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Diet composition, feeding strategy, and diet overlap of 3 sciaenids along the southeastern United States

C. Michelle Willis (contact author)
Jonathan Richardson
Tracey Smart
Joseph Cowan
Patrick Biondo

Email address for contact author: willisc@dnr.sc.gov

Southeast Area Monitoring and Assessment Program–South Atlantic
Marine Resources Research Institute
South Carolina Department of Natural Resources
217 Fort Johnson Road
Charleston, South Carolina 29412

Abstract—From 2008 through 2010, the diets of 3 sciaenid species, the weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*), were examined. Stomach contents were identified, enumerated, and weighed to determine the diet composition and feeding strategy of each species and diet overlap among species. Bony fishes were the most frequently consumed prey of weakfish. Decapods, nondecapod crustaceans, and polychaetes were the most commonly consumed prey of southern kingfish and Atlantic croaker. Some individuals of all species consumed specific prey types and others consumed varying prey types; however, specialization was a more common trait for weakfish than for the other 2 species. Weakfish diets had minimal overlap with diets of the other 2 species; however, the Morisita-Horn index indicated considerable overlap between southern kingfish and Atlantic croaker. Potential for competition could occur between these 2 species, but, because both are often opportunistic feeders, it is unlikely that competition would occur unless shared resources become scarce. Descriptions of feeding strategies, prey resources, and the potential for competition among co-occurring species can provide a framework for management of these species, particularly for ecosystem-based management.

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Ecosystem-based fisheries management is dependent on defining not only target species but the species and habitats with which they interact. Ecosystem-based management models ideally would account for the complexities of ecosystems, allowing managers to incorporate ecosystem relationships in management strategies and decisions (Brodziak and Link, 2002). The Magnuson-Stevens Fishery and Conservation Reauthorization Act of 2006 (Magnuson-Stevens…Act, 2007) highlighted the need for research detailing interdependence among fisheries; trophic relationships can play a key role in understanding ecosystem composition, status, and energy linkages within the system (Link, 2002; Magnuson-Stevens…Act, 2007; Ainsworth et al., 2008). As a result, the South Atlantic Fishery Management Council (SAFMC) has prioritized efforts to characterize fish diets, define relationships between predator and prey, and to better understand how these relationships affect economically important species (SAFMC[1]). Therefore, the South Atlantic component of the Southeast Area Monitoring and Assessment Program (SEAMAP-SA), as part of its Coastal Survey (a long-term, fishery-independent, shallow-water trawl survey from Cape Canaveral, Florida, to Cape Hatteras, North Carolina), began collecting stomachs from 3 common species of Sciaenidae: weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*).

Weakfish, southern kingfish, and Atlantic croaker commonly occur along the eastern coast of the United States, residing in shallow waters over bottoms of sand or sandy mud. Distributions of these species greatly overlap, sharing a geographic range from Cape Cod, Massachusetts, to Florida and into the Gulf of Mexico (only occasionally in the Gulf of Mexico in the case of weakfish) (Goode,

[1] SAFMC (South Atlantic Fishery Management Council). 2009. Fishery Ecosystem Plan of the South Atlantic Region. Volume V: South Atlantic research programs and data needs, 177 p. South Atlantic Fishery Management Council, North Charleston, SC. [Available at website.]

1884; Chao, 2002). In the southeastern United States, these species have a similar life history; they grow rapidly and are capable of spawning as early as 1 year of age (Walton, 1996).

Weakfish generally spawn from March through July in estuarine and nearshore waters, and juveniles use the estuary as nursery grounds. From 2008 through 2010, weakfish with an average age <1 year old and a mean of 21 cm in total length (TL) were captured in SEAMAP-SA trawl surveys, but this species reportedly lives to 8 years and can reach a length of 90 cm TL (Shepherd and Grimes, 1983; Chao, 2002). Adult weakfish migrate seasonally between nearshore and offshore waters, and forage throughout the water column.

Southern kingfish are bottom foragers that spawn on the continental shelf from April through August, live up to 6 years, and can grow to lengths of 60 cm TL (Bearden, 1963; Smith and Wenner, 1985; Chao, 2002). For southern kingfish captured by SEAMAP-SA from 2008 to 2010, the average age was 1 year and the average size was 18 cm TL. Atlantic croaker are shelf-spawners during October–January and can reach an age of 15 years and length of 46 cm TL (Hales and Reitz, 1992; Barbieri et al., 1994; Richardson and Boylan[2]). From 2008 to 2010, the mean age and length for specimens of Atlantic croaker collected by SEAMAP-SA were 1 year and 22 cm TL, respectively. Atlantic croaker are demersal and use their inferior-located mouth to suck prey from the substrate (Overstreet and Heard, 1978). Juveniles of both southern kingfish and Atlantic croaker use estuaries as nurseries, a characteristic similar to weakfish (Musick and Wiley, 1972; Harding and Chittenden, 1987).

Although the life history of these 3 species has been studied extensively, quantitative diet information from the southeastern United States is either lacking or was collected 2 or more decades ago. The potential for diet overlap among sciaenids with similar feeding strategies has not been addressed in this region to date. Merriner (1975) examined the diet of weakfish captured in North Carolina waters and found that penaeid and mysid shrimps, anchovies, and clupeid fishes were the most common food items. He noted a gradual ontogenetic shift from shrimp to clupeids, specifically the Atlantic thread herring (*Opisthonema oglinum*), beginning when weakfish were about 19 cm standard length (SL) and 1 year of age. McMichael and Ross (1987) analyzed the diets of southern kingfish, northern kingfish (*Menticirrhus saxatilis*), and gulf kingfish (*M. littoralis*) in the Gulf of Mexico and found that southern kingfish most frequently consume bivalve siphons and cumaceans, followed by mysids, polychaetes, brachyurans, and gammarid amphipods. Although frequency of prey items seemed to be dependent on season, prey item composition was not found to be significantly different among species within a season in that study. A diet study of species of *Menticirrhus*, conducted near the Patos Lagoon in Brazil, has shown both low species diversity and seasonal differences in prey consumption, with polychaetes, amphipods, and various crustaceans being consumed most frequently (Rodrigues and Vieira, 2010). Overstreet and Heard (1978) studied Atlantic croaker diets in the Gulf of Mexico and found a high diversity of prey items, including polychaetes, mysids, blue crabs, amphipods, and penaeids, among other prey items.

Each of these fish species is important both commercially and recreationally, and each commonly occurs as bycatch in the shrimp trawl fishery (Smith and Wenner, 1985; Murray et al., 1992; Diamond et al., 2000). In addition, Atlantic croaker is harvested for use in the bait industry (Ross, 1988). Management of these species has become necessary as these industries evolve and catch levels increase.

We investigated the diets of weakfish, southern kingfish, and Atlantic croaker off the southeastern United States to provide current regional information on their diets. We also assessed the overlap in prey among the 3 species and examined several factors that may influence this assessment, including spatial and temporal variation in sampling.

Materials and methods

Field sampling

Fishes were collected from 2008 to 2010 during shallow-water trawl hauls conducted as part of the SEAMAP-SA Coastal Survey by staff of the South Carolina Department of Natural Resources. Paired 22.9-m mongoose-type Falcon[3] trawl nets (Beaufort Marine Supply, Beaufort, SC), which had a net body of no. 15 twine with 4.8-cm stretch mesh and a cod end of no. 30 twine with 4.1-cm stretch mesh, were deployed from the RV *Lady Lisa*, a 23-m wooden-hulled, double-rigged St. Augustine Trawlers (St. Augustine Trawlers Inc., St. Augustine, FL) shrimp trawler. Trawl hauls were conducted during daylight hours at target speeds of 1.3 m/s (2.5 kn) for 20 min and at depths between 4 and 10 m (Hendrix and Boylan[4]). For the Coastal Survey, trawl hauls are conducted at randomly selected locations within 6 regions from Cape Canaveral, Florida, to Cape Hatteras, North Carolina (Fig. 1). Regions are

[2] Richardson, J., and J. Boylan. 2013. Results of trawling efforts in the coastal habitat of the South Atlantic Bight, 2012. Report SEAMAP-SA-CS-2012-004, 101 p. [Available from Mar. Resour. Res. Inst., Mar. Resour. Div., South Carolina Dep. Natl. Resour. 217 Fort Johnson Rd., Charleston, SC 29422.]

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4] Hendrix, C., and J. Boylan. 2011. Results of trawling efforts in the coastal habitat of the South Atlantic Bight, 2010. Report SEAMAP-SA-CS-2010-004, 108 p. [Available from Mar. Resour. Res. Inst., Mar. Resour. Div., South Carolina Dep. Nat. Resour, 217 Fort Johnson Rd., Charleston, SC 29422.]

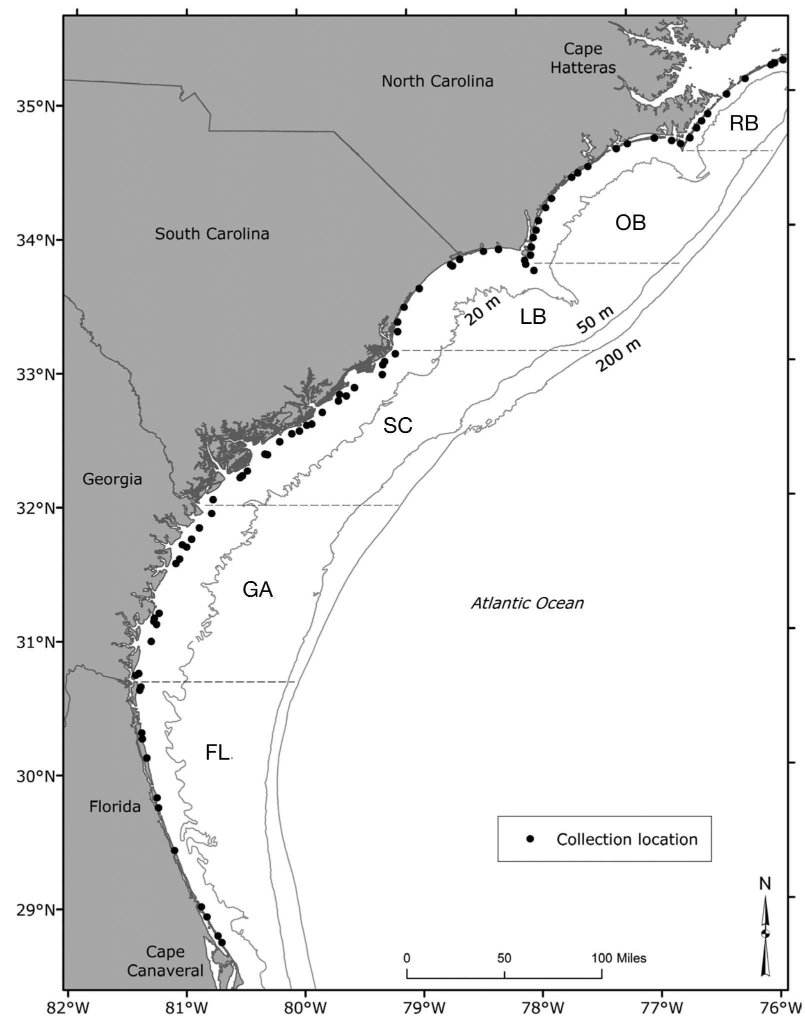

Figure 1

Map of the sampling area of the Coastal Survey of the Southeastern Monitoring and Assessment Program—South Atlantic off the southeastern coastline of the United States, extending from Cape Canaveral, Florida, to Cape Hatteras, North Carolina. The sampling area is divided into 6 regions: Florida (FL), Georgia (GA), South Carolina (SC), Long Bay (LB), Onslow Bay (OB), and Raleigh Bay (RB). Black circles indicate locations where 3 sciaenid fishes— weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*)—were collected from 2008 through 2010 for analysis of their stomach contents.

divided further into strata based on latitude (~0.28° latitude; 2–5 strata per region). The Coastal Survey includes 3 cruises conducted each year during 3 seasons: spring (April–May), summer (July–August), and fall (September–November). Specimens retained for life history research (including diet analysis) were selected from the total catches at a rate of 2 representatives per size class (based on TL in centimeters) per stratum per season. Fish were kept on ice on deck until sample processing began. Total length (in millimeters), SL (in millimeters) and total body weight (in grams) were measured, and otoliths and gonads were extracted. Stomachs, excluding the intestinal tract, were removed from selected specimens, wrapped in cheesecloth and labeled. Stomachs were stored in 10% neutral buffered formalin for a minimum of 14 days, after which they were rinsed with room temperature tap water several times and stored in 70% ethanol.

Laboratory processing

Extraneous tissue was removed from the stomach, the stomach was blotted to remove excess liquid and emptied, and a wet weight of the contents was recorded to the nearest 0.001 g. Each prey item was identified to the lowest possible taxon that could be collapsed into 7 course prey categories: bony fishes, decapod crustaceans, echinoderms, mollusks, nondecapod crustaceans, polychaetes, and other (composed of unidentified animal tissue and rarely seen miscellaneous taxa). Identifications were made from voucher specimens, with staff assistance from the Southeastern Regional Taxonomic Center, and according to various references (e.g., Baremore and Bethea[5]). Small parts were sorted and counted to estimate numbers of individuals whenever possible. When prey were highly digested, key body parts, such as eyes, telsons, or otoliths, were used to make counts. When the number of individuals could not be determined (e.g., from unidentified animal tissue), a conservative count of one individual was assigned. Prey were collectively weighed by taxon to the nearest 0.001 g.

Data analysis

before any analyses, prey items that could not be identified and stomach contents that were incidentally ingested (e.g., sand and gravel) were removed from the data set. To provide the most conservative estimate of overlap in diet, only stomachs from fish collected in trawl hauls that captured all 3 species were included in analyses. Co-occurrence provides the most likely possibility that shared resources were available to each species, regardless of whether they used them. Diet contents were grouped into the 7 prey categories, initially to reduce the number of zero observations in the data set. Data

[5] Baremore, I. E., and D. M. Bethea. 2011. A guide to otoliths from fishes of the Gulf of Mexico. Panama City Laboratory, NOAA Southeast Fisheries Science Center, Panama City, FL. Last modified 29 August 2011. [Available at website.]

were fourth-root transformed, and cluster analysis and nonmetric multidimensional scaling were performed on the resulting Bray-Curtis dissimilarity matrix (McCune and Grace, 2002; Bozzetti and Schulz, 2004) with the packages labdsv and vegan in R software, vers. 2.15.2 (R Core Team, 2012). Predator species, region, year, and season were examined as categorical variables and water depth (in meters), bottom temperature (in degrees Celsius), and salinity were examined as continuous variables by analysis of similarity.

Three metrics of stomach content by prey category were calculated, as percentages, for each predator species, according to Hyslop (1980), where the total sample was defined as all prey within a given prey category: frequency of occurrence, composition by weight, and composition by number. An index of relative importance (IRI) was determined by combining these metrics to eliminate any biases created when each method is analyzed individually (Goldman and Sedberry, 2010; modified from Pinkas et al., 1971):

$$IRI = (N + W) \times F, \quad (1)$$

where F = frequency of occurrence;
N = composition by number; and
W = composition by weight.

IRI has been included only in tabular form as a method of data comparison across diet studies because it is calculated by combining indices that may produce varying results and, therefore, is not necessarily the most robust representation of diet (Cortés, 1997; Hansson, 1998). To provide a more complete picture of prey consumption by each predator, IRI is presented by year.

In additional, mean percent weight and mean percent number were calculated for each predator according to Chipps and Garvey (2007). Prey were analyzed at the lowest possible taxon, and bootstrapping was used to generate bias-corrected 95% confidence intervals for both means with the package boot in R, (vers. 2.15.2). Prey were then grouped into higher prey categories for the purpose of graphical presentation.

Feeding strategy was determined with the method of Amundsen et al. (1996), modified from the method of Costello (1990), where prey-specific abundance (P_i) is plotted against frequency of occurrence. Expressed as a percentage, prey-specific abundance is a given prey taxon's proportion in relation to all prey items observed in only those predator stomachs that contained the given prey taxon:

$$P_i = \left(\frac{\sum S_i}{\sum S_t} \right) \times 100, \quad (2)$$

where S_i = sum of prey i; and
S_t = sum of all prey items found in only those predator stomachs that contained prey I.

Although the summed variable can be composed of the number or the volume or weight of prey items, we used weight and lowest possible prey taxon. The spread and location of points on an Amundsen plot indicate the feeding strategy of the predator population. Data points that cluster near the top of the y-axis indicate specialized feeding by individuals within the population. A cluster close to the origin describes infrequent consumption of a prey type (i.e., prey types that are not an important part of the predator's diet). Data points that are scattered across the graph indicate that a population cannot be characterized as one that employs a single feeding strategy; a population may be specialized sometimes and generalized at other times. Data points clustered in the upper right quadrant of the graph indicate a population with a specialized feeding strategy, where a high percentage of the population consumes one or more specific prey types.

Potential for trophic overlap among each predator pair was tested on mean percent weight and mean percent number with the simplified Morisita-Horn (M-H) index (O):

$$O = (2 \textstyle\sum_i^n P_{ij} P_{ik}) / (\sum_i^n p_{ij}^2 + p_{ik}^2), \quad (3)$$

where n = the total number of prey item groups;
p_{ij} = the proportion of the prey item i used by predator j; and
p_{ik} = the proportion of the prey item i used by predator k (Wolda, 1981; King and Beamish, 2000).

Both mean percent weight and mean percent number were examined to provide the most robust evidence of potential overlap because both variables are biased when viewed independently owing to the broad range of prey sizes (Graham et al., 2007). The M-H index ranges from 0 to 1, with diet overlap increasing as the index approaches 1 (Zaret and Rand, 1971; Labropoulou and Eleftheriou, 1997; King and Beamish, 2000; Graham et al., 2007; Rodrigues and Vieira, 2010).

Results

Analysis of similarity revealed that differences among predator species were significant (goodness of fit: coefficient of determination [r^2]=0.112, P=0.001); however, for a given predator, the differences among years, regions, and seasons were not statistically significant and depth, temperature, and salinity were not correlated with diet composition. Therefore, for the remainder of the analyses, we combined seasons and regions to investigate differences in diet composition among predators and combined years for all analyses except IRI._

Weakfish

For this study, 349 individuals with an average size of 21 cm TL for young-of-the-year fish through adult fish, were examined. Of the 349 stomachs extracted, 276 contained food (79%; Table 1) and prey represented 71 taxa (Table 2).

Table 1

Number of stomachs extracted for this study, according to year, region, and season, from weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*) collected from 2008 through 2010 during nearshore trawl surveys conducted by the Southeastern Monitoring and Assessment Program—South Atlantic.

	2008			2009			2010		
	Weakfish	Southern kingfish	Atlantic croaker	Weakfish	Southern kingfish	Atlantic croaker	Weakfish	Southern kingfish	Atlantic croaker
Spring									
Region									
Florida	5	5	1	4	2	7	7	23	6
Georgia	1	4	1	2	6	6			
South Carolina	1	8	3						
Long Bay				11	14	7	1	6	4
Onslow Bay				9	15	8	15	20	9
Raleigh Bay				8	9	8	16	25	4
All areas	7	17	5	34	46	36	39	74	23
Summer									
Region									
Florida				2	5	8	1	7	1
Georgia	1	2	5	1	4	8	4	9	13
South Carolina	2	3	5	12	24	17	6	4	15
Long Bay				1	1	2	7	5	7
Onslow Bay	4	2	7	4	5	4	10	5	11
Raleigh Bay	4	2	3	7	4	9			
All areas	11	9	20	27	43	48	28	30	47
Autumn									
Region									
Florida				4	11	10	3	22	12
Georgia	9	18	18	7	17	17	5	11	12
South Carolina	7	12	6	9	20	19	7	11	8
Long Bay	1	2	1	6	7	9	12	14	8
Onslow Bay	15	20	25	5	3	7	1	8	2
Raleigh Bay	15	4	6	11	8	6	13	15	6
All areas	47	56	56	42	66	68	41	81	48
Total	65	82	81	103	155	152	108	185	118

Bony fishes, mostly bay anchovy (*Anchoa mitchilli*), striped anchovy (*A. hepsetus*), and other members of the class Actinopterygii, dominated the diet of weakfish, with a frequency of occurrence of 63% in stomachs that contained food (Table 2). The diet composition by weight consisted of 70% bony fishes. The highest diet component by number was nondecapod crustaceans (69%). In addition to bony fishes, the most frequently consumed prey items were mysids, the sergestid shrimp *Acetes americanus carolinae*, and various crustaceans. Values of mean percent weight and mean percent number predictably showed bony fishes to be the dominant prey consumed (44% and 35%, respectively); however, decapod crustaceans (32%) and nondecapod crustaceans (29%) had similarly high values for mean percent number (Fig. 2, A and B).

Results from the use of the Amundsen method indicate that the feeding strategy of weakfish was mixed because individuals sometimes chose specific prey but the population was often opportunistic with regard to what prey were selected. The top left portion of the graph in Figure 3A shows that many individuals chose specific prey types; however, the specific prey selected by each individual differed (Fig. 3A). The data points scattered throughout the center of this graph indicate a mixed feeding strategy, suggesting that, occasionally, the population would feed opportunistically.

Southern kingfish

Stomachs were processed for this study from 486 individuals, with an average size of 21 cm TL (for young-of-the-year fish through adult fish), and 422 of those stomachs contained food (86%; Table 1). Prey representing 86 taxa were identified (Table 2).

Decapod and nondecapod crustaceans were present in the majority of stomachs. Collected stomach sam-

Table 2

Frequency of prey occurrence (*%F*), diet composition by number (*%N*), diet composition by weight (%W), and index of relative importance expressed as a percent (IRI) of prey items found in stomachs of 3 predator species—weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*)—sampled off the Atlantic coast of the southeastern United States from 2008 through 2010.

	Weakfish				Southern kingfish				Atlantic croaker			
	%F	%N	%W	IRI	%F	%N	%W	IRI	%F	%N	%W	IRI
Bony fishes	62.7	7.4	70.27	4869.91	24.5	7.6	21.87	722.02	25.6	7.6	21	732.17
Actinopterygii	39.13	5.1	8.98	550.89	20.1	6.78	9.82	333.68	18.8	5.19	3.62	165.74
Anchoa hepsetus	10.51	0.96	30.1	326.35	0.25	0.09	0.38	0.12	1.42	0.21	8.99	13.11
Anchoa mitchilli	4.35	0.24	5.81	26.32	0.25	0.03	0.3	0.08	1.42	0.46	2.01	3.52
Anchoa spp.	4.35	0.36	3.85	18.3	1.23	0.3	1.19	1.82	2.85	0.88	4.37	14.96
Centropristis striata	1.45	0.08	2.73	4.07								
Clupeiformes	0.36	0.02	0.24	0.1								
Cynoscion nothus	1.45	0.1	2.54	3.82					0.28	0.04	0.79	0.24
Cynoscion spp.	2.17	0.16	1.86	4.39	0.49	0.06	0.35	0.2	1.14	0.17	0.81	1.11
Engraulidae	0.72	0.04	<.01	0.03	0.49	0.06	0.06	0.06	0.57	0.25	0.21	0.26
Harengula jaguana	0.36	0.02	0.23	0.09								
Larimus fasciatus	0.36	0.02	<.01	0.01								
Leiostomus xanthurus	2.54	0.18	9.17	23.72	0.25	0.03	0.27	0.07				
Ophichthidae					0.25	0.03	0.05	0.02				
Mugil cephalus	0.36	0.02	4.17	1.52								
Prionotus spp.	0.36	0.02	<.01	0.01	0.25	0.03	4.28	1.06				
Selene setapinnis					0.25	0.03	0.79	0.2				
Sciaenidae	0.36	0.02	0.01	0.01					0.85	0.38	0.2	0.49
Stellifer lanceolatus	1.09	0.06	0.59	0.7	0.49	0.06	0.21	0.13				
Symphurus plagiusa					0.25	0.03	3.49	0.86				
Syngnathus spp.					0.49	0.06	0.68	0.36				
Decapod crustaceans	54	23.1	20.52	2355.48	67.9	30.9	33.97	4404.99	45.3	18.8	21.53	1826.77
Acetes americanus carolinae	30.43	18.04	5.64	720.7	5.39	4.8	1.38	33.28	8.55	7.37	3.15	89.89
Albunea catherinae					0.49	0.06	0.76	0.4	0.28	0.04	0.26	0.09
Albuneidae					0.25	0.03	0.08	0.03	0.57	0.08	0.89	0.56
Axiidae									0.28	0.04	0.53	0.16
Brachyura	9.78	0.98	0.06	10.22	15.2	2.37	5.21	115.13	7.69	1.47	0.84	17.72
Callianassidae									0.85	0.21	0.09	0.25
Decapoda	1.45	0.1	0.07	0.24	4.9	0.98	0.57	7.59	2.85	0.71	0.1	2.33
Heterocrypta granulata					0.25	0.03	0.04	0.02	0.28	0.04	0.45	0.14
Latreutes parvulus					0.74	0.09	0.01	0.07	1.42	0.29	0.06	0.5
Leptochela sp.	5.8	0.64	0.21	4.93	12.5	3.26	0.83	51.11	7.41	1.38	0.38	13.07
Leucosiidae					0.74	0.09	0.25	0.25				
Lucifer faxoni	2.17	0.12	0.01	0.28	0.74	0.09	<.01	0.07	1.71	0.25	0.01	0.45
Ogyrides sp.	2.17	0.24	0.12	0.77	15.93	4.62	1.33	94.76	8.26	1.63	1.11	22.62
Paguroidea					3.43	0.44	2.52	10.19	3.7	0.59	1.58	8.04
Palaemonidae					0.98	0.12	0.01	0.12	0.85	0.13	0.01	0.12
Panopeidae					1.72	0.3	2.49	4.78	1.42	0.21	1.59	2.56
Pelia mutica	0.36	0.02	0	0.01								
Penaeidae	1.81	0.12	0.18	0.54	17.16	5.15	3.07	141.1	4.27	0.67	4.41	21.7
Pinnotheridae	3.26	0.26	0.1	1.16	9.07	1.69	1.34	27.46	4.27	1.05	0.5	6.61
Porcellanidae	1.81	0.1	0.01	0.19	0.49	0.12	0.6	0.35				
Portunidae	4.35	0.48	0.1	2.54	7.84	1.39	5.37	53.06	0.28	0.13	0.28	0.12
Rimapenaeus constrictus	11.23	1.57	5.6	80.52	14.71	5.21	7.6	188.46	5.98	2.13	1.93	24.32
Sicyonia laevigata					0.25	0.03	<.01	0.01				
Thalassinidea	2.17	0.36	5.87	13.54	0.49	0.06	0.49	0.27	1.42	0.25	1.93	3.11
Xanthoidea	0.36	0.02	<.01	0.01	0.25	0.03	0.02	0.01	0.85	0.13	1.42	1.33
Xiphopenaeus kroyeri	0.36	0.06	2.57	0.95								

Table continued

Table 2 (continued)

	Weakfish				Southern kingfish				Atlantic croaker			
	%F	%N	%W	IRI	%F	%N	%W	IRI	%F	%N	%W	IRI
Echinoderms					0.5	0.1	0.02	0.06	16.5	2.8	4.93	127.58
Echinoidea					0.49	0.06	0.02	0.04	0.57	0.08	0.01	0.05
Holothuroidea									1.99	0.67	1.29	3.91
Ophiuroidea									13.96	2.09	3.63	79.86
Mollusca	5.8	0.3	1.54	10.68	19.1	2.4	1.05	65.84	12.8	1.9	15.84	227.1
Arcidae									0.85	0.13	2.55	2.29
Bivalvia					4.9	0.62	9.97	51.91	4.84	0.71	4.21	23.83
Gastropoda									1.42	0.21	0.18	0.56
Mollusca	5.8	0.32	1.54	10.8	5.88	0.71	1.94	15.62	4.56	0.67	4.69	24.42
Solenidae					8.58	1.1	6.98	69.25	1.14	0.17	4.21	4.99
Nondecapod crustaceans	47.8	68.7	7.29	3632.32	62.3	41	14.73	3472.26	55.8	54.2	5.84	3350.01
Copepoda	8.33	6.26	0.12	53.18	0.74	0.65	0.01	0.48	7.12	7.37	0.08	53.03
Crustacea	18.12	1.1	1.87	53.89	12.5	2.4	1.13	44.06	20.8	4.02	2.6	137.58
Cumacea	2.54	2.63	0.01	6.69	18.87	10.48	0.31	203.76	5.13	1.63	0.06	8.67
Gammaridea	8.33	0.78	0.07	7.08	20.83	5.15	0.19	111.39	20.8	5.23	0.29	114.84
Isopoda	2.9	0.18	0.02	0.57	2.7	0.44	0.04	1.3	1.14	0.21	0.05	0.3
Mysidae	33.33	57.37	5.02	2079.4	35.05	21.23	1.19	785.77	25.64	35.5	2.59	976.51
Stomatopoda	4.35	0.34	0.2	2.34	4.9	0.68	11.87	61.51	1.42	0.21	0.17	0.54
Polychaetes	4.3	0.3	0.38	2.92	44.6	10	18.22	1258.49	51	12.1	28.95	2093.69
Ampharetidae	0.36	0.02	<.01	0.01	6.37	1.21	1.88	19.74	4.27	0.75	7.86	36.82
Aphroditidae					0.49	0.06	2.15	1.08				
Armandia agilis					7.11	1.72	0.37	14.86	4.56	0.96	0.43	6.36
Capitellidae					0.74	0.09	0.49	0.43	0.85	0.13	0.6	0.62
Cirratulidae									0.28	0.04	<.01	0.01
Glyceridae	1.09	0.06	0.06	0.13	3.92	0.47	0.98	5.71	3.7	0.54	3.04	13.26
Goniadidae					1.23	0.18	0.05	0.27	1.42	0.25	0.04	0.42
Lumbrineridae					1.47	0.18	1.27	2.13	0.85	0.13	0.3	0.36
Maldanidae					3.43	0.41	0.99	4.8	7.12	1.21	0.88	14.89
Nephtyidae					3.43	0.44	0.25	2.4	0.28	0.04	0.02	0.02
Nereididae					0.25	0.03	0.01	0.01	1.42	0.33	0.35	0.97
Oenonidae					1.47	0.18	0.08	0.38	2.56	0.38	0.5	2.25
Onuphidae	1.45	0.08	0.29	0.53	9.8	1.75	3.59	52.35	7.41	1.17	2.29	25.62
Opheliidae					0.74	0.09	0.02	0.08	3.13	0.54	0.46	3.16
Orbiniidae					0.49	0.06	0.03	0.04	3.42	0.54	0.18	2.48
Pectinariidae					0.49	0.06	0.19	0.12	0.85	0.13	2.83	2.52
Phyllodocidae					0.98	0.12	0.11	0.23	0.57	0.08	0.01	0.06
Polychaeta	1.45	0.14	0.03	0.24	11.03	1.45	2.18	40.03	16.52	2.43	6.11	141.1
Polynoidae									0.28	0.04	0.06	0.03
Sabellariidae					0.25	0.03	<.01	0.01	2.6	1.09	0.25	3.49
Sigalionidae					0.25	0.03	0.01	0.01	0.57	0.08	0.01	0.05
Spionidae					1.47	1.13	0.29	2.08	5.7	1	1.06	11.76
Terebellidae					2.21	0.36	3.26	7.97	0.57	0.08	0.04	0.07
Trichobranchidae									0.28	0.08	1.63	0.49
Other	0.4	0.2	<.01	0.08	4.2	7.5	1.06	35.95	1.7	0.4	0.19	1
Branchiostoma sp.					1.23	0.24	0.07	0.37				
Chaetognatha	0.36	0.18	<.01	0.07	0.98	6.9	0.13	6.89	0.57	0.17	0.01	0.1
Cnidaria					2.21	0.38	0.16	1.2	3.99	2.26	1.72	15.88
Echiura									0.28	0.04	0.14	0.05
Glottidia pyramidata					1.96	0.36	0.19	1.08	0.57	0.13	0.03	0.09
Sipuncula					0.25	0.03	0.67	0.17				
Tubificidae									0.28	0.08	0.01	0.03
Total		100	100			100	100			100	100	

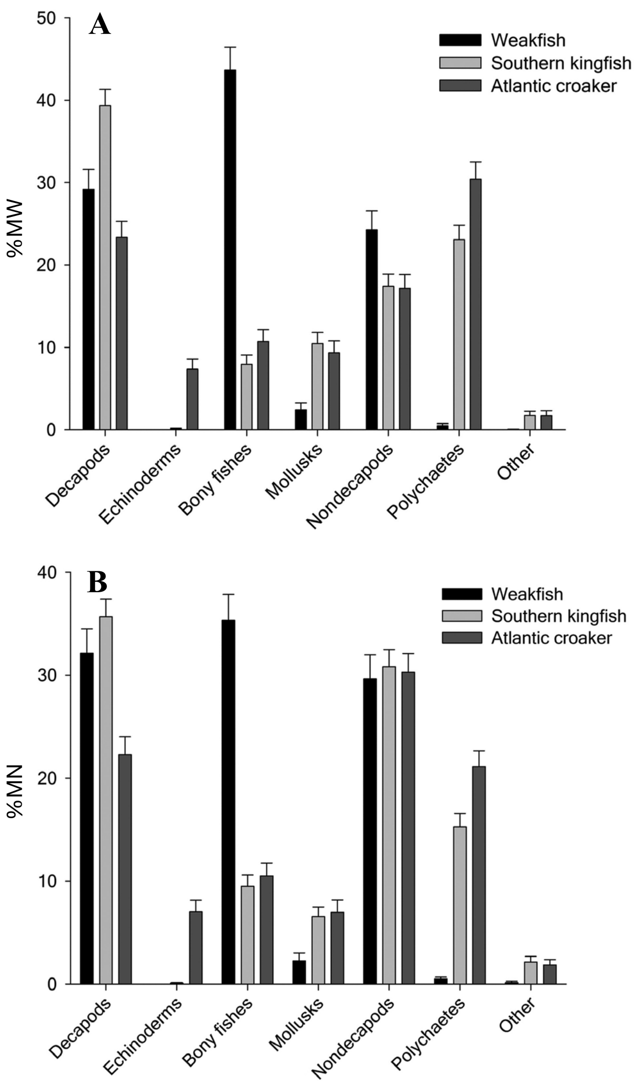

Figure 2

For weakfish (*Cynoscion regalis*; *n*=276), southern kingfish (*Menticirrhus americanus*; *n*=408), and Atlantic croaker (*Micropogonias undulatus*; *n*=351) captured in 2008, 2009, and 2010 off the Atlantic coast of the southeastern United States, (**A**) mean diet composition by weight (%MW) and (**B**) mean diet composition by number (%MN) by prey category: decapod crustaceans, echinoderms, bony fishes, mollusks, nondecapod crustaceans, polychaetes, and other (composed of unidentified animal tissue and rarely seen miscellaneous taxa). Error bars indicate 1 standard deviation of the mean.

ples contained decapod crustaceans 68% of the time and nondecapod crustaceans 62% of the time (Table 2). Polychaetes were identified in more than 40% of southern kingfish stomachs. Identified polychaetes included representatives from 20 different families, primarily Ampharetidae, Glyceridae, Nephtydae, Onuphidae, Opheliidae, and Terebellidae. Decapod crustaceans composed 33% of the composition by weight of the southern kingfish diet. Composition by number was higher for nondecapod crustaceans (41%) than for decapod crustaceans (31%). Mean percent weight and mean percent number were highest for decapod crustaceans (39% and 36%, respectively), compared with the mean values for all other prey categories. Polychaetes had the second-highest mean percent weight (23%), whereas nondecapod crustaceans represented 17% of the diet (Fig. 2, A and B).

Amundsen metrics indicate that the population of southern kingfish displayed a generalized feeding strategy. Although some prey items, including mysids, gammaridean amphipods, and cumaceans, were consumed regularly, most prey types were infrequently observed in the stomachs of southern kingfish (Fig. 3B). The concentration of data points along the *y*-axis in Figure 3B is indicative of prey items that were present in the stomachs of individual southern kingfish but were rarely if ever seen in the stomachs of more than a single animal.

Atlantic croaker

Of the 421 Atlantic croaker selected for diet analysis (with an average size of 18 cm TL for young-of-the-year fish through adult fish), 351 individuals had stomachs that contained prey items (83%; Table 1). Prey representing 91 taxa were identified (Table 2).

Nondecapod crustaceans (56%) and polychaetes (51%) were the prey categories with the highest frequencies of occurrence in the diet of Atlantic croaker in this study (Table 2). Decapod crustaceans (45%) were the third most frequent prey category. Values of composition by weight were comparable for bony fishes, decapods crustaceans, and polychaetes (21%, 22%, and 29%, respectively). Nondecapod crustaceans, most of which were mysids, had the highest value of composition by number (54%). Across all sampling years, polychaetes dominated mean percent weight, composing 30% of the prey weight (Fig. 2A). However, nondecapod crustaceans were numerically dominant, accounting for 30% of the number of prey (Fig. 2B).

Atlantic croaker were the most generalized feeders of the 3 sciaenids, according to the Amundsen plot in Figure 3C. Most of the data points in this figure appear along the *y*-axis, indicating that individual Atlantic croaker consumed many different prey types and that those prey types were rarely seen in the stomachs of other individual fish. The data points in the center of this graph indicate those prey that were more frequently found in the stomachs of Atlantic croaker than in the stomachs of the other 2 species: mysid shrimp, various unidentified crustacean parts, and gammaridean amphipods.

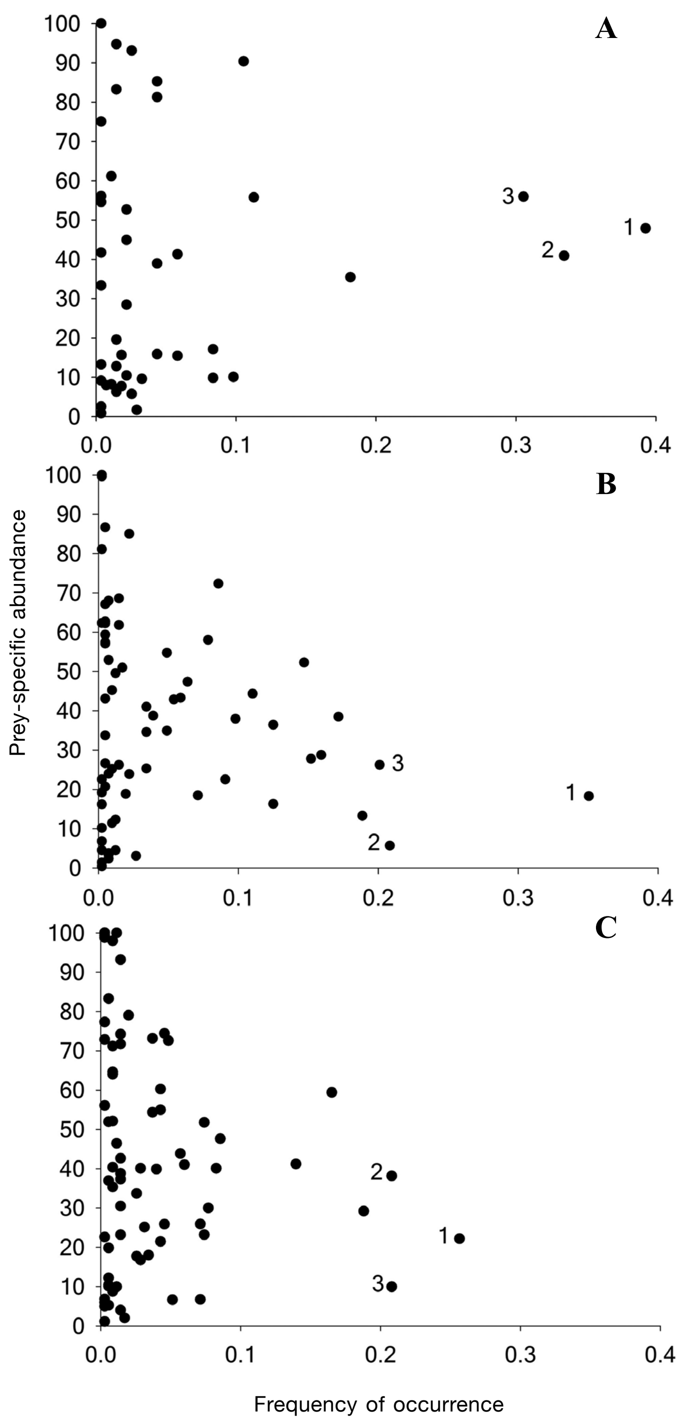

Figure 3

Plots of the feeding strategies of (**A**) weakfish (*Cynoscion regalis*), (**B**) southern kingfish (*Menticirrhus americanus*), and (**C**) Atlantic croaker (*Micropogonias undulatus*) determined with the Amundsen method. Prey consumed most frequently are numbered: 1=Actinopterygii, 2=Mysidae, and 3=*Acetes americanus carolinae* for weakfish; 1=Mysidae, 2=Gammaridea, and 3=Cumacea for southern kingfish; and 1=Mysidae, 2=Crustacea, and 3=Gammaridea for Atlantic croaker.

Overlap

The analysis performed on mean percent weight with the simplified M-H index indicates that some diet overlap was observed between species pairs (Table 3). The overlap was highest between southern kingfish and Atlantic croaker (M-H index=0.74; Table 3). M-H index for mean percent number indicated less diet overlap for all species pairs, although the overlap remained highest between southern kingfish and Atlantic croaker (M-H index=0.56).

Discussion

The diet of weakfish was distinct from that of the 2 other species examined; the most important prey consumed were bony fishes on the basis of both frequency of occurrence and composition by weight. Our findings are similar to those of Merriner (1975), who noted a diet dominated by bony fishes, particularly anchovies and the larger Atlantic thread herring, by occurrence, number, and volume. In contrast to Merriner (1975), we did not specifically identify any Atlantic thread herring in the weakfish stomachs. It is possible that the clupeid Atlantic thread herring was present , but our fish remains were identified only to family. Species of *Anchoa*, mostly striped anchovy and bay anchovy, were observed in 19% of stomachs compared with 58% of stomachs in Merriner's study. Again, it is feasible that species of *Anchoa* were present in a higher percentage of stomachs, but identification of fishes was difficult because specimens were often highly digested.

Although the composition by number indicates that nondecapod crustaceans played an important role in the diet of weakfish (57% of total prey composition by number), this finding may be misleading. Mysids are quite small and known to occur in aggregations (Omori and Hamner, 1982). It is very possible that the high numerical occurrence that we found is the result of opportunistic encounters with mysid patches rather than an indication of targeted prey selection or high nutritional importance in weakfish diets. Bony fishes were the largest dietary component by weight, and weight is a more relevant measurement of energetic importance of organisms in fish diets than is number (Bowen, 1983; Chipps and Garvey, 2007).

The diet of southern kingfish is similar across the range of this species and includes polychaetes, amphipods, and mysids. However, the frequency of occurrence of various prey items differs with location. Off the southeastern United States, we found that various taxa of crustaceans were the most important prey

Table 3

Results from the simplified Morisita-Horn index used for analysis of diet overlap for pairs of 3 species: weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), and Atlantic croaker (*Micropogonias undulatus*). An asterisk (*) denotes a value that indicates biologically significant potential for diet overlap between species in a pair. Analyses were performed for both mean percent weight (%MW) and mean percent number (%MN).

Predator cross pairs	Weakfish and southern kingfish	Southern kingfish and Atlantic croaker	Atlantic croaker and weakfish
%MW	0.46	0.74*	0.50
%MN	0.40	0.56	0.43

items according to all 3 of the diet metrics analyzed (frequency of occurrence, composition by number, and composition by weight). Polychaetes were also important, occurring in nearly half of the stomachs for all years of this study, compared with polychaetes ranking fourth in the diet of southern kingfish in a study in the Gulf of Mexico (McMichael and Ross, 1987). Clam siphons were the most frequently occurring prey item in our study, but, in another study in Brazil, amphipods were the most common prey item in spring, followed by polychaetes and mysids (Rodrigues and Vieira, 2010). The Gulf of Mexico and Brazilian study defined juvenile fishes as those ranging in TL between 2 and 6 cm, but few fishes less than 10 cm TL were observed in our study. A possible explanation for the differences in diet are ontogenetic changes in foraging behavior and swimming ability that, in turn, increase foraging areas and feeding opportunities for larger fishes (Graham et al., 2007).

The diet of Atlantic croaker was the most diverse of among the diets of the 3 sciaenids and our findings are comparable with those of Overstreet and Heard's (1978) study of this species in the Gulf of Mexico. The diet patterns that we observed are most similar to those of Atlantic croaker captured in nearshore waters, at depths consistent with the depth range of our sampling. Statistical analyses indicated no seasonal shift in diet in either our study or in that of Overstreet and Heard (1978), but we found that the diet of Atlantic croaker included a markedly higher frequency of occurrence for echinoderms, specifically ophiuroids, which were present in an average of 16% of stomachs, compared with <4% of the stomachs in the Gulf of Mexico study (Overstreet and Heard, 1978). This difference could be a result of variance in the distribution of ophiuroids, which are quite common off the southeastern coast of the United States, or may be the result of other prey types being more readily available to Atlantic croaker populations in the Gulf of Mexico.

Foraging habitats and feeding strategy varied among the 3 species in this study. Southern kingfish and Atlantic croaker consumed prey that are associated with the seafloor, whereas weakfish generally fed on prey items that occur in the water column. Furthermore, southern kingfish and Atlantic croaker can be characterized as having a more generalized feeding strategy. Despite the variation in feeding strategy, a few prey items were consumed by all 3 species, such as the amphipods *Erichthonius brasiliensis* and *Microprotopus raneyi* and the mysid *Promysis atlantica*. Mysids were the most frequently consumed individual prey item for both southern kingfish and Atlantic croaker, and the second-most frequently consumed individual prey item of weakfish. Some animals, such as most mysid species, exhibit diel vertical migrations, spending daylight hours on the seafloor and migrating toward the surface at dusk to forage throughout the night or vice versa (Robertson and Howard, 1978). These vertical migration patterns provide an opportunity for predatory fishes to encounter and consume prey that may only temporarily dwell in their foraging habitat (Goldman and Sedberry, 2010), therefore, creating an opportunity for diet overlap between bottom-feeding fishes and water-column–feeding fishes.

The 3 species examined here did not exclusively employ a single feeding strategy (e.g., generalist or specialist). Individuals of all 3 species consumed specific prey items, but, at the population level, each species showed a proclivity to feed opportunistically—a finding that could be interpreted as indicating that they fed on whatever was both available and abundant. In comparison with the populations of the other 2 fish species, the weakfish population showed a trend toward more specialized feeding, shifting to more mobile, pelagic prey earlier in their ontogeny. Weakfish also have the potential to reach the greatest size, and changes in their diet as they grow would be expected to reduce diet overlap with species that have a smaller terminal size (Schoener, 1974; Werner and Gilliam, 1984). Alternatively, the morphological features of the 3 species indicates that weakfish would be more likely to feed in the water column than the other 2 species, regardless of body size.

The highest potential for resource competition exists between southern kingfish and Atlantic croaker on the basis of the simplified M-H index. Morisita-Horn index values exceeding 0.60 are generally accepted as biologically significant in the literature (Zaret and Rand, 1971; Labropoulou and Eleftheriou, 1997; King and Beamish, 2000; Graham et al., 2007; Rodrigues and Vieira, 2010). Assuming this value is significant, southern kingfish and Atlantic croaker showed significant diet overlap by mean percent weight, at 0.74, but not on the basis of mean percent number, at 0.56 (Table 3). Most southern kingfish and Atlantic croaker that were sampled had prey in their stomachs, indicating that sufficient prey were readily available to both species and the generalized (opportunistic) feeding strategy employed by these benthivorous species likely reduces any competition for resources, even when there are relatively high levels of diet overlap.

Ecosystem-based management is dependent on defining interactions among species and, in particular, on identifying trophic links for priority species (NMFS[6]). Weakfish, southern kingfish, and Atlantic croaker are swept up regularly in commercial shrimp trawl nets, are targets of bait fisheries, and play important roles in the nearshore food web. If exploitation increases, their large-scale removal could alter some fundamental ecosystem processes (Kumar and Deepthi, 2006). The sciaenids in this study overlap spatially; therefore, ecosystem-based principles require that we determine whether competitive interactions occur among them for prey resources. Ignorance of predator–prey relationships will result in fisheries managers overlooking important ecosystem-based complexities that could drive population trends (Ruckelshaus, 2008).

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