 1991–1992: z = 3.01, P = 0.007; 1981–1982 versus 2005– 2013: z = 2.62, P = 0.024) and the largest size-class (1981– 1982 versus 1991–1992: z = 2.91, P = 0.010; 1981–1982 versus 2005–2013: z = 3.20, P = 0.004). A greater proportion of empty stomachs was observed for size-class 3 in 1981–1982 compared with 1991–1992 (z = 2.72, P =(0.017), but none of the other comparisons for the intermediate size-classes indicated significant differences.

DISCUSSION

Using data from three studies, we were able to describe patterns and changes in the diets for juvenile Spotted Seatrout at two temporal scales: (1) ontogenetic shifts within each



FIGURE 2. Canonical analysis of principal coordinates (CAP), illustrating diet composition for juvenile Spotted Seatrout belonging to each size-class (defined in Table 1). Symbol shading denotes the study period for each Tampa Bay study (black = 1981–1982 [McMichael and Peters 1989]; gray = 1991–1992 [Peebles and Hopkins 1993]; open = 2005–2013 [present study]). Superimposed vectors indicate the prey taxa that contributed to observed differences in diet composition.

TABLE 3. Expanded taxonomic resolution of diets consumed by juvenile Spotted Seatrout in Tampa Bay, as reported in summary tables from three studies conducted in different decades: 1981–1982 (McMichael and Peters 1989); 1991–1992 (Peebles and Hopkins 1993); and 2005–2013 (present study). The "X" denotes each study in which the given prey type was identified. Other pooled categories that are not shown in the table include Ostracoda, Cumacea, and Isopoda; these categories were rare and had no further resolution across studies.

Prey group	1981–1982	1991–1992	2005–2013	Bowmaniella di Bowmaniella fi
Mollusca ^a			Х	Taphromysis bo
Bivalves	Х		Х	Taphromysis sp
Gastropods	Х			Decapoda (shrii
Copepoda ^a	Х	Х	Х	Alpheus norma
Acartia bermudensis	Х			Alpheus spp.
Acartia spp.	Х		Х	Ambidexter sym
Calanoids	Х	Х	Х	Caridea
Harpacticoids	Х		Х	Farfantepenaeu
Harpacticus obscurus	Х			duorarum
Oithonidae			Х	Farfantepenaeu
Oithona spp.	Х			Hippolyte zoste
Pseudodiaptomus	Х		Х	Hippolyte spp.
coronatus				Leander tenuico
Pseudodiaptomus spp.			Х	Leptalpheus for
Temora turbinata	Х			Lucifer faxoni
Amphipoda ^a		Х		Palaemon florid
Americorophium spp.			Х	Palaemonetes p
Ampeliscidae			Х	Palaemonetes
Ampelisca abdita			Х	vulgaris
Ampelisca holmesi			Х	Palaemonetes s
Ampelisca vadorum	Х		Х	Penaeus spp.
Ampelisca verrilli			Х	Periclimenes
Ampelisca spp.			Х	americanus
Ampithoidae			Х	Periclimenes sp
Ampithoe spp.			Х	Processa spp.
Apocorophium			Х	Rimapenaeus s
louisianum				Tozeuma caroli
Aoridae			Х	Decapoda (crab
Cerapus spp.			Х	Albuneidae
Corophiidae			Х	Panopeidae
Corophium spp.	Х			Pinnotheridae
Cymadusa compta			Х	Porcellanidae
Cymadusa spp.			Х	Portunidae
Erichthonius punctatus			Х	Xanthidae
(E. brasiliensis)				Crab zoeae
Eusiridae			Х	Crab megalopa
Gammaridae		Х	Х	Actinopterygii ^b
Gammarus mucronatus			Х	Striped Anchov
Gammarus spp.			Х	Anchoa heps
Grandidierella bonnieroides			Х	Bay Anchovy A mitchilli
Hartmanodes nvei			Х	Anchovies Anci
Ischyroceridae			Х	Silver Perch Ba
Monocorophium spp.			x	chrvsoura
Oedicerotidae			Х	Sand Seatrout
Rudilemboides naglei			X	Cynoscion ar

Prey group	1981–1982	1991–1992	2005-2013
Mysidacea ^a		Х	
Americamysis almyra	Х		Х
Americamysis bahia			Х
Americamysis stucki			Х
Bowmaniella dissimilis			Х
Bowmaniella floridana			Х
Taphromysis bowmani			Х
Taphromysis spp.	Х		Х
Decapoda (shrimps) ^b	Х	Х	Х
Alpheus normanni			Х
Alpheus spp.			Х
Ambidexter symmetricus			Х
Caridea	Х		Х
Farfantepenaeus			Х
duorarum			
Farfantepenaeus sp.			Х
Hippolyte zostericola	Х		Х
Hippolyte spp.			X
Leander tenuicornis			x
Lentalnheus forcens			x
Lucifer faxoni		x	
Palaemon floridanus		21	x
Palaemonetes nugio	x		x
Palaemonetes	21		X
vulgaris			Λ
Palaemonetes spp.	Х		Х
Penaeus spp.	Х		Х
Periclimenes			Х
americanus			
Periclimenes spp.			Х
Processa spp.			Х
<i>Rimapenaeus</i> spp.			Х
Tozeuma carolinense	Х		Х
Decapoda (crabs) ^b			Х
Albuneidae			Х
Panopeidae			Х
Pinnotheridae			Х
Porcellanidae			Х
Portunidae			Х
Xanthidae			X
Crab zoeae	х		x
Crab megalonae	X		x
Actinontervaii ^b	X	x	x
Strined Anchowy	21	X	24
Anchoa hensetus		21	
Bay Anchowy Anchoa	v	v	v
mitchilli	Λ	Λ	Λ
Anchovies Anchos and		\mathbf{v}	\mathbf{v}
Silver Derch Dairdiella	\mathbf{v}	Λ V	Λ V
shiver reich Dalralella	Λ	Λ	Λ
Chrysouru Sand Saatraut		\mathbf{v}	
		Λ	
Cynoscion arenarius			

TABLE 3. Continued.

Prey group	1981–1982	1991–1992	2005-2013
Spotted Seatrout		Х	
Cynoscion nebulosus			
Seatrout and corvinas		Х	Х
Cynoscion spp.			
Mojarras	Х		Х
Eucinostomus spp.			
Striped Mojarra			Х
Eugerres plumieri			
Striped Killifish		Х	
Fundulus majalis			
Longnose Killifish	Х		
Fundulus similis			
Killifishes		Х	
Fundulus spp.			
Goldspotted Killifish			Х
Floridichthys carpio			
Gobiidae		Х	
Naked Goby		X	
Gobiosoma bosc			
Code Goby Gobiosoma	х	х	х
robustum		21	
Gobiosoma spp		x	x
Rainwater Killifish		21	x
Lucania parva			21
Killifishes <i>Lucania</i> spn			x
Silversides <i>Menidia</i> spp.	x		X
Kingfishes	24		X
Monticirrhus spn			Λ
Clown Goby	v	v	v
Microgobius gulosus	Λ	Λ	Λ
Green Goby			v
Microgobius			Λ
thalagginug			
Gobies		v	v
Microgobius spp		Λ	Λ
Sordinos Saudinalla ann			v
Dualas Dirafah			
Summer athus flowid as			А
Cult Directed			v
Guil Pipensn			А
Syngnathus scovelli		V	
Pipensnes		А	
<i>Syngnathus</i> spp.	V	V	
lanaldacea"	X	Х	37
Hargeria rapax	Х		X
Kalliapseudes spp.			X
Leptochelia longimana			X
Tanaidomorpha			Х

^aDue to differences in taxonomic resolution among studies, some taxa were combined into larger categories for analysis.

^bCombined to the family level for analysis.

study and (2) decadal shifts across studies. Spotted Seatrout that were collected during three decades exhibited relatively consistent ontogenetic diet shifts among common and abundant prey types (mysids, decapod shrimps, and bony fishes), whereas they displayed more subtle differences in the importance of less-common prey among study periods (1981–1982, 1991–1992, and 2005–2013). Differences in diet composition among the three time periods are likely attributable, at least in part, to significant differences in the areal extent of seagrass coverage. Alterations in seagrass quantity and distribution varied among the different regions of the Tampa Bay estuary, but the direct effects of seagrass quantity and distribution on diet composition could not be rigorously quantified because data from McMichael and Peters (1989) and Peebles and Hopkins (1993) were aggregated across the entire estuary.

Diet composition for juvenile Spotted Seatrout consistently differed among size-classes across all three decades and generally corroborated the results of previous work (Mercer 1984; Johnson and Seaman 1986; Hettler 1989; Mason and Zengel 1996; Llanso et al. 1998). Generalist piscivores like the Spotted Seatrout commonly undergo ontogenetic shifts in diet (Mittelbach and Persson 1998; Scharf et al. 2000; Juanes et al. 2002), which help to optimize energetic return (Pyke et al. 1977). In general, the youngest Spotted Seatrout consume small zooplankton (primarily copepods); over ontogeny, Spotted Seatrout display a shift in diet to larger benthic invertebrates and fish (Mercer 1984; Johnson and Seaman 1986; Hettler 1989; Mason and Zengel 1996; Llanso et al. 1998), ultimately availing themselves of a drastic increase in energy to grow quickly while protecting themselves from being preyed upon by many piscivorous fishes (Sogard 1997; Post and Parkinson 2001; Waggy et al. 2007). Given the importance of rapid growth, especially for the smallest juvenile fish (Sogard 1997; Stallings et al. 2010), the significantly higher proportion of empty stomachs during the McMichael and Peters (1989) study, which possibly reflected reduced prey availability in 1981-1982 relative to later years, may have resulted in slower growth and higher mortality among juvenile Spotted Seatrout.

Mysids and copepods were found in all diet samples from the smallest size-class in all three study periods, but they varied in importance through time. Mysids were prominent in the diets of 15–30-mm SL juveniles during 1981–1982 (McMichael and Peters 1989), whereas they were present throughout the full size range examined (15–120 mm SL) in our (2005–2013) study. Mysids are often used as indicator species of environmental contamination due to their high sensitivity to sewage and inorganic discharge, and the presence of mysids in the diets of larger Spotted Seatrout size-classes during our study may reflect improved water quality (Lussier et al. 1999). Small Spotted Seatrout (15–30 mm SL) also consumed significantly more copepods than did other size-classes, and the overall volume



FIGURE 3. Stacked bar graphs of taxa (pooled across finer levels of taxonomic resolution) used in the comparison of percent volume for prey types consumed by each size-class (defined in Table 1) of juvenile Spotted Seatrout in Tampa Bay during three study periods: 1981–1982 (McMichael and Peters 1989); 1991–1992 (Peebles and Hopkins 1993); and 2005–2013 (present study). Families of shrimp, crabs, and fishes were combined into the larger categories of decapod shrimps, decapod crabs, and Osteichthyes, respectively.



FIGURE 4. Stacked bar graphs displaying the percent volume of fish prey consumed by each size-class (defined in Table 1) of juvenile Spotted Seatrout in Tampa Bay during the three study periods (defined in Figure 3). These graphs depict a subset of Figure 3 data for visual purposes and do not represent all of the prey types that were consumed by each size-class.



FIGURE 5. Stacked bar graphs displaying the percent volume of shrimp prey consumed by each size-class (defined in Table 1) of juvenile Spotted Seatrout in Tampa Bay during the three study periods (defined in Figure 3). These graphs depict a subset of Figure 3 data for visual purposes and do not represent all of the prey types that were consumed by each size-class.



FIGURE 6. Canonical analysis of principal coordinates (CAP), illustrating diet composition for juvenile Spotted Seatrout sampled during three Tampa Bay studies. Symbol shading denotes the study period (black = 1981–1982 [McMichael and Peters 1989]; gray = 1991–1992 [Peebles and Hopkins 1993]; open = 2005–2013 [present study]). Size-classes are defined in Table 1. Superimposed vectors indicate the prey taxa that contributed to observed differences in diet composition.

of copepods in the diet for this size-class was more prominent during our study period. Copepod communities vary, in part, as a function of nutrient loads (Gannon and Stemberger 1978; Livingston 1984), so some of the observed differences in the overall volume of copepods among the three studies could be explained by differences in water quality (Johansson 1991). During the late 1970s and early 1980s, Tampa Bay was described as being grossly polluted, experiencing eutrophication, and having lost over 50% of its seagrass coverage (only 8,800 ha remained in 1981–1982, when the study by McMichael and Peters 1989 took place; Johansson 1991; Greening and Janicki 2006). In addition, concentrations of ammonia (which fuels macroalgae and phytoplankton blooms) relative to inorganic nutrient concentrations were higher in Tampa Bay than in other estuarine and coastal areas around the world (Fanning and Bell 1985). Only after wastewater treatment facilities were improved and human-influenced nitrogen loading was reduced did water quality and subsequently seagrass coverage improve in the estuary (Johansson 1991; Johansson and Lewis 1992). Indeed, seagrass coverage in Tampa Bay had expanded to 12,000 ha by 2008 (Tampa Bay Estuary Program 2013).

Overall, amphipods represented a larger percent volume of stomach contents for juvenile Spotted Seatrout in 2005– 2013 than in previous years, especially for the 30–130-mm fish. The observed amphipods were predominantly epibenthic or endobenthic species that are known to be strongly associated with seagrass systems and clear water (Zimmerman et al. 1979; Pardal et al. 2000; Burghart et al. 2013). Although macroalgae may be beneficial to many amphipod species, the prevalence of amphipods is generally reduced in highly eutrophic systems (Pardal et al. 2000). Amphipods can also often serve as bioindicators because (1) they are sparse in muddy habitats and (2) many species are sensitive to sediment contaminants and low dissolved oxygen levels (Bellan-Santini 1980; Thomas 1993). Few amphipod species were observed by McMichael and Peters (1989), and only gammarideans were found by Peebles and Hopkins (1993). The greater diversity and overall volume of amphipods we observed in the 2005-2013 diet study may be partly attributable to the aforementioned improvements in water quality and seagrass coverage within Tampa Bay. Amphipod species such as Erichthonius punctatus (E. brasiliensis) and Cymadusa compta, which are sensitive to contaminants and low dissolved oxygen (Grabe et al. 2006), were present during our study; therefore, these species may reflect improvements in water quality and clarity (Johansson 1991; Greening and Janicki 2006). Before LeCroy's (2000) relatively comprehensive dichotomous key was published, the identification of amphipods was difficult; this may have influenced amphipod identification and thus measures of amphipod diversity, but the overall volumetric composition would not have been affected.

Peebles and Hopkins (1993) did not observe shrimps from the family Hippolytidae in the diets of Spotted Seatrout. Species from this family, such as the arrow shrimp Tozeuma carolinense, are commonly found in seagrass beds (Main 1987; Bauer 1989; Zupo and Nelson 1999), so their absence from the Peebles and Hopkins (1993) study was somewhat unexpected. Similar findings were noted by Mason and Zengel (1996) when they compared their analysis with that of Moody (1950), who documented the presence of hippolytid shrimps in the Spotted Seatrout diet. However, despite the lack of hippolytid shrimps in their diet analysis of Spotted Seatrout, Mason and Zengel (1996) detected hippolytid species in their invertebrate collections from seagrass beds. In addition, shrimps Tozeuma spp. have been noted to be underrepresented in diet studies due to their size and predator avoidance behavior (Main 1987). Furthermore, the absence of hippolytid shrimps in the 1991-1992 diet composition (Peebles and Hopkins 1993) may not be due to the absence of hippolytid shrimps in Tampa Bay. Predatory fish are exposed to a range of potential prey with varying levels of mobility, and they use a range of feeding tactics in capturing prey (Wenner and Archambault 1996; Scharf et al. 2000; Juanes et al. 2002; Hall-Scharf and Stallings 2014). Potential prey may not be selected by a predator, and the presence of a prey item in a predator's stomach does not necessarily indicate that the diet item is the predator's preferred prey type (Hall-Scharf and Stallings 2014). Nevertheless, observing what a predator consumes

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and its preference for any prey type can be informative as to how that predator interacts with and uses its habitat.

McMichael and Peters (1989) reported a higher prevalence of unidentifiable fish and shrimp than did Peebles and Hopkins (1993) and the present (2005-2013) study. Fish can be difficult to identify in dietary analysis because they lack many of the relatively indigestible and readily identifiable external structures that are often diagnostic for invertebrate species (e.g., the chelae of a crab or the carapace of a shrimp). Skeletal components of fish are resistant to digestion and have the potential to be diagnostically valuable, but there are relatively few morphological descriptions of bones for fishes in the greater tropical western Atlantic region, including Tampa Bay (Traynor et al. 2010). An increase in the number of observed fish families for 2005-2013 relative to the previous study periods could have been an artifact of better taxonomic indexing, especially due to improvements in the use of jawbones as a means of identification (Gabriel Ramos-Tafur, Florida Fish and Wildlife Conservation Commission [FWC], Fish and Wildlife Research Institute [FWRI], unpublished data). Such higher taxonomic resolution can be valuable when determining the effects of habitat degradation and pollution on the diet. For instance, fish (e.g., anchovies Anchoa spp. and mojarras Eucinostomus spp.) that fed primarily on plankton and polychaetes were observed to be dominant in the polluted Fenholloway River system, Florida (Livingston 1984); in contrast, fish species that were benthic omnivores and carnivores dominated the nearby and relatively pristine Econfina River system (Livingston 1984). Because the Tampa Bay estuary has undergone habitat degradation and pollution comparable to the degradation levels in the Fenholloway River system, a higher taxonomic resolution of fishes in our study would have been valuable for providing further insight. Therefore, more effort should be invested to improve fish identification through methods such as genetic analyses and morphological descriptions of bones.

Teasing out the mechanisms that drove differences in the diets of juvenile Spotted Seatrout across size-classes and studies was complicated due to environmental factors, a lack of specific site data, and limitations in taxonomic resolution (Hooks et al. 1976; Livingston 1984; Gratwicke and Speight 2005; Flaherty-Walia et al. 2015). Nevertheless, these results suggest explanatory hypotheses that can be tested. Spotted Seatrout in Tampa Bay spawn from April to October; thus, various size-classes are present throughout all seasons (McMichael and Peters 1989). In all three studies, Spotted Seatrout were collected throughout the year (i.e., during all seasons), so seasonal differences in sampling likely had minimal effects on our results.

Seagrass beds contain a higher species richness and higher abundances of both prey and predators than other habitats, such as mangrove forests and unvegetated areas (Heck and Westone 1977; Bloomfield and Gillanders 2005; Gratwicke and Speight 2005). Therefore, the loss or expansion of these habitats could affect many organisms (Hooks et. al. 1976; Livingston 1984; Bell et al. 1988; Mason and Zengel 1996). High nutrient inputs and poor water quality can cause phytoplankton blooms, fuel macroalgal growth, and alter food webs and the abundance of benthic organisms (Hooks et al. 1976; Livingston 1984; Switzer et al. 2011; Burghart et al. 2013). Although macroalgae can provide structural habitat for many organisms, it is not equivalent to and should not be deemed a replacement for seagrass (Sogard and Able 1991; Switzer et al. 2011). Such alterations in habitat, abundance, and species richness due to pollution and anthropogenic influences may not be immediately apparent; therefore, long-term monitoring is essential (Switzer et al. 2011; Flaherty et al. 2013). Invertebrates, such as mysids and amphipods, are key components of the diet for juvenile Spotted Seatrout; although the occurrence of these species in a predator's diet can exhibit seasonal shifts, the diversity of mysids and amphipods in an ecosystem is considered a measure of biological balance (Mercer 1984; Hettler 1989; Mason and Zengel 1996). The Spotted Seatrout, like other predatory fishes, is considered a good indicator species representing the overall health of an estuary because it is a generalist predator that relies on an estuary at all life stages (McMichael and Peters 1989; Wenner and Archambault 1996; Bortone 2002; Hall-Scharf and Stallings 2014). The evaluation of predator diets may therefore provide further insight on the health of a system.

The ability of the Spotted Seatrout to adapt to a changing prey community may have contributed to this generalist predator's ability to persist during periods of environmental degradation. Although we were limited in our analysis and interpretations due to the lack of raw diet data, water quality measurements, and taxonomic detail, this study helps to further the understanding of a recovering seagrass system and the interaction among organisms residing within it (Lewis et al. 1999; Johansson 2002; Greening and Janicki 2006). Fish diet studies can provide data that are useful in tracking the health of ecological systems (Hanson and Chouinard 2002; Cook and Bundy 2012). In the case of juvenile Spotted Seatrout within Tampa Bay, the data are still inadequate to permit the conclusion that environmental changes have directly caused changes in feeding habits. This is largely due to the general lack of multiyear diet monitoring and the low level of taxonomic resolution that has been traditionally accepted by fisheries biologists.

Long-term monitoring has proven beneficial in the assessment of commercially and recreationally important species and marine preserves (Blossey 1999; Shears et al. 2006; Magurran et al. 2010; Matheson et al. 2010). In addition, most benthic invertebrates have population turnover rates that are faster than the rate at which ecosystems tend to change, possibly making these taxa good indicators of an ecosystem's health (Livingston 1984; Lussier et al. 1999; Pardal et al. 2000; Hodkinson and Jackson 2005; Grabe et al. 2006). Thus, the long-term monitoring of benthic invertebrates should be considered as well. To gather applicable data on fish feeding habits, studies should be designed with multiyear sampling and high taxonomic resolution so that the results can be correlated to environmental factors, such as anthropogenic perturbation and global warming.

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Appendix: Correlation Results from Canonical Analysis of Principal Coordinates

TABLE A.1. Correlation coefficients for the canonical axes that were used to compare diet composition among Spotted Seatrout size-classes (defined in Table 1). Fish were sampled during three study periods: 1981–1982 (McMichael and Peters 1989); 1991–1992 (Peebles and Hopkins 1993); and 2005–2013 (present study). Output is provided for only four of the axes.

Study period	Axis 1	Axis 2	Axis 3	Axis 4
		Size-class 1		
1981-1982	-0.4661	0.1453	-0.0560	0.0112
1991–1992	-0.4090	0.1634	0.0746	0.0045
2005–2013	-0.5207	-0.0091	0.1353	-0.0165
		Size-class 2		
1981-1982	0.0274	0.0521	-0.1957	-0.0094
1991–1992	0.2146	0.1741	-0.2255	-0.0311
2005–2013	0.0566	0.2377	-0.2992	0.0533
		Size-class 3		
1981-1982	0.3386	0.2013	0.2069	0.0027
1991–1992	0.1774	0.1069	-0.1100	-0.0250
2005-2013	0.1507	0.4214	0.1564	0.0074
		Size-class 4		
1981-1982	0.0388	-0.2472	-0.1385	-0.0617
1991–1992	0.0016	-0.4992	-0.0685	0.0088
2005–2013	-0.0065	-0.3161	-0.1701	0.0426
		Size-class 5		
1981-1982	0.0754	-0.0751	0.1221	-0.0462
1991–1992	0.1113	-0.1578	0.5341	0.0161
2005–2013	0.2100	-0.1978	0.0342	0.0435

TABLE A.2. Correlation coefficients for the canonical axes that were used to compare the diet composition of Spotted Seatrout among three study periods: 1981–1982 (McMichael and Peters 1989); 1991–1992 (Peebles and Hopkins 1993); and 2005–2013 (present study). Size-classes are defined in Table 1. Output is provided for only two of the axes.

Size-class	Axis 1	Axis 2
	1981–1982	
1	-0.3172	0.1162
2	-0.4260	0.0626
3	-0.3793	0.1358
4	-0.2910	-0.0112
5	-0.2844	-0.2836
	1991–1992	
1	0.1894	-0.3283
2	0.1645	-0.1544
3	0.0867	-0.2967
4	0.2403	-0.1968
5	0.1465	-0.2083
	2005–2013	
1	0.1300	0.3190
2	0.2413	0.3020
3	0.2309	0.1064
4	0.0237	0.1069
5	0.2447	0.3302

APPENDIX REFERENCES

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