# SHOREBIRD DIET AND SIZE SELECTION OF NEREID POLYCHAETES IN SOUTH CAROLINA COASTAL DIKED WETLANDS

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Abstract.—Coastal wetlands that are diked and managed may supplement declining natural habitat for migrating shorebirds (Charadriiformes). However, data on shorebird diet in these diked wetlands are scarce. We examined shorebird diet and prey size selection in brackish diked wetlands at the Yawkey Center on South Island, South Carolina, USA. Gut contents of seven Lesser Yellowlegs (*Tringa flavipes*) and seven Short-billed Dowitchers (*Limnodromus griseus*) were examined. The most common items in gut contents were mandibles of the nereid polychaete, *Laeonereis culveri*, followed by insects. *L. culveri* eaten by Short-billed Dowitchers were significantly larger than those eaten by Lesser Yellowlegs. This difference may be related to differences in bill length and feeding tactics. We make suggestions on how to maintain high numbers of *L. culveri* in diked wetlands, but more research on the timing of colonization by invertebrates is needed in shorebird conservation efforts.

## DIETA DE PLAYEROS Y SELECCION DEL TAMAÑO DE POLIQUETOS EN ÁREAS ANEGADAS FORMADAS POR DIQUES EN CAROLINA DEL SUR

Sinopsis.—Los anegados costaneros que son manejados y a los cuales se les construyen diques, pueden suplementar a habitats, que estan desapareciendo para playeros (Charadriformes) migratorios. No obstante, datos sobre la dieta de playeros en este tipo de anegados es escasa. Examinamos la dieta de playeros y la selección del tamaño de la presa en anegados con diques en el Centro Yawley, South Island, de Carolina del Sur. Se examinó el contenido estomacal de siete playeros de patas amarillas (*Tringa flavipes*) y de siete chorlos de pico corto (*Limnodromus griseus*). Los artículos alimentarios más comunes fueron mandíbulas del poliqueto *Laeonereis culveri*, siguiéndole insectos. Los poliquetos que se comieron los chorlos fueron significativamente de mayor tamaño que los que ingirieron los playeros. La diferencia podría atribuirse a diferencias en el tamaño del pico y a tácticas para alimentarse. Se hacen sugerencias para mantener altos números de poliquetos en anegados formados por diques. No obstante, se necesitan estudios adicionales, para determinar el momento más apropiado para la colonización de estas áreas por parte de los invertebrados.

Quantity and quality of natural intertidal habitat for migratory shore-birds (Senner and Howe 1984) and numbers of some shorebird species (Morrison et al. 1994, Page and Gill 1994) are in decline. As a supplement to natural intertidal areas, coastal wetlands that are diked and managed (sometimes called impoundments) can provide shorebird habitat if managed appropriately (Burger et al. 1982, Erwin et al. 1994, Weber and Haig 1996). Of the 0.5 million ha of marshes along the Atlantic coast of the southeastern United States, about 11% are diked and managed for mosquito control or waterfowl management (Montague et al. 1987). This

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represents a potentially vast supplemental shorebird area if integrative management strategies are adopted. Efforts to manage diked wetlands for shorebirds should include the maintenance of high prey abundance if, as at our study site, shorebird density is positively correlated with prey density (Weber and Haig 1997). However, only a few studies have published shorebird diet in coastal diked wetlands (Rehfisch 1994, Wenner 1986). Thus, our goal was to identify gut contents of migratory shorebirds in South Carolina to determine the preferred prey species that would be the target of management in brackish, coastal diked wetlands of the Atlantic coast.

We also investigated prey size selection for Short-billed Dowitchers (Limnodromus griseus) and Lesser Yellowlegs (Tringa flavipes). At our study site, both species fed in the same  $30 \times 30$  m plots (Weber 1994), fed at similar water depths (Short-billed Dowitcher mean = 4.8 cm, SD = 3.7; Lesser Yellowlegs mean = 2.7 cm, SD = 3.2; Weber and Haig 1996), and had similar body size. It is often assumed that there is little diet overlap for species foraging in the same habitat (Lack 1954). Yet, some studies have found a striking overlap of shorebird diet among species (Holmes and Pitelka 1968, Recher 1966). Our search of the literature found no comparison of the prey size of Short-billed Dowitchers and Lesser Yellowlegs feeding in the same habitat. Thus, after finding that both species fed on the same major prey item, we measured and compared the size of the main prey species taken to determine if diet overlap extended to size.

#### METHODS

Study site.—Field work was conducted on South Island (79°15'W, 33°10'N) at the Tom Yawkey Wildlife Center in Georgetown County, South Carolina managed by the South Carolina Department of Natural Resources. There are twelve brackish diked wetlands on South Island ranging in size from 9-98 ha. Water levels are regulated by wooden water control structures (Williams 1987). The management strategy is an integrative shorebird-waterfowl technique in which high water depths (35-45 cm) are provided for overwintering waterfowl. In spring, depths are drawn down to sheet water and temporary dry bed to encourage germination of waterfowl food plants and to provide mudflat and shallow water habitat for shorebirds. More complete management details are described elsewhere (Weber and Haig 1996). In the three diked wetlands from which shorebirds were collected, the following mean salinity values (ppt) were recorded from weekly measurements taken from 17 Jan.-17 April 1992: Gibson Pond mean = 16.1, SD = 4.8; Upper Reserve mean = 12.2, SD = 1.8; Wheeler Basin mean = 16.6, SD = 2.7. Salinity varied weekly because of rainfall. Bottom sediments appeared similar to those in diked wetlands of Cat Island, which was separated from South Island by a small tidal creek. The bottom sediments of Cat Island's diked wetlands were fine-grained (<0.062 mm in diameter), and ranged from silty clay (up to 82% clay) to clayey silt (up to 86% silt) with a sand fraction ranging from 0-5% (May and Zielinski 1986).

On South Island, about 3000 shorebirds overwintered each year from 1991–1993 (Weber and Haig 1996). Shorebird numbers increased throughout the spring and peaked in late May at approximately 15,000–19,000 migrants. Most common migrants (in decreasing order of abundance) were Semipalmated Sandpiper (Calidris pusilla), dowitchers (Limnodromus griseus and L. scolopaceus), Dunlin (Calidris alpina), Semipalmated Plover (Charadrius semipalmatus), Lesser Yellowlegs, Western Sandpiper (Calidris mauri), Least Sandpiper (C. minutilla), and Black-bellied Plover (Pluvialis squatarola).

Gut analysis.—From 14-18 Apr. 1992, seven Lesser Yellowlegs and seven Short-billed Dowitchers were collected as they fed during mid-afternoon in three of the most highly used diked wetlands (Gibson Pond, Upper Reserve, and Wheeler Basin). Within 30 min after death, the entire digestive tract was removed, the proventriculus pierced, and the entire tract placed in formalin. Shorebird mass, sex (identified by internal anatomy), and culmen (bill) length were recorded in the field. Contents of esophagus and proventriculus were identified and counted in the laboratory using a 30 × stereomicroscope. Only hard-bodied prey parts remained because soft parts are quickly digested in shorebirds (Pienkowski et al. 1984). Large polychaete jaws were from the family Nereidae and identified as Laeonereis culveri, a 28-45 mm worm (Mazurkiewicz 1975) similar in appearance to those in the genus *Nereis* (see Gosner 1978, plate 38). To estimate size of L. culveri ingested by the birds, lengths of all (or a maximum of twenty randomly selected) whole left L. culveri mandibles from each gut were measured (straight line distance between base and tip) using a stereomicroscope (25 or  $50 \times$ ).

Head width of L. culveri was estimated from jaw length using a regression equation. We derived the equation from a reference collection obtained from 13 core samples (5-cm diameter, 10-cm deep) taken from Wheeler Basin and Gibson Pond in April 1993. Core samples were washed through a 0.5 mm mesh sieve and preserved in buffered 10% formalin stained with Rose Bengal. All large nereids in the samples were identified as L. culveri. Head widths of all uninjured L. culveri were measured at the widest part of the prostomium using an ocular micrometer at 30 ×. One mandible was removed and the length measured as already described. Mandible length plotted against head width (Fig. 1) was predicted by the equation (in mm): head width = 1.3 (mandible length) + 0.026;  $r^2$  = 0.91. L. culveri head width was related to body length as follows: length = 4.3 (width) - 0.7,  $r^2$  = 0.68, n = 114. Head width was thought to be a more accurate measure of size than length because of variable longitudinal contractions by polychaetes. We compared the mean head width of L. culveri eaten by Short-billed Dowitchers and Lesser Yellowlegs by first calculating the average for each bird and then using an unpaired ttest to compare species using each bird as a replicate.

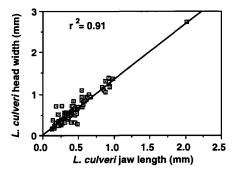


FIGURE 1. Regression between jaw length and head width for *L. culveri* at the Yawkey Center on South Island, South Carolina in April 1993.

### RESULTS

L. culveri mandibles were the most conspicuous and numerous food item in the diet of shorebirds from the diked wetlands (Table 1). L. culveri head width consumed by Short-billed Dowitchers (mean = 1.36 mm, SE = 0.09) was wider (t = 5.24, P < 0.001) than in Lesser Yellowlegs (mean = 0.77 mm, SE = 0.07; Fig. 2). We assume the length of L. culveri consumed by Short-billed Dowitcher was also longer because of the positive correlation between head width and length in L. culveri. Greater size of prey consumed occurred even though the mass of Short-billed Dowitchers (mean = 102.1 g, SE = 2.5, n = 7) was not different (t = 1.35, P = 0.20) from Lesser Yellowlegs (mean = 95.1 g, SE = 4.5, n = 7). Bill length in Short-billed Dowitchers (mean = 5.95 cm, SE = 0.18) was longer (t = 12.9, P < 0.001) than Lesser Yellowlegs (mean = 3.51 cm, SE = 0.06).

During collection, two shorebirds were taken incidentally. A male Dunlin (37.5 g) contained 11 pairs of *L. culveri* jaws, and a male Greater Yellowlegs (*Tringa melanoleuca*) (180.0 g) contained 1 pair (Weber 1994).

#### DISCUSSION

Diked wetlands in South Carolina are not the only sites in which nereid polychaetes are the favored prey of shorebirds. In California, nereids dominated the diets of dowitchers, Dunlin, Marbled Godwit (Limosa fedoa), and Semipalmated Plover (Recher 1966). In Europe, Africa, and Australia, large nereids (particularly Nereis diversicolor, N. virens, and Ceratonereis spp.) are important dietary constituents of Dunlin (Bengtson and Svensson 1968, Goss-Custard et al. 1977, Mouritsen 1994, Pienkowski et al. 1984, Rands and Barkham 1981, Wolff 1968), Black-bellied Plover (Durell and Kelly 1990, Evans et al. 1979, Goss-Custard et al. 1977, Kalejta 1993), Eurasian Curlew (Numenius arquata; Evans et al. 1979, Goss-Custard et al. 1977, Kent and Day 1983, Zwarts and Esselink 1989), Curlew Sandpiper (Calidris ferruginea, Kalejta 1993), Bar-tailed Godwit (Limosa lapponica; Evans et al. 1979, Goss-Custard et al. 1977), Black-tailed Godwit (Limosa, Moreira 1994), Redshank (Tringa totanus, Goss-Custard et al.

TABLE 1. Gut contents of Lesser Yellowlegs (LEYE) and Short-billed Dowitchers (SBDO) in Upper Reserve (UR), Wheeler Basin (WB), and Gibson Pond (GP) collected during spring migration on South Island, South Carolina. Laeonera's culver head width is predicted from jaw length to head width regression (Fig. 1).

Miscellaneous contents								3 Gammarus, 21 Corix-	idae wings, 3 Cole-	optera adults, white	seed			amphipod		clam, mosquito larvae		
Individuals present <sup>a</sup>	Snails			2		8	30	4										က
	Corix. Seeds											જ	9	4		56		9
		1					2	12										
	Ost.	2			4	8	œ	сC				19	30	21	107	14	œ	9
	Chi.	96	9					1				18	63	84	243	130	75	49
Pairs of jaws in gut		2	4	62	68.5	15	119	22				256.5	59.5	19	127.5	294.5	26	247
L. culveri head width	n	1	2	15	20	13	20	19				20	50	14	20	20	50	20
	SD		0.24	0.71	0.20	0.13	0.14	0.92				0.56	0.37	0.53	0.42	0.41	0.38	0.59
	×	98.0	0.69	1.03	0.85	1.25	1.31	1.41				2.40	1.90	1.96	1.44	1.62	1.87	1.76
Culmen.	(cm)	3.48	3.56	3.33	3.36	3.48	3.63	3.75				5.22	5.45	6.36	6.27	6.49	5.96	5.96
Mass	(g)	103.0	85.0	94.5	81.0	92.5	93.0	117.0				96.5	103.5	108.5	110.5	102.0	91.0	103.0
	Sex	놴	Z	Σ	M	Ŧ	Z	Σ				M	Z	Ŧ	ΙŦ	ĮΉ	ᄺ	ī
	Site	UR	UR	UR	UR	UR	WB	GP				UR	UR	UR	UR	UR	UR	UR
	<u> </u>	LEYE1	LEYE2	LEYE3	LEYE4	LEYE5	LEYE6	LEYE7				SBDO1	SBDO2	SBDO3	SBDO4	SBDO5	SBDO6	SBDO7
Date		4/14	4/14	4/14	4/14	4/14	4/18	4/18				4/14	4/14	4/14	4/14	4/18	4/18	4/18

<sup>a</sup> Chi. = chironomid, Ost. = Ostracod, Corix. = Corixidae.

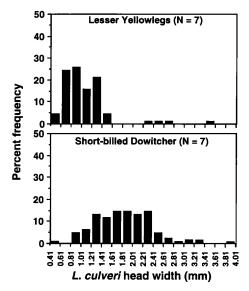


FIGURE 2. Size-frequency distribution of *L. culveri* head widths in two shorebird species at the Yawkey Center on South Island, South Carolina.

1977), and Eurasian Oystercatcher (Haematopus ostralegus, Boates and Goss-Custard 1989). Although most other North American shorebird diet studies do not report nereids as the dominant prey item, this may be explained by a preponderance of alternative prey in natural sites on the Atlantic coast available during shorebird migration. Most notable of these prey are horseshoe crab eggs (Limulus polyphemus) (Botton et al. 1994) and the amphipod, Corophium spp. (review by Wilson 1991). Other dominant prey items in North America include isopods and sand crabs (Myers et al. 1980), insects (Holmes and Pitelka 1968), or a variety of other annelids, crabs, shrimp, clams, and invertebrates (Quammen 1984, Schneider 1985, Schneider and Harrington 1981, and see further review by Wilson 1991). Crustaceans associated only with sand and horseshoe crabs that require beaches would be excluded in diked wetlands. Thus, we expect nereids to be the dominant shorebird prey in other brackish diked wetlands if the sediment is fine, soft, and flocculent.

Our data show that Lesser Yellowlegs and Short-billed Dowitchers ate a variety of other prey besides *L. culveri*. However, *L. culveri* may be preferred because of its size which can have more than 20 times the drymass of an average chironomid. Our diet analysis may have omitted some important prey items because soft-bodied prey items were excluded. Benthic core samples at our site indicated that soft-bodied organisms were present in the sediment including polychaetes with no or very small hard parts, oligochaetes, a sea anemone (*Nematostella vectensis*), nematodes, and nemertines (Weber 1994). Because of the variety known to be consumed

and possibly consumed, management strategies should include other prey types as well as *L. culveri*.

Management for *L. culveri* may be possible over a wide geographic range including Connecticut to Florida, the Gulf of Mexico, Central America, and the east coast of South America, in a wide range of salinities and temperatures in fine flocculent soft-sediments (Mazurkiewicz 1975). Female *L. culveri* spawn by depositing eggs within their mucoid tubes; larvae then migrate to the sediment surface and swim or crawl to adequate habitat before burrowing (Mazurkiewicz 1975). Colonization may have occurred at the Yawkey Center because there was a small amount of continuous exchange between diked wetlands and tidal creeks. At sites without continuous exchange, *L. culveri* colonization might be achieved by timing water exchange with spawning. Additional research to determine polychaete and chironomid survival rates, the timing of colonization, and hardiness in coastal diked wetlands could provide more specific management recommendations.

A variety of factors may explain why Short-billed Dowitchers ate larger L. culveri than Lesser Yellowlegs. Short-billed Dowitches feed mainly by rapid vertical probing like a sewing machine, often submerging the head, while Lesser Yellowlegs tend to pick prey from the surface (L. Weber, personal observation; Hayman et al. 1986). Short-billed Dowitchers may capture larger L. culveri than Lesser Yellowlegs if worm size tends to increase with sediment depth. Bill length may also determine prey length. Compared to Lesser Yellowlegs, mean length of L. culveri eaten by Shortbilled Dowitchers was approximately twice as long (length calculated by using the L. culveri head width to length conversion equation). Correspondingly, mean bill length in Short-billed Dowitchers was 1.7 times longer than in Lesser Yellowlegs. A combination of bill length and depth to which the species probe along with other factors might best explain prey size selection. Other field studies have found that important factors determining prey size include bill length, foraging mode, gape width, prey profitability, prey availability, tarsal length, social context of foraging, and habitat preference (Goss-Custard 1977a, 1977b; Zwarts and Blomert 1992).

In conclusion, *L. culveri* at various sizes provide prey for shorebirds in coastal diked wetlands. Maintaining high numbers of these invertebrates in managed wetlands could be a key to shorebird conservation.

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#### LITERATURE CITED

- BENGSTON, S., AND B. SVENSSON. 1968. Feeding habits of *Calidris alpina L.* and *C. minuta* Leisl. (Aves) in relation to the distribution of marine shore invertebrates. Oikos 19:152–157.
- BOATES, J. S., AND J. D. GOSS-CUSTARD. 1988. Foraging behavior of oystercatcher *Haematopus ostralegus* during a diet switch from worms *Nereis diversicolor* to clams *Scrobicularia plana*. Can. J. Zool. 67:2225–2231.
- BOTTON, M. L., R. E. LOVELAND, AND T. R. JACOBSEN. 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of horseshoe crab (*Limulus polyphemus*) eggs. Auk 111:605–616.
- BURGER, J., J. SHISLER, AND F. H. LESSER. 1982. Avian utilisation on six salt marshes in New Jersey. Biol. Conserv. 23:187–212.
- DURELL, D., AND C. P. KELLY. 1990. Diets of Dunlin *Calidris alpina* and Gray Plover *Pluvialis squatarola* on the Wash as determined by dropping analysis. Bird Study 37:44–47.
- ERWIN, R. M., J. S. HATFIELD, M. A. HOWE, AND S. KLUGMAN. 1994. Waterbird use of salt-marsh wetlands created for open marsh water management. J. Wildl. Manage. 58:516–594.
- EVANS, P. R., D. M. HERDSON, P. J. KNIGHTS, AND M. W. PIENKOWSKI. 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. Oecologia 41:183–206.
- GOSNER, K. L. 1978. A field guide to the Atlantic seashore. Houghton Mifflin Company, Boston, Massachusetts. 329 pp.
- Goss-Custard, J. D. 1977a. Optimal foraging and the size selection of worms by redshank, *Tringa totanus*, in the field. Anim. Behav. 25:10-29.
- -----. 1977b. The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density. J. Anim. Ecol. 46:1–19.
- ——, R. E. JONES, AND P. E. NEWBERRY. 1977. The ecology of the Wash I. Distribution and diet of wading birds (Charadrii). J. Appl. Ecol. 14:681–780.
- HAYMAN, P., J. MARCHANT, AND T. PRATER. 1986. Shorebirds. An identification guide to the waders of the world. Houghton Mifflin Company, Boston, Massachusetts. 414 pp.
- HOLMES, R. T., AND F. A. PITELKA. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. Syst. Zool. 17:305–318.
- KALEJTA, B. 1993. Intense predation cannot always be detected experimentally: a case study of shorebird predation on nereid polychaetes in South Africa. Netherlands J. Sea Res. 31:385–393.
- Kent, A. C., and R. W. Day. 1983. Population dynamics of an infaunal polychaete: the effect of predators and an adult-recruit interaction. J. Exp. Mar. Biol. Ecol. 73:185–203.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, United Kingdom. 343 pp.
- MAY, J. P., AND P. B. ZIELINSKI. 1986. Sedimentology, hydrogeology and hydrology. Pp. 79–101, in M. R. DeVoe and D. S. Baughman, eds. South Carolina coastal wetland impoundments, Vol. II: Technical Synthesis, Publication #SC-SC-TR-86-2. South Carolina Sea Grant Consortium, Charleston, South Carolina.
- MAZURKIEWICZ, M. 1975. Larval development and habits of *Laeonereis culveri* (Webster) (Polychaeta: Nereidae). Biol. Bull. 149:186–204.
- MONTAGUE, C. L., A. V. ZALE, AND H. F. PERCIVAL. 1987. Ecological effects of coastal marsh impoundments: a review. Environ. Manage. 11:743–756.
- MOREIRA, F. 1994. Diet, prey-size selection and intake rates of Black-tailed Godwits *Limosa lapponica* feeding on mudflats. Ibis 136:349–355.
- MORRISON, R. I. G., C. DOWNES, AND B. COLLINS. 1994. Population trends of shorebirds on fall migration in eastern Canada 1974–1991. Wilson Bull. 106:431–447.
- MOURITSEN, K. N. 1994. Day and night feeding in Dunlins *Calidris alpina*: choice of habitat foraging technique and prey. J. Avian Biol. 25:55–62.
- MYERS, J. P., S. L. WILLIAMS, AND F. A. PITELKA. 1980. An experimental analysis of prey availability for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. Can. J. Zool. 58:1564–1574.

- PAGE, G. W., AND R. E. GILL. 1994. Shorebirds in western North America: late 1800s to late 1900s. Studies in Avian Biol. 15:147–160.
- PIENKOWSKI M. W., P. N. FERNS, N. C. DAVIDSON, AND D. H. WORRALL. 1984. Balancing the budget: measuring the energy intake and requirements of shorebirds in the field. Pp. 29–56, *in* P. R. Evans, J. D. Goss-Custard and W. G. Hale, eds. Coastal waders and waterfowl in winter. Cambridge University Press, Cambridge, United Kingdom.
- QUAMMEN, M. L. 1984. Invertebrates in intertidal mudflats: an experimental test. Ecology 65:529-537.
- RANDS, M. R. W., AND J. P. BARKHAM. 1981. Factors controlling within-flock feeding densities in three species of wading bird. Ornis Scan. 12:28–36.
- RECHER, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.
- REHFISCH, M. M. 1994. Man-made lagoons and how their attractiveness to waders might be increased by manipulating the biomass of an insect benthos. J. Appl. Ecol. 31:383–401.
- SCHNEIDER, D. C. 1985. Predation on the urchin *Echinometra lucunter* (Linnaeus) by migratory shorebirds on a tropical reef flat. J. Exp. Mar. Biol. Ecol. 92:19–27.
- ——, AND B. A. HARRINGTON. 1981. Timing of shorebird migration in relation to prey depletion. Auk 98:801–811.
- SENNER, S. E., AND M. A. HOWE. 1984. Conservation of nearctic shorebirds. Pp. 329–421, *in* J. Burger and B. L. Olla, eds. Shorebirds: breeding behavior and populations. Plenum Press, New York, New York.
- Weber, L. M. 1994. Foraging ecology and conservation of shorebirds in South Carolina coastal wetlands. Ph.D. Dissertation, Clemson University, Clemson, South Carolina. 126pp.
- ——, AND S. M. HAIG. 1996. Shorebirds use of South Carolina managed and natural coastal wetlands. J. Wildl. Manage. 60:73–82.
- ——, AND ———. 1997. Community structure associated with shorebirds in South Carolina coastal soft-sediments. Can. J. Zool. 75:245–252.
- Wenner, E. L. 1986. Benthic macrofauna. Pp. 255–293, *in* M. R. DeVoe and D. S. Baughman, eds. South Carolina coastal wetland impoundments, Vol. II: Technical Synthesis, Publication #SC-SC-TR-86-2. South Carolina Sea Grant Consortium, Charleston, South Carolina.
- WILLIAMS, K. R. 1987. Construction, maintenance and water control structures of tidal impoundments in South Carolina. Pp. 138–167, in W. R. Whitman and W. H. Meredith, eds. Proceedings of a symposium on waterfowl and wetlands management in the coastal zone of the Atlantic flyway. Delaware Department of Natural Resources and Environmental Control, Dover, Delaware.
- WILSON, W. H. 1991. The foraging ecology of migratory shorebirds in marine soft-sediment communities: the effects of episodic predation on prey population. Am. Zool. 31:840–849.
- WOLFF, W. J. 1969. Distribution of non-breeding waders in an estuarine area in relation to the distribution of their food organisms. Ardea 57:1–28.
- ZWARTS, L., AND A.-M. BLOMERT. 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. Mar. Ecol. Prog. Ser. 83:113–128.
- ——, AND P. ESSELINK. 1989. Versatility of male curlews *Numenius arquata* preying upon *Nereis diversicolor*. deploying contrasting capture modes dependent on prey availability. Mar. Ecol. Prog. Ser. 56:255–269.

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