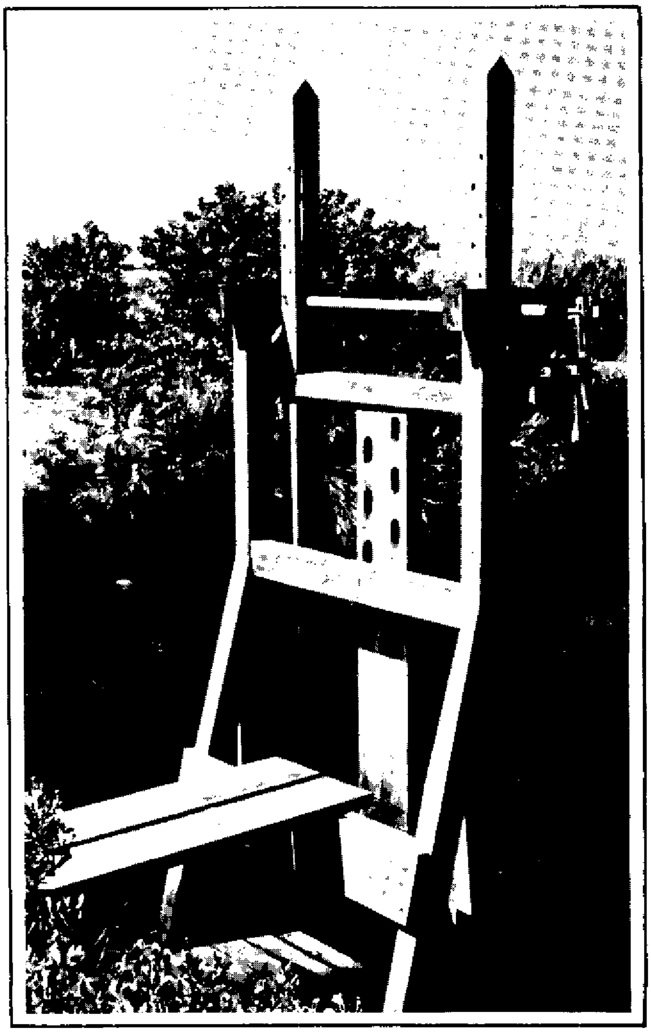
South Carolina
Sea Grant Consortium

SOUTH CAROLINA COASTAL WETLAND IMPOUNDMENTS:

Ecological Characterization, Management, Status, and Use

Volume II: Technical Synthesis

Edited by
M. Richard DeVoe
Douglas S. Baughman



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PREFACE

Coastal wetland impoundments, remnants of a once-flourishing rice culture industry, are the focus of a wetlands management controversy in the State of South Carolina. At one time, impoundments comprised approximately 29% of the State's 504,000 acres of tidal wetlands. Approximately 15% of these wetlands are currently impounded and are managed primarily for waterfowl habitat. Recent interest in reimpounding formerly impounded wetlands for additional waterfowl habitat and aquaculture has raised a number of ecological, policy and management questions. The controversy has focused on the question of how the state should regulate and monitor activities proposed for wetland areas which had been or are now impounded.

The Coastal Wetland Impoundment Project (CWIP) was designed to generate the first comprehensive characterization of a coastal impoundment system in South Carolina. The purpose of this investigation was to develop an information base which could be used by policy-makers and regulatory agencies to address the complex questions surrounding this valuable state resource.

The CWIP, a multi-institutional effort, was conducted at the Tom Yawkey Wildlife Center, near Georgetown, S. C., from summer 1982 to spring 1985. Each element of this four-year effort was reviewed by a peer group of scientists in each area to maintain scientific quality. The results of the CWIP are presented in three volumes: Volume I - Executive Summary; Volume II - Technical Synthesis; and Volume III - Technical Appendix. Volume I provides a concise statement of the research findings, along with a summary of research, management, and policy recommendations. Volume II contains the detailed results of the CWIP and has been organized up into nine sections. Volume III provides supplemental technical data and information which support the results presented in Volume II. As a whole, the three-volume synthesis represents the efforts of a variety of individuals involved in the CWIP during the last four years.

Due to the number of perspectives represented in the CWIP synthesis, the terms "coastal wetland impoundments", "impoundments", "former rice fields", "diked wetlands", "impounded wetlands" and "managed wetlands" have been used interchangeably.

Any opinions expressed within the chapters of Volume II are those of the individual authors and not necessarily those of the editors or the South Carolina Sea Grant Consortium.

ACKNOWLEDGEMENTS

In a large research project such as the CWIP the list of individuals that deserve acknowledgement can be very long. During the four years of this study, the assistance of many persons was critical to the success and completion of this project; we would like to thank each person for his/her assistance. Additionally, each chapter in Volume II acknowledges the individuals associated with the research task. The acknowledgements cited here are those of the editors and the South Carolina Sea Grant Consortium.

We would like to thank the Trustees of the Tom Yawkey Wildlife Center and the South Carolina Wildlife and Marine Resources Department for allowing the research to be conducted on the Cat Island Impoundments. Special thanks are extended to Mr. R. Joyner, Resident Biologist and Project Leader, Tom Yawkey Wildlife Center, for his cooperation throughout the four years of the study.

We are indebted to S. Olsen, J. Kraeuter, L. Barclay, W. Kitchens, R. E. Turner and R. Hodson for critical review and comment on the scope and direction of the project. Additionally, a number of scientists assisted in reviewing the individual chapters in Volume II. Their efforts are greatly appreciated. Phil Wilkinson, G. Reeves and K. Williams are acknowledged for providing technical assistance on impoundment management.

Special thanks are due to Carole Olmi for her assistance in the synthesis and preparation of Volume II. Andrew Mount also assisted in the preparation of the three-volume document, while Anne Hill provided writing, editorial and production assistance. Their efforts are gratefully acknowledged.

We are especially appreciative of the efforts of Annette Wilson, who spent many hours and exhibited extreme patience in typing and word processing the document. Monica Mulvey and Pattie Christian are thanked for providing additional assistance with the typing effort. Thanks also to Wyatt Coon of the S. C. Wildlife and Marine Resources Department for his assistance with the computer system used for word processing. Karen Swanson and Lucy Hollingsworth are commended for the production of the numerous figures and graphs.

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SECTION I

INTRODUCTION AND BACKGROUND

Chapter 1

Historical Review of South Carolina's Impoundments

M. E. Tompkins

South Carolina's coastal lands, and especially its wetlands, have long served as one of the state's greatest natural resources. The U.S. Fish and Wildlife Service reports that with over 504,000 acres of wetlands, South Carolina has about 20% of the wetlands acreage on the East Coast and 11% of the remaining acreage in the United States (Tiner, 1977; O.T.A., 1984). These studies also indicate that approximately 8% of the nation's coastal wetlands were lost between the mid-1950s and mid-1970s. Recent Interior Department estimates suggest that more than 400,000 wetland acres are disappearing every year. Consequently, how to best use, manage, and conserve this threatened stock of coastal wetlands has become a question of increasing interest. In South Carolina, the use and activities in coastal wetland impoundments have posed a number of important questions for the state and its citizens for several years. These managed sites, often called impoundments in recent years, provide the focus for the research reported here.

Settlement of the state began in the coastal communities, where it was supported by trade, production of naval stores, and, subsequently, lucrative rice and indigo crops (Weir, 1983). Most of the diked wetland sites in the state can be traced back to the days of rice culture. As Weir notes, "at first, rice was sometimes grown on dry land like other crops, but planters soon learned that irrigation could be used to stimulate growth, control weeds, and drown insects" (Weir, 1983). Apparently first grown as early as 1670 (McCrady, 1901; Heyward, 1937), rice had emerged as a profitable staple crop by 1695 (Ackerman, 1977; Sirmans, 1977). By the beginning of the 1700s, a substantial rice culture, based on waterfront plantations, had already emerged in the Goose Creek area (Heitzler, 1983). For years, the entire colony's growth was driven by the expanding rice culture. "In 1700 slightly under 400,000 pounds [of rice] were exported; during each of the next two decades exports quadrupled and then nearly tripled again during the 1720's... In all probability, the amount of new land cleared and planted in rice during the 1730's matched the total brought under cultivation during the previous forty years" (Weir, 1983). Much of this rice was produced for export, with ports in Holland, Germany, and Portugal dominating the market (McCrady, 1899). The market for rice declined dramatically in the 1740s, but the problems this created for South Carolina's rice planters were ameliorated by the emergence of markets for indigo and later after the Revolutionary War, for cotton. Rice and indigo flourished along the upper part of the coast, with Georgetown defining the northern limit of rice culture (apart an area around the Cape Fear River), while in the Beaufort area, rice culture competed with sea island cotton (Rogers, 1970; Kovacik and Mason, 1985). Rogers (1970) estimated that the Georgetown area of the state alone produced nearly half the nation's total rice crop by 1840.

THE RICE-CULTURE PERIOD

As rice became a valuable crop, the land it was grown on grew in value. In the early colonial period, land policy was shaped by the Lords Proprietors, who received their charter in 1663. They granted land to individuals, often on request, viewing their grants as serving four purposes according to Ackerman (1977): "as a means of encouraging immigration, a reward for services beneficial to the colony, a return on investments in the colony, and a source of revenue." A grant was obtained by petitioning the Governor and Council, who would then issue a warrent authorizing a survey of the tract (generally ranging from 50 to 100 acres per family member, although much larger grants were assembled in some cases). The resulting survey provided the basis for the grant from the

Proprietors or the Crown, usually after fees and "quitrents" were paid (Weir, 1983). However, some were allowed to purchase their lands outright.

Conflict over the payments owed the proprietors and their land policies produced increasing controversy in the colony. The passage in 1695-1696 of what became known as Archdale's Laws conceded a greater role to the colonial assembly (Ackerman, 1977). The proprietors increasingly sought to restrict grants of land and to ensure the payment of quitrents they felt they were due. The assembly responded by refusing to recognize proprietary authority in the so-called Revolution of 1719 (McCrady, 1899). Ackerman (1977) attributed the revolution, in part, to the "chaotic land system." "Although they did not give up legal possession until 1729, the proprietors' actual control of the colony ended in 1719" (Ackerman, 1977). The Crown took provisional control of the colony in 1720 and returned the land to royal control through the purchase of seven of the eight proprietor's shares in 1729 through an act of Parliament (Ackerman, 1977).

The new Royal Governor, a substantial landholder with ties to the proprietors, moved after his arrival in 1730 to restore order to the land system. In 1731, the Quit Rent Act was passed, establishing the basis for new grants and for the resolution of old claims to land. When the royal government began granting land, there "was a rush to grab potential rice lands at the periphery of settlement. In less than two years, for example, the entire areas between the Combahee and Coosawatchie rivers, which would become Prince William's Parish, passed into private hands" (Weir, 1983). The resulting controversy over the interpretation of old grants, the speculation encouraged by the new act, and the application of the Quit Rent Act in general, "ended in a general victory for those favoring a liberal land system" (Ackerman, 1977). The resulting expansion proceeded so rapidly that "...those who wanted additional rice land in South Carolina by the mid-eighteenth century almost had to buy, inherit, or marry it" (Weir, 1983).

This rush was stimulated by the developing craft of rice culture, which had quickly developed into an enterprise requiring extensive irrigation. This initially lead to the use of fields located next to inland waters, then subsequently to fields in which water levels could be manipulated through the influence of tidal cycles. The development of this tidal culture (sometime before the middle of the eighteenth century) roughly doubled the productivity of field hands (Heyward, 1937; Weir, 1983). By the end of the century, these tidally influenced fields dominated the production of rice. It was, nonetheless, difficult to prepare a rice field, because swamps and hardwood bottomland forests had to be cleared, and dikes, level beds, drainage ditches, water reservoirs, and surrounding embankments had to be prepared. All of this was done with hand implements no different from those used for hundreds of years (Heitzler, 1983). Much of the work was done by slaves. Consequently, slavery played a critical role in the rice economy.

During the early part of the nineteenth century, rice culture continued to play an important role in South Carolina's economy. Its growth was facilitated by the development of mechanical mills, which replaced the wooden mortar and pestle, for preparing the rice for market (Heyward, 1937). Prices peaked in 1805 and continued at high levels for the next decade in response to the European wars (Heyward, 1937). Prices rose again late in that decade, then stabilized during the 1820s (Freehling, 1965).

Sea island cotton also played an important role in the development of coastal plantations along the lower portion of the coast during the early part of the nineteenth century. Much of this cotton was grown on lowland or drained sites protected by dikes, which would later become a part of the state's impoundment resource. By the 1840s some planters were draining salt marshes to create cotton fields (Kovacik and Mason, 1985). This cotton did not compete with the short-staple cotton grown elsewhere and, as a result, did not suffer from the problems of overproduction that plagued the regular cotton crop. Ramsay dates its emergence as an important crop in the state to the period following the Revolution, with the first big export crop emerging in 1795 (Ramsay, 1809, in Bruchey, 1967). Export records for the entire country suggest that the peak years for sea island cotton production occurred in 1823 and 1827 (Bruchey, 1967). Problems with control of the fiber's quality emerged during this period, but Freehling (1965) and Smith (1958) suggested that production had improved enough by the early 1830s for cotton to become a significant crop for low-country planters. Smith (1958) provided some evidence from export data suggesting that production of these fine fibers declined gradually until the 1850s, then suddenly grew dramatically in 1852 and continued to grow until 1860 (also see: Bruchey, 1967). Smith attributed this growth in production to the use of guano-based fertilizers introduced during this period. His evidence also suggests that sea island cotton production remained secondary to rice culture even in the Beaufort District in the 1850s (Smith, 1958).

Rogers reported that rice production continued to grow during the period from 1840 to 1860. Production figures from Charleston and Georgetown county (Table 1.1) reveal the dominance of the South Carolina plantations in the nation's rice production during this period. Difficulties emerged during this period; South Carolina's rice production grew until the Civil War, but the nation's production was also growing. This competition grew sharply following the Civil War as rice emerged as an important crop in Arkansas, Louisiana, and Texas. A more favorable climate in these states, coupled with upland planting and pumped irrigation water, produced rice at a lower cost than South Carolina planters were able to achieve.

THE DEMISE OF RICE CULTURE

The aftermath of the Civil War brought new disruptions to rice culture. Economic difficulties, including crop failures in 1865, 1866, 1867 (Rogers, 1970), and an unreliable labor supply handicapped planters who tried to continue rice cultivation. Natural catastrophes, including storms and more frequent freshets attributed to "the draining of fields and destruction of forests in the upper part of the state" (Rogers, 1970) created further difficulties that eventually proved insurmountable. In Georgetown County, for example, the peak harvest during Reconstruction came in 1872, when 16,900 acres were planted (compared to an average of 46,000 up to 1860), and the harvest amounted to an estimated 9,105,000 pounds (compared to the peak harvest of 57,077,000 pounds in 1859). This harvest was preceeded by a wet harvest in 1871 and followed by a heavy and protracted freshet from August to mid-October in 1873 (Roger, 1970).

In spite of several attempts to revive the declining industry, it essentially died out in the years that followed. Doar (1936) reported that the harvest had declined to 418,722 pounds in 1906. Heyward (1937) attributed the beginning of the final decline to competition from crops in Louisiana, Texas, and Arkansas which he dated to 1885. Ravenel (in Doar, 1936), one of the last planters, attributed the decline to competition for the labor supply, notably with phosphate mining and the timber industry. Heyward reported planting his last commercial crop in 1913, with storms in the several preceding years damaging the fields beyond repair. Mrs. Elizabeth W. Allston Pringle ("Patience Pennington") abandoned her efforts to grow rice at White House Plantation in 1906 (and earlier at Chicora Wood) (Pennington, 1961). Burton (in Doar, 1936) identified Theodore D. Ravenel as the "last large commercial rice planter in South Carolina"; he planted rice on the Cooper River, then the Edisto, and finally the Combahee, until 1927.

Table 1.1
Rice production (in pounds) in the U.S.
and selected South Carolina counties (Rogers, 1970).

Location	1840	1850	1860
National production	80,841,422	215,313,497	187,167,032
South Carolina			
Georgetown District	36,360,000	46,765,040	55,805,385
Charleston District	11,938,750	15,700,603	18,899,512
Beaufort District	5,629,402	47,230,082	18,790,918
Colleton District	5,483,533	45,308,660	22,838,984

The sea island cotton industry remained important in the decades following the Civil War, although the acreage devoted to its cultivation declined (Kovacik and Mason, 1985). Planters remained optimistic about the value of the crop through the turn of the century, but "the boll weevil in 1919 struck the Sea Island cotton crop such a devastating blow (90 per cent crop failure) that the planters gave up the crop" (Lander, 1960). Wallace quoted a 1932 story in the Charleston News and Courier which indicated that the crop had been "virtually abandoned" (Wallace, 1934); according to Kovacik and Mason (1985), the last crop was grown on John's Island in 1956.

IMPOUNDMENTS IN THE TWENTIETH CENTURY

Interest in another resource often identified with the coast emerged in the post-Reconstruction era. President Grover Cleveland visited a friend on South Island in 1884 for a duck-hunting expedition; his unwelcome but widely publicized swim (and timely rescue), coupled with articles in the popular press, drew attention to the old plantations. By 1905, Bernard Baruch had completed the purchase of the various properties at the foot of Waccamaw Neck recreating what he called, "Hobcaw Barony," (Rogers, 1970), while the properties comprising what is now known as Brookgreen Gardens were assembled in 1930. Rogers (1970) has detailed the sale of many other plantations over these years: "By 1931 there was scarcely a plantation left in the hands of native South Carolinians. The final spate of purchases had taken place after the stock market crash of 1929. Money in land was safer than money in stocks."

The waterfowl resource had not gone unnoticed in earlier years; indeed, its great abundance required little comment. Heyward (1937) suggested that the reason planters before the Civil War"... did not care for duck shooting was that these birds were then so plentiful in their fields, and hence so easily killed, that their killing was not considered good sport."

Other industries identified with the coastal areas also grew in importance after the beginning of the twentieth century. Sawmills became an important industry in the state, to the point that after 1900, it became one of the state's top producers of wealth. With the development of technologies for the manufacture of wrapping paper and cardboard from softwood pulp, the coastal regions turned to these related industries (Lander, 1960). These would later become particularly important in the Georgetown area (Rogers, 1970) following the construction of International Paper's facility. As a result, a number of old plantation sites were acquired for the extensive forests located on them.

Interest in waterfowl hunting continues to play an important role in shaping the use of these wetland fields and the old plantations. The timber industry also remains interested in these sites. Other uses have emerged as well. Substantial areas have been granted to the state, for public preservation and game management. Because the old plantations consist of large contiguous tracts of land, with substantial waterfront acreage, they have also been used as the sites for developments for residences, vacation homes, and resorts. Each of these activities is, nonetheless, based on the fields created for rice and cotton culture during the eighteenth and nineteenth century -- but now used for other purposes.

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Chapter 2

Coastal Wetland Impoundment Project: Problem Identification and Project Description

M. R. DeVoe and D. S. Baughman

PROBLEM IDENTIFICATION

Although extensive activities have placed pressures on South Carolina's wetlands resource, estimates indicate that less than 300 acres of the state's 504,000 acres of coastal wetlands have been destroyed or lost since 1978 (J. Smith, personal communication). Recent attention, however, has focused on the fate of the state's managed wetlands, or impoundments, remnants of the once-flourishing rice culture industry of the nineteenth century. Representing approximately 29% of South Carolina's wetlands, over 70,000 acres remain encompassed by earthen dikes with functional water-control structures, and another 74,000 acres represent previously impounded areas that have lost their structural integrity through natural deterioration and neglect by man.

The abundance of this rice-field acreage had been viewed in the past as a coastal resource for which no development or improvement modifications were sought. Recent interest, however, in converting these unutilized areas for waterfowl management, aquaculture, and other uses has increased significantly. Those individuals who claim title of ownership or, at the least, assume ownership are now realizing that converting unused diked wetland areas or reimpounding former rice fields for active management can result in economic benefits.

This surge in interest in South Carolina resulted in some 20 permit applications for the repair or reconstruction of over 3000 acres of former rice fields between 1967 and 1981. Since 1981, at least another half dozen impoundment applications have been submitted to the State of South Carolina for consideration. It has been through the permitting process at both the state and federal levels that the major issues surrounding the current impoundment controversy have emerged.

Regulatory and Policy Issues

Current South Carolina policies clearly state that the construction of impoundment dikes is prohibited in natural wetland areas. Construction activities within existing impoundment systems do not require permit approval unless cross diking is involved. The condition of cross dikes in an existing impoundment requires a letter of approval from the South Carolina Coastal Council and a Section 404 permit (Clean Water Act of 1977, et seq.) from the U.S. Army Corps of Engineers, which allows an applicant to conduct dredge-and-fill activities in navigable waters.

The permit and decision-making process becomes more complex when the proposed activity involves formerly impounded wetlands. Regulations are in place to allow for the reimpoundment of former rice fields as long as a series of permits are acquired at both the state and federal levels. However, the activity must be shown to be in the public interest.

The complexity of the regulatory process is evident when the process is examined in more detail. At least 13 state and federal agencies are involved in the permit and decision-making process regarding impoundments, primarily through public notices. At the state level, the following agencies have played a major role: South Carolina Wildlife and Marine Resources Department, South Carolina Department of Health and Environmental Control, and the South Carolina Attorney General's Office. On the federal side, the U.S. Fish and Wildlife Service (Department of the Interior), the National Marine Fisheries Service (Department of Commerce), and the U.S. Environmental Protection Agency in particular have voiced strong concerns during public-notice periods of several impoundment permit applications.

Also intimately involved in the impoundment controversy are the coastal landowners and impoundment managers (e.g., the Historic Ricefields

Association), environmental organizations (e.g., the Sierra Club, and the S.C. Wildlife Federation), and concerned citizen groups (e.g., the S.C. League of Women Voters). These groups have also taken the opportunity to state their respective positions on the issues in the public-notice period.

During the consideration of recent permit applications, the lack of available scientific information on impoundment systems emerged as a major obstacle in the decision-making process. This lack of data has affected the ability of state and federal regulatory agencies to make well-informed decisions on permit applications for impoundment activities, and hence the arguments used by all parties either opposed to or in favor of impoundments have been based primarily on data gathered from research on estuarine wetland systems. This situation has led to a number of disagreements among scientists, managers, and regulators on how best to interpret and apply these data to the current controversy. To further complicate this situation, the available literature suggests conflicting opinions among the scientific community.

One case, now before the S.C. Supreme Court, illustrates the dilemma clearly. In December 1981, after eight years of consideration, the S.C. Coastal Council issued a permit to allow the reimpoundment of 660 acres of wetlands in the Santee Delta region of South Carolina. The permit was immediately appealed by the S.C. Attorney General's Office and by several environmental and public-interest groups. The matter was referred to a hearing officer for the purpose of developing a "Findings of Fact" document. A hearing was held, and many experts in environmental science were called to testify. It was apparent from the "Findings of Fact" (Smith, 1982) that a large data gap existed with respect to marsh impoundments and subsequent effects on adjacent natural wetlands: "Opinions concerning the impact of the impoundment on the Santee Delta varied from expert to expert and in some respects depended upon whether or not the opinion came from a waterfowl biologist or from a marine biologist....It was conceded by all of the scientists...that far more research is needed with regard to impoundments in general, and in particular their effects on adjacent undisturbed wetlands [and] their productivity..." This situation illustrates one of the key factors in the impoundment controversy: the development of consistent impoundment policies and the process by which permit decisions are made are hindered by the lack of fundamental scientific data.

One additional factor that requires attention is the issue concerning ownership. While ownership of submerged lands is a complex subject and is dealt with only briefly in Chapter 3, it has become more entwined within the impoundment controversy because of complexities inherent in the state regulatroy process. The state's agencies do not require proof of ownership form applicants seeking permits to repair or restore formerly impounded areas, despite the fact that the State of South Carolina, through the S.C. Attorney General's Office, assumes ownership over all tidelands within its borders. On the other hand, private landowners who claim ownership over these lands base their claims on the fact that they can trace title back to King's Grants or grants by the state in the seventeenth and eighteenth centuries. As a result, each application submitted to the state permit agencies for impoundment repairs or restoration has been challenged by the attorney general's office on the basis of ownership. Each application may require a formal opinion by the attorney general's Office to validate claims of ownership while the state permit agencies are acting on the application.

Ecological and Scientific Issues

Numerous studies have been conducted on estuarine and salt-marsh systems on the East and Gulf coasts of the United States (see: Sandifer et al., 1980 for a review). Schelske and Odum (1962) attributed the high productivity of these waters to tidal action, abundant nutrient supplies, conservation and rapid turnover of nutrients, three units of primary production (macrophytes, benthic algae, and phytoplankton), and year-round production. The "outwelling" of nutrients and organic detritus from salt marshes has been compared with the "upwelling" of nutrients from deep water in supporting the productivity of the adjacent waters and coastal fisheries.

In addition to the multitude of studies on salt-marsh productivity, considerable research has focused on the utilization of salt marshes by larval and juvenile stages of finfish and shellfish (e.g., Giles and Famora, 1973; Weinstein, 1979; Epifanio et. al., 1984; Zimmerman et al., 1984). This research suggests that estuarine marsh habitat is essential to the life cycle of a large number of transient estuarine species.

It is not known to what degree these ecological attributes are characteristic of coastal wetland impoundments; however, some information is available. Work by Copeland (1974) has suggested that new ecological systems replace old ones when a portion of an estuary is impounded, and significant changes in hydrography occur simultaneously. Overall, it appears that water circulation is decreased and in some cases may become virtually nonexistent; the nature of the substrate changes as a result of increased sedimentation, aquatic vegetation may be smothered, and water salinity, temperature, oxygen, pH, and nutrient levels are affected (Copeland, 1974; Dean, 1975). Draining and filling practices and variations in hydrographic variables may affect the diversity of species occuring within shallow rice-field impoundments. Several studies (Gilmore et al., 1981; Harrington and Harrington, 1982; Rogers and Herke, 1985) have shown that wetland impoundment and weir systems significantly affect the abundance and diversity of estuarine fish species which characterize adjacent open wetland areas. Although such areas are able to support a limited variety of estuarine species, their productivity is reportedly high (Dean, 1975).

We have very little direct knowledge of how the basic functional processes of impoundment systems related to those of natural wetland ecosystems. Nevertheless, some important background information is available from South Carolina. For well over a decade, scientists at the state's Wildlife and Marine Resources Department have conducted research emphasizing development of better habitat management procedures for waterfowl (e.g., Wilkinson, 1970, 1976; McKenzie et al., 1980). Other research by department scientists has included the use of marsh impoundments for mariculture (Lunz, 1951, 1968; Bearden, 1967; Anderson, 1976; Manzi et al., 1977), the importance of impoundments to endangered species (Murphy and Coker, 1978; Wilkinson, 1985; Endangered Species Section, unpublished reports), and general ecology and productivity of impoundments (Tiner et al., 1976; Tiner, 1977; Manzi et al., 1977; Sandifer et al., 1980).

At the University of South Carolina, extensive field studies have been conducted on the ecology of intertidal habitats and old rice fields

(Dean, 1973, 1975, 1979; Dennis, 1977; Shenker and Dean, 1979; Bozeman and Dean, 1980; and Reis and Dean, 1981). A group of researchers at The Citadel has studied the vegetation associated with abandoned rice-field impoundments and adjacent wetlands in freshwater areas to determine possible successional patterns (Kelley, 1982). Investigators at Clemson University's College of Engineering have studied impoundment design and construction (Zielinski et al., 1978; Zielinski and Castro, 1979).

Managed impoundment systems appear to be quite productive. Sandifer and Miglarese (1982) have suggested that impounded wetlands may enhance the productivity of estuarine areas by "providing nursery grounds and spawning sites for zooplankton, which are then periodically released into the open estuary when water is released" from the impoundment. Relative to export from impoundments, Joyner (personal communication) indicates that full consideration is not given to the amount of nutrients that are removed from these systems by organisms that "fly, swim or crawl away"; for example, tens of thousands of wintering ducks can fly away with a great quantity of nutrients. Conversely, conflicting statements, based on early estuarine ecological studies, have been offered to dismiss arguments for the restoration and repair of impoundment systems. In a 1984 letter from the U.S. Fish and Wildlife Service to the U.S. Army Corps of Engineers, Charleston District, requesting that a permit application be elevated to the corps office in Washington, D.C., the productivity in impoundments was attributed to the closed system functioning as a nutrient sink. Basing their argument on reports by Teal (1962) that tidal flushing removes 45% of the nutrient material from the open-marsh system, the U.S. Fish and Wildlife Service maintains that impoundment productivity is due to the fact that there is little or no export of nutrient material available for recycling. Related to this are arguments that organic materials, which serve as foundational elements in the food chain, are introduced into the open wetlands system through detrital export and phytoplankton production during normal tidal flushing. It has been suggested that the creation of impoundments removes acreage from the open system, thereby diminishing the export of detrital material and the productivity of the overall system.

What complicates the situation even more is the current reevaluation by estuarine scientists of the role wetlands play in contributing to the productivity of estuarine and coastal waters. Scientists at the Institute of Ecology, University of Georgia indicate that recent studies conducted by the institute have led to a reevaluation of earlier conclusions concerning carbon and nutrient export from marshes; that is, the degree to which marshes export carbon and nutrients to their associated estuaries is "an open question, in large part depending on site-specific hydrological factors." They go on to suggest that agency concerns over the use of marshes as nursery grounds for marine organisms are valid, but that uncertainty exists as to the "quantification of this value." Nixon (1980) suggested, in reference to the importance of outwelling from salt marshes to expanded or intensive fisheries in coastal waters where upwelling is not a factor, that the argument first put forward in support of the trophic importance of outwelling is not very convincing.

Nevertheless, our understanding of impoundment processess and productivity is fragmentary at best, and comparisons with the processes and productivity of open marshes are completely lacking. In a comprehensive ecological characterization of the sea islands coastline of South Carolina, Sandifer et al., (1980) concluded that "Despite their abundance and the increased pressure for reclamation, little research is presently underway to study the ecological processes of impounded wetlands. The general lack of knowledge concerning saltmarsh impoundments makes this area of marsh ecology a principal data gap."

Impoundment Management Concerns

The management of existing impoundment systems has increasingly received attention over the last five to ten years. Management techniques employed by managers vary from one system to another; there is no "cookbook" approach to management. Although debate has centered or whether the impoundment of former rice-fields results in the isolation of the wetland from the surrounding estuarine system, little attention has been paid to the effects of various impoundment management schemes currently employed throughout South Carolina. It appears that different management regimes can significantly affect the ecological attributes of the "local" estuarine system. Thus, the quality of management has become the focus of some concern. Indeed, several South Carolina authorities have estimated that less than 50 percent of all functional impoundments are actually being effectively managed. However, nowhere does there exist a source of information on the current distribution, management, use, and overall status of impoundment fields in South Carolina.

Impoundments in South Carolina: The Issues

The major issues in this wetland controversy have touched on important aspects of our knowledge of wetland ecology and how this knowledge is translated into public policies and refinement of impoundment management techniques. Major concerns regarding the restoration of wetland impoundments include (1) the purported impacts on tidal exchange (including biomass and nutrient fluxes), nursery and habitat for aquatic organisms, and overall wetlands productivity; (2) the issues regarding the diverse and vague nature of state and federal impoundment policies; and (3) the lack of knowledge on the status of existing and formerly impounded wetlands and the variety of techniques employed by impoundment managers. Unfortuately, the information base on which the impoundment controversy has been argued is fragmentary at best, and comparisons between open-marsh and impoundment systems are completely lacking. This large data gap stimulated the South Carolina Sea Grant Consortium to develop and undertake the Coastal Wetland Impoundment Project.

THE COASTAL WETLAND IMPOUNDMENT PROJECT - PURPOSE AND SCOPE

The Coastal Wetland Impoundment Project (CWIP) was designed and initiated by the South Carolina Sea Grant Consortium in September 1982. The overall goal of this trans-disciplinary and multi-institutional effort was to provide an initial comprehensive characterization of coastal impoundment distribution, management, use, and ecology.

The ecological study components of the CWIP were initiated to identify to what degree the impoundment of intertidal wetlands alters wetland processes and to evaluate whether this modification has an impact on the resources dependent on the ecological functioning of adjacent wetlands. This identified need provided the basis for the development of the CWIP as an integrated research and extension project to examine the issues with respect to (1) state and federal impoundment policies, (2) the relationship of impoundments to wetland ecology, and (3) the effects of impoundment management on wetland systems. However, these issues are extremely broad in scope, largely because of the complex nature of the problem. Thus, the CWIP represents the inital stage of investigation on these systems and, by necessity, the study findings can not be extrapolated to all systems. The study does, however yield information relevant to the resolution to the complex questions surrounding impoundments.

General Ojectives

Upon a thorough review of the available information on coastal impoundments and detailed discussions with representatives of natural resource and regulatory agencies, impoundment managers, and environmental organizations, the following objectives were identified as the principle points for study. Each served as the basis for the development of research task initiatives. The objectives were:

(1) to determine stratigraphy, characterize hydrology, and identify and compare the major floral and faunal components of the impoundments under study;

(2) to characterize the nutrient dynamics and determine primary productivity of the study impoundments and the adjacent open wetlands;

(3) to determine and compare the recruitment, growth rates, and standing crop biomass of commercially important species in impoundments with those in adjacent open wetland areas;

(4) to determine the flow of nutrients and biomass between the study impoundments and the adjacent open wetland areas; and

(5) to determine the public-policy issues affecting impoundments: ownership, current and proposed uses, management techniques, and federal and state policy.

The primary goal of this four-year research effort was to provide an initial ecological data base on impoundment systems and their spatial relationship to adjacent tidal wetlands within the context of the many public-policy issues that have emerged. This data base has been organized and structured to provide decision makers additional information related to the complex questions currently under debate in South Carolina.

To address the five major objectives outlined above, a team of fourteen doctoral-level researchers from five of the Consortium's seven member institutions was organized to perform twelve research tasks. A list of the researchers, their affiliations, and their respective research efforts is provided in Table 2.1. More-detailed descriptions of the individual research tasks are presented in the following chapters. Taken together, the multi-disciplinary nature of the CWIP has enabled the research team to obtain a holistic view of the ecological characteristics of an impounded wetland system within a tidal wetland complex.

Project Management

Realizing the goals and objectives of this multi-investigator, multi-task project has been facilitated by the inclusion of a centralized management and coordination function. The principal investigator was responsible for overall project administration, coordination, and oversight, and the project manager provided the day-to-day coordination and oversight of the research tasks, the field and laboratory research efforts, and the preparation of draft reports. In addition, a CWIP "core group", consisting of the principal investigator, the project manager, and technical advisors, met regularly to review progress, assess project goals, and refine project tasks. The project-management team also actively solicited peer review on an annual basis to assist in the reevaluation of project thrusts and priorities and to enhance the technical quality of the study.

The most critical aspect in coordinating the CWIP involved the analysis, integration, and synthesis of project data and information. Each team of investigators prepared a draft report on the results of their research task, incorporating data and information from other tasks as appropriate. Each report was then distributed to at least three peer reviewers for detailed review and comment. Upon revision of the draft reports, detailed abstracts were prepared, highlighting the major findings and conclusions. These abstracts, along with the reports themselves, provided the information base used by the CWIP core group to prepare Section VIII, Integration of Research Results.

Table 2.1
The Coastal Wetland Impoundment Project:
Team Members and Research Tasks

Investigator/Affiliation	Research Tasks
1. Mark E. Tompkins, University of South Carolina	1. Identify and conduct analyses of impoundment policy concurrent to the ecological studies, and determine the current status (extent, management, use) of impoundment systems in South Carolina
2. James P. May, The Citadal Paul Zielinski, Clemson University	2. Characterize impoundment and wetland sediments and determine hydrologic and hydraulic attributes of the study system.
3. Hank N. McKellar, University of South Carolina	3. Determine hydrography, budgets, and submerged aquatic productivity of the study system.
4. B. Joseph Kelley, The Citadel Richard D. Porcher, The Citadel	4. Determine distribution and primary productivity of macrophyte vegetation in the study area.
5. Richard G. Zingmark, University of South Carolina	5. Determine seasonal abundance and productivity of benthic microalgae in the study area.
6. A. Keith Taniguchi, University of South Carolina	6. Determine micro- and meso-zooplankton abundances, seasonal cycles, and dynamics of the study system.
7. Bruce Coull, University of South Carolina	7. Characterize the meiofauna population of the study impoundments.
8. Elizabeth L. Wenner, S.C. Wildlife and Marine Resources Dept. Paul A. Sandifer, SCWMRD Robert Van Dolah, SCWMRD	8. Determine the composition, structure, and population dynamics of macrobenthic invertebrates and decapod crustacean communities of the study area.
9. Charles A. Wenner, S.C. Wildlife and Marine Resources Dept.	9. Determine the composition, structure, and trophic dynamics of fishes at the study area.

Table 2.1 Continued

10. John Mark Dean, University of South Carolina	10. Estimate and compare individual growth rates of ecologically importants and adjacent tidal wetland area.
11. Robert L. Joyner, Tom Yawkey Wildlife Center, SCWMRD Marc Epstein, Tom Yawkey Wildlife Center, SCWMRD	11. Determine the utilization of the managed and unmanaged areas by waterbirds and alligators.
12. Jack M. Whetstone, Clemson/Sea Grant Marine Extension Program	12. Disseminate project results through the C/SG Marine Extension Program and assist nonprofit organizations in developing sound impoundment strategies.

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SECTION II

SURVEY OF COASTAL WETLAND IMPOUNDMENTS IN SOUTH CAROLINA

Chapter 3

Scope and Status of Coastal Wetland Impoundments in South Carolina

M. E. Tompkins

INTRODUCTION

Before discussing the ecological characteristics of these wetland systems, the extent of the affected resource must be examined. Clearly, the character of many of the fields cultivated before the Civil War changed once intensive management was no longer practiced. For example, Morgan et al. (1975) found that 39% of the acreage "under water control during the era of rice culture" in the South Edisto, Ashepoo, and Combahee estuary was no longer under control in 1972-1973. Nevertheless, remnants of the old fields are still visible, and some fields are still managed all along the coast.

To provide some measure of the extent of this resource, the S.C. Wildlife and Marine Resources Department conducted a substantial study of the state's coastal marshes in 1975-1976 (Tiner, 1977). Using aerial photographs and subsequent ground truthing, USGS topographic maps (primarily the 1:24,000 scale series) were employed to record the sites of wetlands and impounded fields. The wetlands inventoried were divided into seven types: (1) beach zone, (2) low salt marsh, (3) high salt marsh, (4) brackish-water marsh, (5) freshwater marsh, (6) impoundments, and (7) diked disposal areas. Subsequent field investigations were conducted from August 1975 to May 1977 "to obtain descriptive information about the plant ecology of the various marsh types." Salinity regimes were also classified in this process. This inventory was supplemented with a "form letter requesting information on managed waterfowl impoundments" sent to "several knowledgeable individuals" (Tiner, 1977).

In 1984, a supplement to this report was prepared by the S.C. Coastal Council, using the same USGS map series and more-recent S.C. Coastal Council color infrared aerial photographs (1:20,000 scale) (S.C. Coastal Council, 1984, unpublished report). In this project, an inventory of formerly impounded sites was also included, with salinity regimes identified (based on the earlier classification of salinities) and three major types of construction (ricefields, waterfowl impoundments, and cotton fields) distinguished.

Although two earlier studies had examined particular watersheds along the coast (Gresham and Hook, 1982; Morgan et al., 1975), no previous study has examined the entire state coast. Apart from these earlier partial studies, anecdotal information drawn from the (often extensive) experience of particular site managers has provided our best evidence about current use and management practices. Thus the objective of this portion of the CWIP was to complete a survey of impoundment owners and managers to determine the current ownership, management techniques, uses, and status of coastal impoundments in South Carolina.

METHODS

In this study, an extensive survey of S.C. Coastal Council aerial photographs (using only the photography available as of December of 1983) was undertaken to identify the sites of current and formerly impounded wetland fields. Any possible sites, including problematic ones identified through the aerial photographs, were marked on USGS maps. This information was related to the county tax records for the eight coastal counties of the state (Berkeley, Beaufort, Charleston, Colleton, Dorchester, Georgetown, Horry, and Jasper) during March through July, 1984. The names and addresses of those paying taxes on areas that appeared to be diked or to have been diked in the past, along with the addresses of those adjacent to these areas (where no obvious claimant to the site of a current or former diked field could be identified), were incorporated into a master name-and-address file.

This name-and-address file was then divided into two segments. One group included those evidently claiming these fields. This group was sent a four-page survey aimed at describing the site and a three-page survey aimed at describing the management of currently impounded sites. The other group, much larger in number, included those near apparently unclaimed sites, evidently claiming small sites (less than 10 acres), or claiming sites that appeared to be formerly impounded fields that had fallen into disrepair. This group was contacted with a brief, two-page questionnaire primarily to ensure that sites that were not clearly identified from aerial photographs were not overlooked. When respondents to the brief questionnaire indicated that they were actively managing sites larger than ten acres, a followup letter was sent asking them to complete the more extensive questionnaire.

In all, more than 1500 individual sites were identified. Up to three separate inquiries were sent to each identified respondent. After dropping those sites where respondents could not be contacted, and combining cases where a single respondent controlled more than one site, 1294 individual names remained. Of these, 659 responded (including more than 40% from each county), for an overall response rate of 50.93% (Table 3.1). In addition, 14 national corporations, with more than one site involved, were contacted separately to ask for their cooperation. Nine of those responded, including all but one known to be actively managing impounded land in the state. Finally, each of the sites managed by state agencies was incorporated into the study, through a combination of formal inquiries, telephone discussions, and site visits. As a result of these contacts, over half the impounded acreage along the state's coast and perhaps as much as three-fourths of the total area identified in aerial surveys is incorporated in the results (see Table 3.2).

As a check on these estimates, a list of waterfowl impoundments in Georgetown County was obtained and compared to the confidential list of respondents. The list incorporated 44 sites, with 16,494 acres of fields included. Twenty-eight of these sites were included among the responses (reporting 22,697 acres of managed fields, rather than the 12,005 acres of fields attributed to these sites on the list). In addition, responses were received from nine other sites in the areas covered, not mentioned in this outside list, incorporating an additional 1199.5 acres of managed wetland fields.

A few sites were missed in this process: aerial photography was inadequate for a few areas and errors in photointerpretation were undoubtedly made; tax records were erroneous in some instances; the mails were not delivered in some others; and county records could not be located for a few sites.

Table 3.1

Response rates to mailed survey instrument.

County	Number of Responses*	Response Rate
Berkeley	40	42.1%
Beaufort	40	48.8%
Charleston	256	51.4%
Colleton	109	48.2%
Dorchester	6	60.0%
Georgetown	137	54.8%
Horry	10	47.6%
Jasper	61	54.5%

* (Multiple sites controlled by a single respondent considered to be a single response in this summary.)

RESULTS

Extent of Impounded Wetlands

Table 3.2 displays the distribution of sites, as reported in the Tiner (1977) and Coastal Council (1984) studies, and the distribution of acreage covered in this survey. In the Tiner study, actively managed fields were reported, whereas the Coastal Council study identified former impoundment sites. In this study, three types of fields were identified:

Table 3.2

The distribution of impounded and formerly impounded wetlands along the coast of South Carolina (acres of land)

	Tiner Study (1977)	Coastal Council Study (1984)	Tompkins/Sea Grant Survey Responses*		
			Impounded		
Watershed or System	Impounded	Formerly Impounded	Intact	Need Repair	Formerly Impounded
Little River, Myrtle Beach, Murrells Inlet, Pawleys Island, North Inlet	565	258	0.0	0.0	0.0
Winyah Bay	4,055	21,067	6,578.5	770.0	11,167.6
Santee River	9,837	14,337	8,838.0	11,476.0	8,309.6
Bulls Bay	2,493	484	1,362.2	41.0	23.0
Charleston Harbor	5,111	8,860	674.0	789.5	2,621.2
Stono-Kiawah	2,285	3,676	139.5	529.0	776.7
North Edisto	1,132	464	187.7	0.0	152.0
St. Helena Sound	5,843	15,098	13,540.0	2,771.1	11,878.5
Fripp-Trenchards	72	3	0.0	0.0	0.0
Port Royal Sound	1,329	866	1,037.0	8.0	2,271.0
Calibogue Sound	113	117	0.0	0.0	0.0
New-Wright	1,688	789	222.0	0.0	310.0
Savannah	4,321	7,903	4,082.0	0.0	4,101.0
TOTALS	70,451	73,922	36,660.9	16,384.6	41,610.6

*In addition, some fields were reported without the status of the dikes being described (including acreage in Winyah Bay [1224.1 acres], Bulls Bay [50 acres], Charleston Harbor [16 acres], St. Helena Sound [3,600 acres], Port Royal Sound [85 acres]) for an additional 4975.1 acres incorporated into the survey; where such responses are involved, they appear in other calculations as "actively managed" fields. "Spoil" areas are not included in these figures.

(1) intact fields, which included those with intact dikes and water-control structures (although some of these fields were reported to be fully enclosed and never drained); (2) fields needing repair (either to the dikes or water-control structures); and (3) former impoundments (meaning formerly diked wetland fields; they are reported separately in the table).

Many of today's managed impoundments lie in a few watersheds. These managed sites, in general, are located in the old rice fields. Although questionnaires were mailed to people in each watershed, no responses were received from owners or managers in several systems with only a few managed fields. Even so, the response rate to this survey of private individuals and the distribution of responses provided good coverage of the state in a variety of settings. In Winyah Bay, survey responses indicated that more coastal wetlands were being actively managed than aerial photography suggested; this probably reflects both the ambiguity of aerial photography and the casual management of some sites. County assessor's records have provided some check on the acreage figures reported, which are not always precise but appear to be generally accurate.

The Status of Impounded Wetlands

The fields reported in the survey vary dramatically in their size, ranging from 1 to 1168 acres. In addition, a number of responses were received that did not report individual field sizes (including one response incorporating 3600 acres in diked fields). Field sizes are reported in Fig. 3.1a and distributed across four categories. As in Morgan, et al. (1975), many relatively small fields were identified. Experienced managers believe that these fields are more readily controlled than larger fields and, as a result, are more responsive to intensive management practices. However, Fig. 3.1b shows that much of the managed acreage occurs in relatively large fields. Similarly, Fig. 3.1c and 3.1d show that this is also true of formerly diked fields: in numbers, these former fields are distributed relatively evenly across the size categories, but in acreage, most of the resource occurs in large fields.

Because virtually all the managed coastal wetlands resource is derived from fields created years ago, the current condition of these

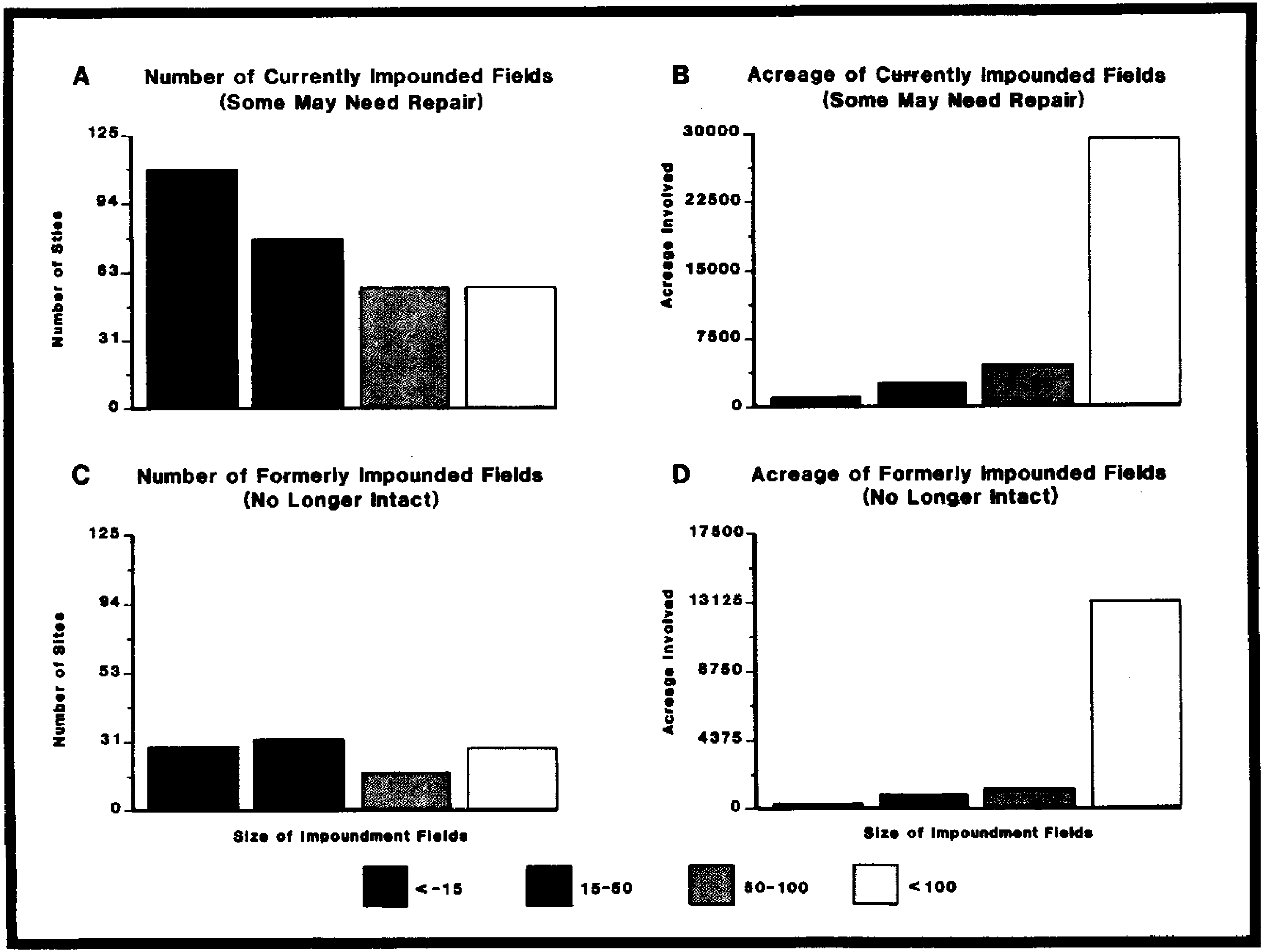

Figure 3.1 Number and acreage of currently (A & B) and formerly (C & D) impounded sites.

sites has proved to be an important factor in shaping our understanding of their resource potential. The condition of the fields described in the responses is portrayed in Fig. 3.2. Substantial acreages of diked wetlands (34,265.1 acres) are reported to be in working order. Fewer fields are reported to be fully enclosed with no tidal exchange permitted (2396 acres); in Table 3.2, these are listed as intact fields. Sites totaling 14,758.5 acres (with 11,161 acres located on a public site) are reported in which the dikes and/or water-control structures need repairs, although the impoundments are enclosed and the water controlled. For a small number, 1626.1 acres, the water-control structures are broken or there are breaks in the dikes; these two groups are listed with fields that need repairs in Table 3.2. Most of the fields in this second group (including the 11,161 acres under public management) are actively managed sites; as a result, subsequent reports will treat both intact fields and those needing repair together. Apart from these fully enclosed fields, an additional 387 acres are reported in which the dikes have been washed over. In addition, a substantial number of formerly enclosed sites (former impoundments) are reported (totaling 41,611 acres). Thus, if we consider only the fields claimed by private parties, we find that they can be divided into two major groups, currently intact fields and formerly enclosed fields which would generally require a substantial expenditure to restore them to operating condition. In addition, a much smaller group of fields exists in which repairs of one sort or another are required to restore them to fully satisfactory condition. The distribution of fields by their reported condition and the salinities at the site are given in Table 3.3.

These responses provide an imperfect guide to field salinities and also reflect the consequences of the effort to control salinity, because that is one purpose of impoundment management. Generally, fresh or brackish water is viewed as the desired outcome. Several respondents reported that the current rediversion of the Santee-Cooper River Systems had begun to affect the salinity of the water in their fields. Still, these salinity reports vary from those reported in Tiner (1977), which are often used for regulatory purposes and which were employed in the S.C. Coastal Council study (1984) as well. Tiner (1977) classified 27% of the sites as fresh and 27% as salty for those who reported that their fields

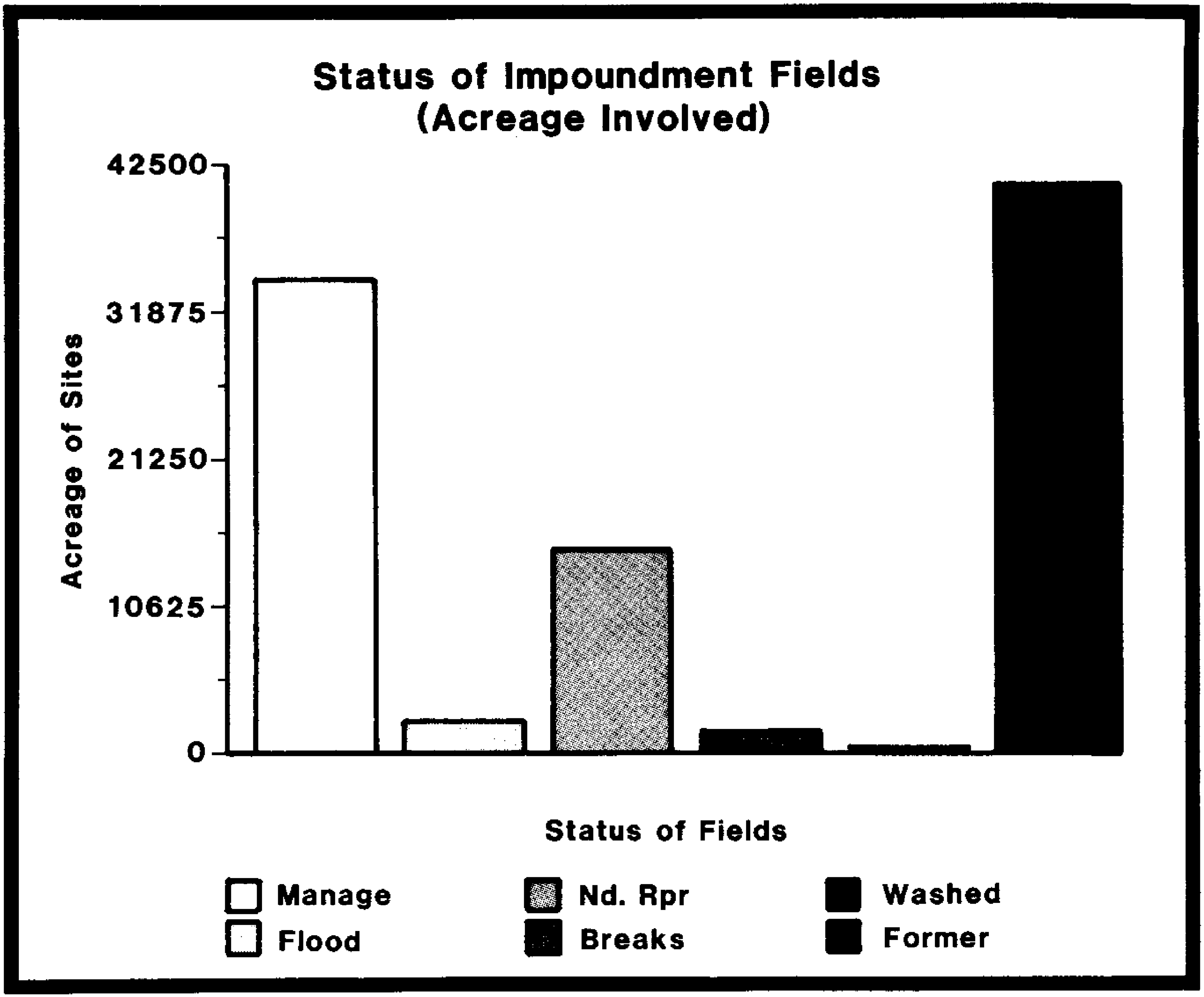

Figure 3.2 Condition of the impoundment sites described by the survey responses.

contained brackish water. This means that the standard classification of salinity regimes and the reports of those actually managing the fields agreed on the salinities at a site only about 46% of the time for this survey. Changes in salinities,disagreements over interpretation, and local and seasonal variations all may be involved in accounting for these differences.

Table 3.3

Salinities and status of

coastal impoundments (in acres).

Status of Fields	Fresh Water	Fresh to Brackish Water	Brackish Water	Brackish to Salty Water
Intact and flooded fields	19,891.8	4,506.0	11,426.4	598.7
Fields need repairs	4,396.6	22.0	11,771.5	100.0
Dikes are washed out and formerly impounded	15,692.2	4,561.4	14,985.8	474.0
Field status unreported	721.5	98.0		
Totals	40,702.1	9,187.4	38,183.7	1,172.7

*238 acres of intact fields are reported to be saline; 64.5 acres of fields needing repairs are reported as saline; 4075.2 acres of former impoundment are reported as saline; remaining acreages reflect nonresponses. 1852 acres (30 in fields needing repair, 1822 in former impoundments) did not include salinities. For 4155.6 acres neither field status nor salinity was reported.

Ownership of Impoundments

A substantial controversy has emerged in recent years over the question of wetland ownership in South Carolina. The state government has laid claim to all lands below the mean high water mark, "subject to the private claimant's ability to prove that the original Crown or State grant contained language specifically evincing an intent to convey to the low water mark" (Woodington, 1982). As Woodington further points out, "The fundamental irony in South Carolina's tidelands situation is that the cases of the late nineteenth century and of the twentieth century deny the existence of that private ownership which from all appearances was axiomatic in the eighteenth century and first half of the nineteenth century." After all, as we have seen, plantation owners freely managed their rice fields, many of which lie in the tidal zone, without objection from the state.

The controversy extends over a series of issues. First, how specific must the language of a grant be to demonstrate the requisite intent to grant title to a specific tideland area (Cheshire, unpublished Baldwin, 1976; Woodington, 1982)? Many of these grants, written in colonial times, are quite general or vague about their scope. Second, do grants include (or are they bounded by) navigable waters -- and how is a "navigable water" defined (Baldwin, unpublished report and 1976; Woodington, 1982)? Third, must the private claimant demonstrate an "unbroken chain of title" from the original grant? Attorneys who have represented private claimants argue that this standard is stronger than ordinarily imposed and that it is especially burdensome because critical records were destroyed by fire in Georgetown, Colleton, and Beaufort counties during the Civil War (Cheshire, 1971, unpublished report; Woodington, 1982). A recent appeals court decision, in State of S.C. v. Sloan Construction Company, Inc., suggests that this standard may be relaxed. Apart from these issues, does the doctrine of adverse possession apply to such lands? South Carolina law provides that unchallenged possession for a period of years establishes a valid private claim to title; because the rice fields were clearly under the control of the landowner, the doctrine might apply to them (Middleton, 1975). Finally, does the claimant hold tidelands in public trust, that is, with some residual public interest in the use of the sites remaining, even though they are privately owned (Woodington, 1982; see also Stevens, 1980)?

These issues are both complex and ambiguous enough to lie outside the domain of this study. Suffice it to say that title to tidal lands is often subject to a state ownership claim, but that the prevailing precedents are ambiguous enough to make their application to a specific case uncertain in most instances. Nonetheless, the survey of those paying taxes on such lands (presumably a necessary, if not sufficient, condition for successfully claiming them) does provide some information of interest. Specifically, the distribution of owners can be examined to learn more about the beneficiaries of such claim. Table 3.4 shows the acreages claimed by various types of owners who responded to the survey.

Table 3.4

Current ownership of diked wetlands

Type of Respondent*	Diked Land (in acres)	Formerly Diked Land (in acres)
Traditional owner	3,884	4,474
New owner	10,410	10,098
Owner not classified		
Uncertain	5,534	5,032
Third-party manager	10,141	2,052
Group ownership	3,923	2,777
Corporate owner	716	9,525
Public ownership	23,800	7,266
Totals	58,408	41,224

*A traditional owner is a respondent who reported inheriting the property or having it transferred to her or him by a living relative. Thus these cases include all second-generation owners. New owners are those who purchased the property during their life times. Many owners could not be classified, for a variety of reasons; if an ownership group or a third-party manager could be identified, those cases are noted. The remaining cases are classified as uncertain.

Corporate owners include only those cases in which a mult-state enterprise is identified as the owner of the field; many of these cases involve timber companies.

Substantial evidence of turnover in ownership is apparent. Still, only 17% of those responding purchased the property within the last five years. To be sure, some of this turnover can be attributed to the state's pursuit of its claim to these lands. Any enterprise that required substantial investment would be perilous in the absence of a clear title.

Those already managing wetland fields have not been impeded by the state, in spite of its apparent claim to ownership, unless an attempt is made to obtain permits to repair or restore dikes or water-control structures. Moreover, the cost of maintaining a claim is small, because these lands are assessed by state law at $10.00 per acre. As a result, the situation strongly favors low-intensity uses such as waterfowl hunting.

One possibility that might reduce the uncertainties involved would be an effort to bring "quit claim" actions in specific cases. Claims that are not strongly established or forcefully advanced, would be abandoned, reducing the scope of the potential controversies to a more specific set of grants. Of the private owners responding (excluding multi-state corporations), 44.4% reported that they had not undertaken any historical research of the sort that would be required to identify a valid grant. On the other hand, 52.8% of those responding reported that they have traced the title to their sites back to the period before the 1860s, which suggests that they have undertaken a search for their original grant (and 36.1% report that they have traced ownership back to an original grant from the State or the Crown or Lords Proprietors). A substantial record of these grants exists, and expertise in identifying the grants and linking them to specific sites has already been developed.

Other states, notably New Jersey and California, have found efforts to review tidelands grants systematically to be complex, costly, and controversial. Their experience suggests that this would also be true in South Carolina, because a substantial number of managers and owners have already undertaken the research they would need to contest any state claim. Notwithstanding disputes over ownership, managed wetland fields currently serve as an important resource in South Carolina, where they have been actively managed for a variety of purposes over the years.

Management of Impoundments

Many people favor intensive management of diked wetlands because that permits owners to enhance their value for particular uses. Management practices are generally aimed at restricting the growth of undesirable plants, notably various coarse emergent perennials, and improving the production of other plants more readily consumed by waterfowl. These management practices generally employ some combination of manipulation of salinity (seeking fresh to brackish water in various cases) and water levels (including draining and flooding cycles), and disturbance of the bed (primarily through cultivation and/or burning of the vegetation).

Four general types of water-level manipulation are reported in the survey. In some cases, managed fields remain flooded throughout the year, creating an enclosed pond which permits no direct water exchange. At the other extreme, some managers permit continuous exchange with the surrounding waters, often maintaining a constant water level over the field's bed by restricting inflow or outflow during the tidal cycle. However most managers adopt a strategy which involves draining the field (generally following the waterfowl season), then flooding it again late in the summer or early in the fall: some of these managers employ a one-time draw down process, followed by later reflooding; while other managers manage more intensively, raising and lowering water levels over several stages and permitting multiple flushing and filling cycles. These latter two approaches may need to be distinguished, since one strategy provides what amounts to a single pulse from the impounded waters into the surrounding tidal waters, while the other strategy provides for more extensive exchange between the managed fields and the surrounding waters. Within these broad categories, managers vary the depth of the water in their fields, the length of the draw-down period, and the amount of exchange permitted during flooding and draw-down cycles.

Managers also vary their treatment of the bed of these fields during the period that water is excluded. While some managers allow the bed to rest without disturbance, others burn, mow or cultivate it during this phase. Only one report was received of a manager allowing cattle or other livestock to graze on the bed during draw down. In an earlier study by Morgan et al. (1975) of the South Edisto/Ashepoo/Combahee estuary, this use appeared more prevalent (reported on 21 ponds of 213 studied). As they pointed out, "good production of duck food was assured only when cattle were removed by mid- August so that plants... could mature seed before duck season" (Morgan et al., 1975). The difficulty of providing an alternative grazing site during the waterfowl season may have made this secondary use too difficult for managers to accommodate.

In fresh water fields, managers generally seek annual emergent duck foods such as smartweed, _Polygonum_ spp.; wild millet, _Echinochloa_ spp.;

panic grasses, *Panicum* spp.; and redroot, *Lachnanthes caroliniana*. They also encourage water shield, *Brasenia schredberi*; spikerushes, *Eleocharis* spp.; pondweeds, *Potamogeton* spp.; arrow-arum, *Peltandra virginica*; southern naid, *Najas quadalupensis*; asiatic dayflower, *Aneilema keisak*; soft-stem bulrush, *Scirpus validus*; wild rice, *Zinzania aquatica*; and water grass, *Hydrocholoa caraolinensis*. In brackish ponds, widgeon grass, *Ruppia maritima*, or in shallower ponds, salt-marsh bulrush, *Scirpus robustus*, and dwarf spikerush, *Eleocharis parvula*, are often sought, while sago pondweed, *Potamogeton pectinatus*; soft-stem bulrush, *Scirpus validus*; muskgrass, *Chara hornemannii*; and duckweeds, *Lemna* and *Spirodela*, are also accepted (Morgan et al., 1975; Hull, 1983).

Examining only the six major categories of management regimes implied by the management of water levels (no exchange, continuous exchange, one-pulse drawdown and reflood, and multiple-pulse drawdown and flood), and manipulation of the bed (either cultivate and/or burn or leave the beds undisturbed), we find that management strategies have shifted dramatically since the Morgan et al. (1975) survey. The reported acreages devoted to each are displayed in Fig. 3.3. There are 3394 acres managed without exchange and 810 acres managed with continuous exchange. Of the impoundments managed with a single drawdown-reflood cycle, 6243 acres are drained without any further disturbance of the beds, whereas 11,161 acres are drawn down, with the beds burned or cultivated periodically. Of those impoundments managed with several drawdown-reflood cycles, 401 acres are managed without any further disturbance of the beds, whereas in 26,776.4 acres, the beds are also burned or cultivated.

In Fig. 3.4a and 3.4b, the type of manager involved also is reported. These data reveal that public management is typically the most intensive. Third-party managers (nonowners managing the site for another party) often manage intensively, but a substantial number resort to the less-demanding management practices identified. Similarly, private managers vary dramatically in the intensity of their management practices.

A typical freshwater single-drain cycle proceeds as follows: from late October to March, water is held on the impoundment beds at a constant depth. In March, the fields are drained, and the impoundment beds allowed to dry. In June, the beds are plowed. Finally, in October, the impoundments are reflooded again; the depth is brought up to level desired

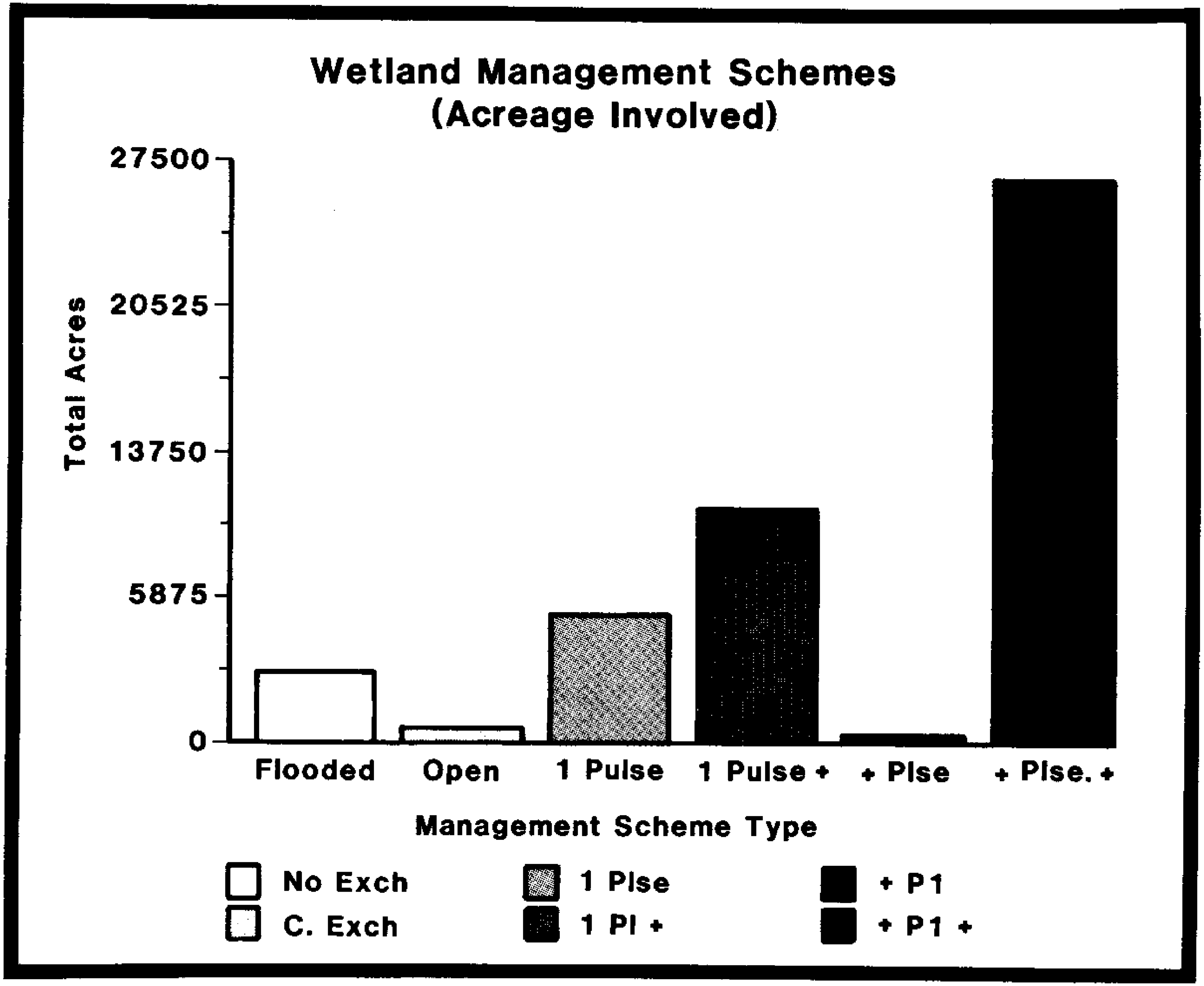

Figure 3.3 Acreage of impoundment sites categorized by management regimes. Scheme types: No exchange; continuous exchange; one pulse drawdown and flood; one pulse drawdown and flood with manipulation of the bed; multiple pulse drawdown and flood; and multiple pulse drawdown and flood with manipulation of the bed.

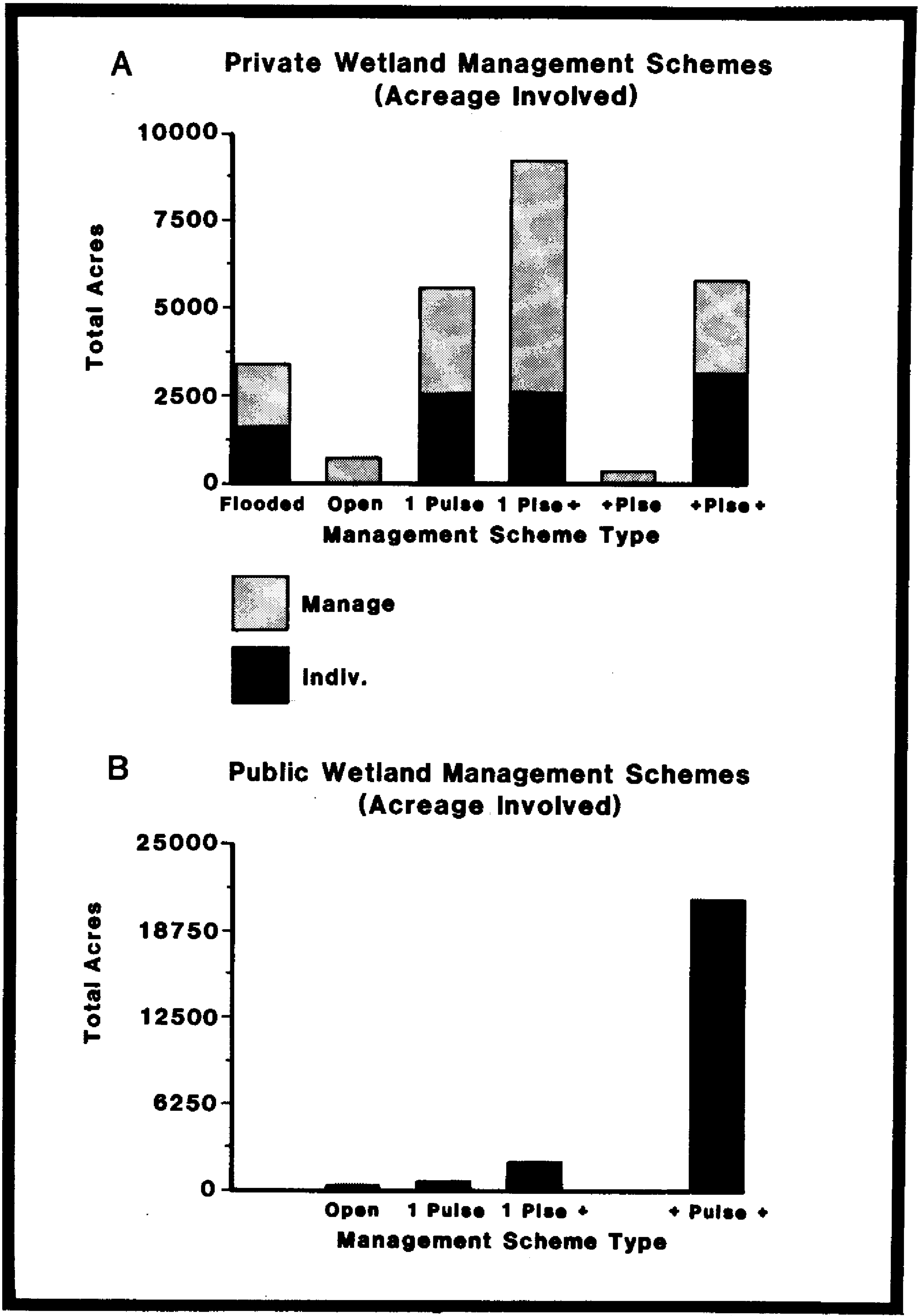

Figure 3.4 Acreage of private (A) and public (B) impoundment sites categorized by management regime. Manage = third party manager; individual = owner/manager.

for waterfowl feeding during the winter season. A typical freshwater multiple-drain-and-flush cycle proceeds as follows: Water is held in the impoundments at a constant depth from November to February. Vegetation is burned off during January and February. From March to May, partial tidal exchange is permitted, with the fields drained in late May. From June to September, the fields are left dry, with plowing undertaken during the summer months. During October and November, the fields are flooded and the cycle begins again.

The overall figures suggest that important shifts in management strategy have taken place in the last decade. Morgan et al. (1975, Table 2), report that widgeon grass ponds were "drained only once every two or three years for a short time for water quality and pest-plant control"; current waterfowl management practice apparently involves periodic drawdowns (on a yearly basis in some areas, less often in others), with a more lengthy drain cycle. Further, Morgan and his colleagues found that over half the acreage they studied was "permanently flooded," although most managed acreage is now drained periodically.

Results of the Morgan survey indicated that brackish water-management schemes were dominated by permanent flooding, but in this survey, cycles of multiple drain/flush and fill are now most common. About half of all impoundments are burned or plowed at some point during the year: cycles of multiple drain, flush, and flood are somewhat more common in brackish water management, whereas the single-cycle drain-flush-and-flood technique is somewhat common in fresh-water management. Permanent flooding is now almost completely confined to fresh-water fields. A relatively small number of sites in both fresh and brackish water are managed with continuous flushing schemes.

Impoundment managers also were asked whether they have experienced several problems commonly associated with managed wetland systems. Responses to these questions are doubtless colored by the personal pride of the manager, because a manager who admitted that he had "problems" may feel he is admitting "ineffective management." However, the responses do indicate some continuing problems with the effectiveness or implementation of the management techniques. Of the total respondents, 15% reported problems with fish kills, 23% with algal "blooms," 28% with water control, 22% with cat clays or acidic soils; and 75% of the respondents reported problems with undesirable plants, suggesting that this is among the most prevalent problems that wetland field managers must address.

There were no noteworthy differences among management strategies in the frequency of reports of these problems, although this evidence is not clear enough to establish whether these strategies have an impact on the problems involved. Personal observation of several sites indicated that some particularly effective managers reported having these "problems", whereas other less energetic and less effective managers failed to report these "problems," even though they were present.

Another consequence of the management strategy employed involves its effectiveness in mosquito control. Officials and scientists interested in the problem suggest that management schemes that require the bed of the field to remain dry during a portion of the spring, and then be flooded, will produce large numbers of salt-marsh mosquitos, unless they are quickly flushed following the initial flooding (Tidwell, 1984; see also Carlson and Carroll, 1986). Large fields also provide substantial salt-marsh mosquito breeding grounds while drained, because periodic rainfall on the uneven bed of a larger field will provide the moisture needed to hatch the mosquitos whose eggs are deposited in the soil. Local managers report some success in mosquito control through active management of the beds, paralleling the California success in controlling salt-marsh mosquito production through systematic cross-ditching together with the application of insecticides (Resh and Balling, 1983). Florida's experience with mosquito impoundments, aimed at controlling mosquito populations, while enhancing fish and wildlife habitat, suggests a similar conclusion (Carlson and Carroll, 1986).

As we have seen, many South Carolina sites are large, which suggests that systemic management of the beds is needed to control mosquito production during periods when the fields are drained. Many fields are drained, then subsequently flooded, but a substantial number of those are not subsequently flushed again, which may result in the hatching of a substantial number of salt-marsh mosquitos during the flooding cycle (Tidwell, 1984). In general, this survey of management practices suggests that a noteworthy number of the managed wetlands treated in the survey are contributing to the coastal area's problem with mosquitos (see also Rubin, 1985).

The Use of Impounded Wetlands

Wetlands have been diked to permit more careful and focused management, which should make more-intensive use feasible. Those contacted in the survey were also asked about their use of these diked wetlands. When substantial holdings were involved, respondents were asked to estimate the percentage of the use of their sites devoted to eight different activities, but respondents with small holdings were merely asked to check the uses involved.

This inquiry suggests that the use of these sites has changed little in recent years. Morgan, et al. (1975) reported that 72% of the fields (and 85% of the acreage) were managed for waterfowl hunting in the South Edisto, Ashepoo, and Combahee basin. In the Gresham and Hook study (1984), conducted along the other end of the state's coast during the mid-1970s, 63% of the 68 respondents indicated that they were managing for waterfowl hunting. In the responses reported from this project, waterfowl hunting was the primary objective (at least as important as any other use of the site) for 43,716 acres of the managed fields, with other objectives more important for the remaining 12,176 acres. (Non-responses excluded 503 acres from this calculation.) The relative proportions are displayed in Fig. 3.5.

More generally, some suggest that managed wetland fields can make an important contribution to intensive conservation efforts. More-intensive management improves the habitat for birds and threatened and endangered species, thus providing sanctuaries for wildlife, and enhancing areas suitable for hiking, bird watching, and other related forms of recreation. Analyses of natural resource utilization sometimes distinguish between "consumptive" uses, such as hunting, fishing, and shellfishing, and "nonconsumptive" uses, such as hiking, bird watching, and wildlife preservation which do not use up the resource. Examining the reported uses of impoundments, we find that consumptive uses dominate. In Fig. 3.6, the breakdown among these uses is displayed; 44,610 acres are dominated by consumptive uses, 4518.5 acres by nonconsumptive uses, and they are equally important on 6763 acres.

Finally, interest has grown in the use of impoundments as potential sites for aquaculture and mariculture. Our inquiry suggested that this

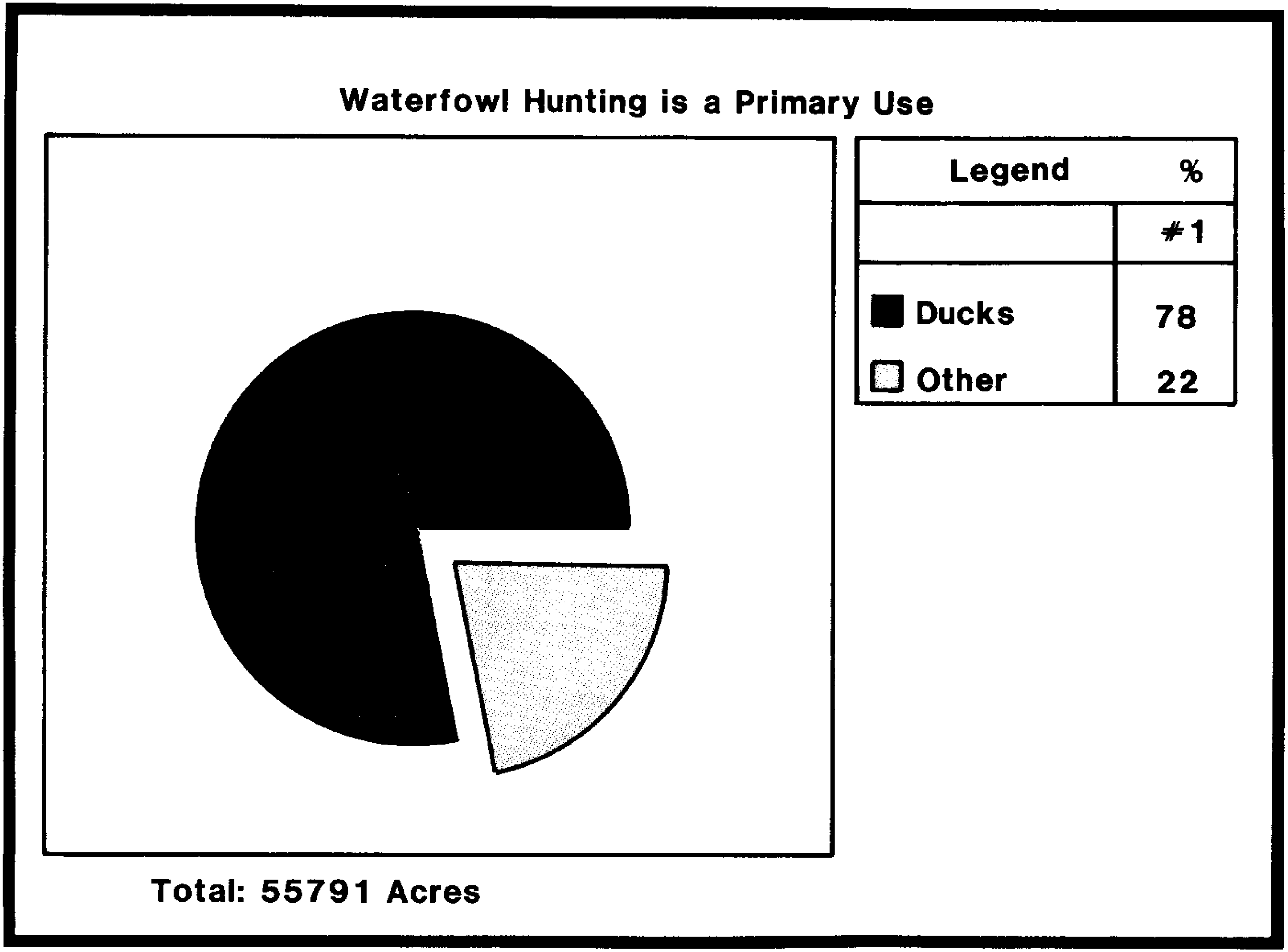

Figure 3.5 Proportion of responses indicating waterfowl hunting is the primary management objective.

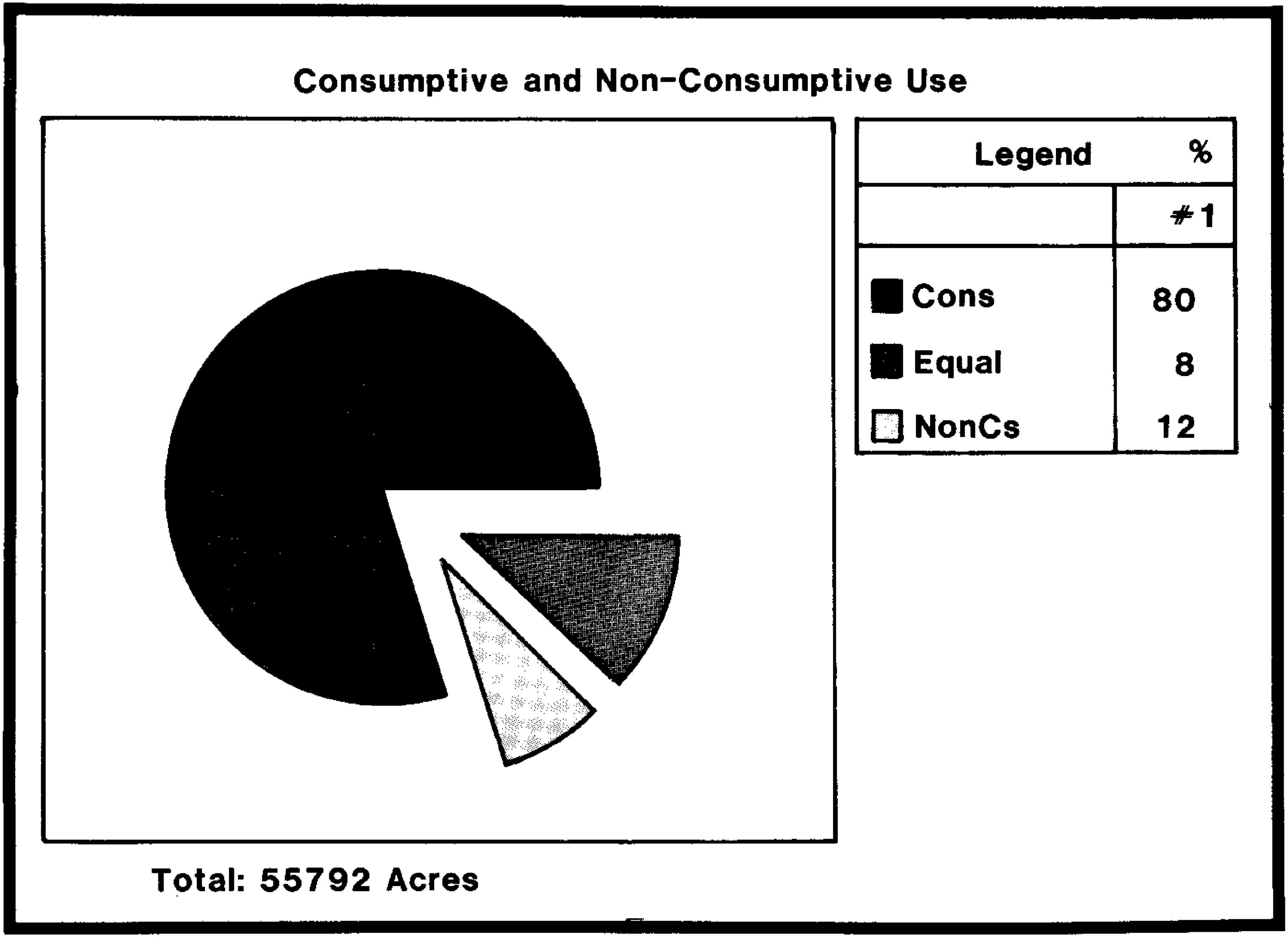

Figure 3.6 Proportions of reported consumptive and non-consumptive uses of impoundments.

use is not yet substantial; only 1680 acres are reported to be utilized for the culture of any marine or freshwater organisms (either shellfish or finfish). Much of the culture of shellfish is concentrated in the Georgetown area (625 of 705 acres), and finfish culture occurs along the entire coast. As Fig. 3.7 suggests, this is a rather small proportion of the overall acreage treated in this survey.

The interest in coastal wetlands also raises the question of the public's access to these resources. In Table 3.5, the number of acres controlled by various types of owners is summarized according to whether they allow the public to use their sites. If the public is permitted on a site, there are sometimes restrictions imposed as to the times open and numbers permitted. As the table indicates, public access is ordinarily restricted to the privately controlled sites. The public does have access to over 20,000 acres of publicly or charitably owned sites. It is important to recall the distribution of responses, however. Virtually all the publicly managed sites are included in this tabulation, and most of the corporately controlled sites are included. On the other hand, between half and two-thirds of the sites controlled by private individuals and groups appear to be included. Thus, extrapolation of these results to the total acreage along the coast suggests that the public has access to 30,000 to 35,000 acres of impounded lands. Other fields are accessible, particularly for waterfowl hunting, but only through the payment of lease fees which have been reported to run as high as $1500 per blind for two shooting days per week for the six weeks of the hunting season.

Other evidence suggests some conflict over "whose marshes" these are. Eighty percent of the private owners report difficulties with the public coming on to their land without permission. Many of these trespasses are related to hunting; controlling access to these fields during that time is particularly difficult. Nonetheless, these problems suggest conflicting perceptions of who can appropriately control access to a wetland.

This evidence demonstrates the conflicts posed by various interests involved in discussions of managed wetlands. Some uses, notably waterfowl hunting, provide direct benefits to the landowner or user, whereas other uses such as those supporting the marshes as nursery habitat, which are generally regarded as conflicting with waterfowl management, provide

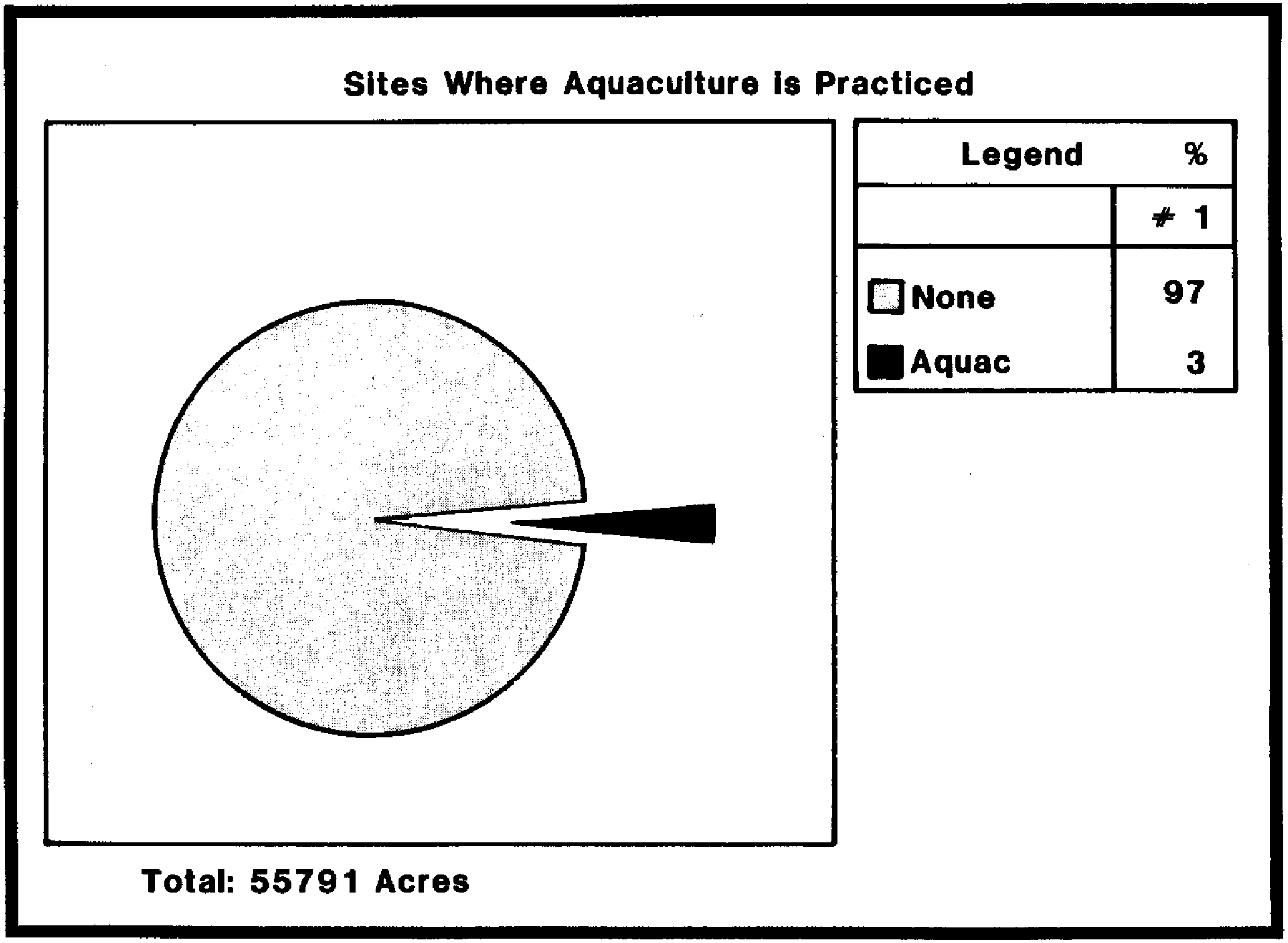

Figure 3.7 Proportion of the reported impoundment sites managed primarily for aquaculture purposes.

Table 3.5

Reported Public Access To Impoundment Fields

By Type Of Ownership

Type of Owner	Acres with Public Access Reported (%)	Number of Acres Reported
Corporation	0.0	329
Private group	15.6	4,407
Private individual	5.9	14,816
On-site manager, not otherwise identified	61.6	6,551
Publicly owned	100.0	23,746

Only reported managed fields (not "former impoundments") are treated in this tabulation. No response was recorded for the question of public access for 8563 acres (indirect evidence suggests that public access to many of these sites may be limited). Public access may be permitted but regulated in some cases noted.

benefits that the community at large enjoys more directly. These conflicts parallel the conflicts over formal ownership of these fields, which have been raised in recent years, and the conflicts over the use of this extensive resource, which have emerged in recent regulatory policy disputes.

CONCLUSIONS

This survey of current use and management of impoundments points to a number of findings that enrich our scientific understanding of the management of these sites and its consequences, and the implications of our perspective on these resources for public policy. Substantial resources in managed coastal wetland fields are concentrated in several watersheds along the coast of South Carolina. Although a large number of small, easily managed fields exists, most of the acreage being managed lies within large fields. Most of these large impoundments lie either in currently managed sites in acceptable condition or in formerly diked fields that would require substantial investment to restore to manageable status. A significant exception to this involves one substantial public site where the dikes are reported to need repair. This suggests that regulatory policies focusing on "repairs" will affect a modest amount of wetland acreage, where policies affecting "reimpoundment" involve much more substantial wetland areas.

The controversy over ownership is likely to continue. Some of those responding to this survey have completed ownership studies needed to support litigation, but nearly half of those responding have not. Apart from the legal controversy, continuing problems with trespassing suggest that the right of access continues to be an important question for those interested in managed coastal wetlands.

The use of these sites is dominated by waterfowl hunting. Management practices are focused on the growth of plants known to attract waterfowl. Although these regimes have changed dramatically in recent years, private managers have updated their management schemes to reflect current knowledge less often than public managers, leaving a number of sites in which management practices could clearly be improved to reflect current understanding. Even though management practices have improved, noteworthy numbers of respondents continue to report a variety of problems with their fields. In addition, a number of privately controlled fields are apparently not being managed effectively to control mosquitos. The state of scientific knowledge about the origin and management of the problems associated with these various management practices, as well as the various uses for which these sites are managed, clearly needs further assessment.

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SECTION III

PHYSICAL CHARACTERIZATION OF THE CAT ISLAND IMPOUNDMENTS

Chapter 4

Study Site Description

M. B. Epstein and D. S. Baughman

CAT ISLAND STUDY AREA

The study site area is located in the southwestern corner of the Cat Island portion of the Tom Yawkey Wildlife Center, Georgetown, South Carolina (Fig. 4.1). Historically, the area was a totally fresh, pristine cypress, *Taxodium* sp., wetland. With the advent of the rice-culture industry in South Carolina in the late 1600s, the cypress swamps were cleared and cultivated for rice (see Chapter 1).

The study site was part of the Hume Island Plantation (Alexander, 1915, unpublished MS) during the rice-culture period and was last cultivated for rice in 1898 (Alexander, 1908). After the rice fields were abandoned, the property eventually became part of the South Island Game Preserve and provided excellent feeding grounds for large numbers of migratory waterfowl. Alexander (1915b) noted that wild rice, *Zizania aquifica*, first colonized the abandoned rice fields, attracting "unbelievable" numbers of waterfowl. Giant cutgrass, *Zizaniopsis milicea*, or white marsh as it is referred to locally, along with several other freshwater plant species, eventually succeeded the wild rice (Alexander 1915b). The property was acquired by the Yawkey family in 1911 and subsequently bequeathed to the South Carolina Wildlife and Marine Resources Department (SCWMRD) in 1976, along with North and South Islands, by Thomas A. Yawkey, who stipulated that the area be used for wildlife management, education, and research.

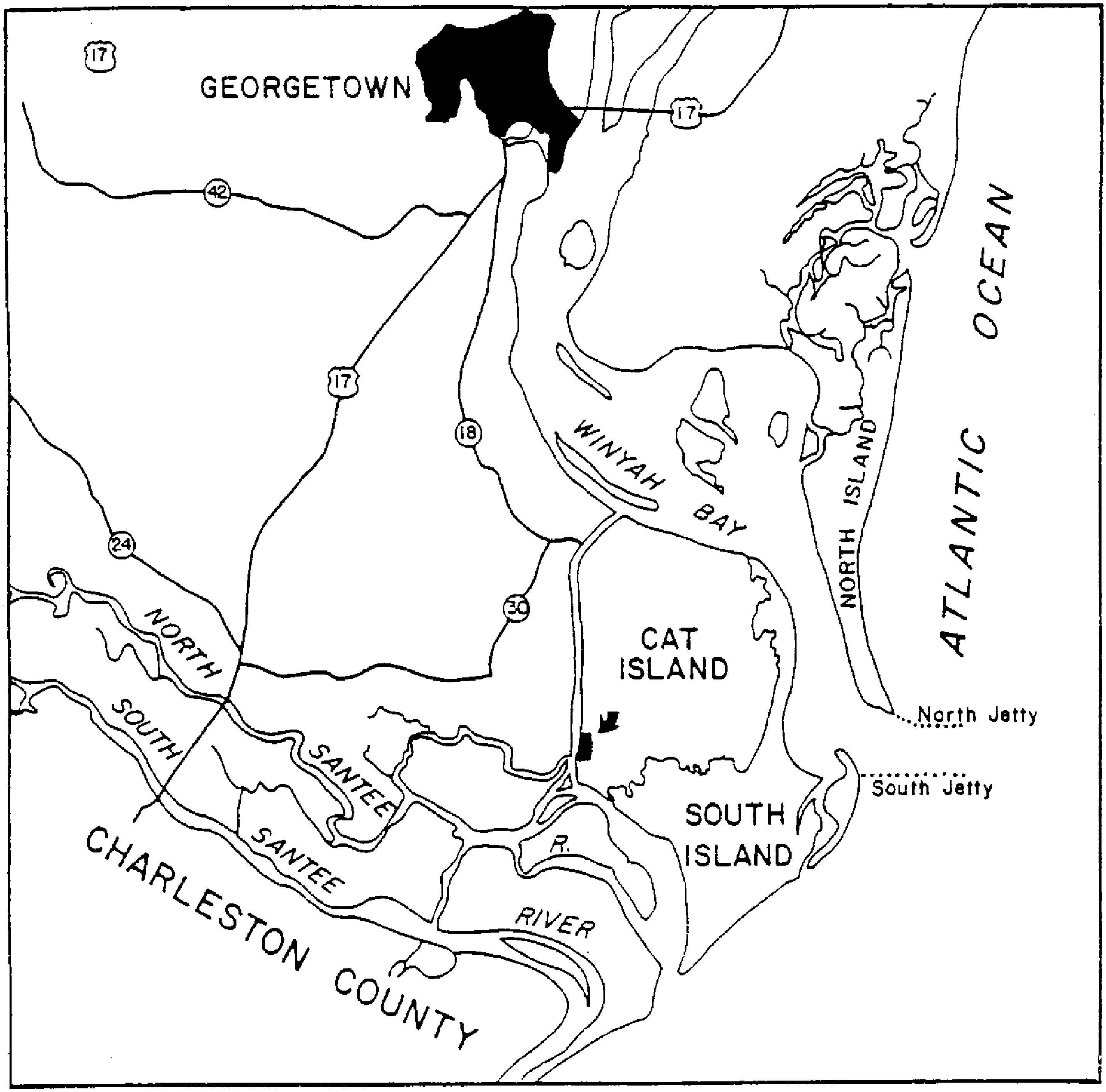

Figure 4.1 Map of the Georgetown, South Carolina area showing the general location of the study site.

During the construction of the Atlantic Intracoastal Waterway (ca. 1900), the study site was used as a spoil deposit by the U.S. Army Corps of Engineers (USACOE) (B. Joyner, personal communication). In 1945 the USACOE diverted a major portion of the freshwater flow from the Santee River to the Cooper River in Charleston, causing the saltwater/freshwater wedge to move up the Santee River. The Santee River delta was thus converted from a fresh to a brackish environment. In 1967, six brackish water impoundments (units 1 to 5 and Cooperfield) were reconstructed from the previously impounded marsh for a study by the Division of Marine Resources, SCWMRD to examine the effects of different water-level management strategies on plant succession (Wilkinson, 1970). One other previously impounded site (unit 6) was not reconstructed and was used as a control area during the Wilkinson study. The reconstructed impoundments have been managed to attract waterfowl since 1970.

The study site consists of a series of five contiguous impoundments, referred to as the Paddy Field complex, ranging from 3.5 to 7.8 ha in size ($\bar{x}$ average = 5.1 ha); one contiguous unmanaged tidal impoundment (7.9 ha); a 13.8-ha managed impoundment (Cooperfield) adjacent to unit 1; and the open marsh located east of the impoundment complex (Fig. 4.2). The five small impoundments are bordered on the east by an earthen dike directly adjacent to Chainey Creek, a contiguous tidal creek, and the open tidal marsh, characterized primarily by low marsh and mud flat habitat. On the western side of the complex is a narrow red cedar/scrub oak forest which separates the impoundments from the Atlantic Intracoastal Waterway.

Each unit contains a shallow mud flat area, occupying 30 to 60% of its total surface area, which supports submergent vegetation. A perimeter ditch, produced when burrow material was excavated to build the dikes, borders each impoundment bed on the north, south, and east sides. Each impoundment is equipped with traditional water-control structures, called trunks, of the flashboard-riser type (Fig. 4.3). Each trunk can be set to control water exchange between the Paddy Field impoundments and Chainey Creek, and water levels on the impoundment beds. Spillways (plug-trunks) located between the units are used to facilitate additional circulation. However, during this study these spillways were left closed, and the water level in each of the study impoundments was controlled through the main trunk on Chainey Creek so that each unit could be studied individually.

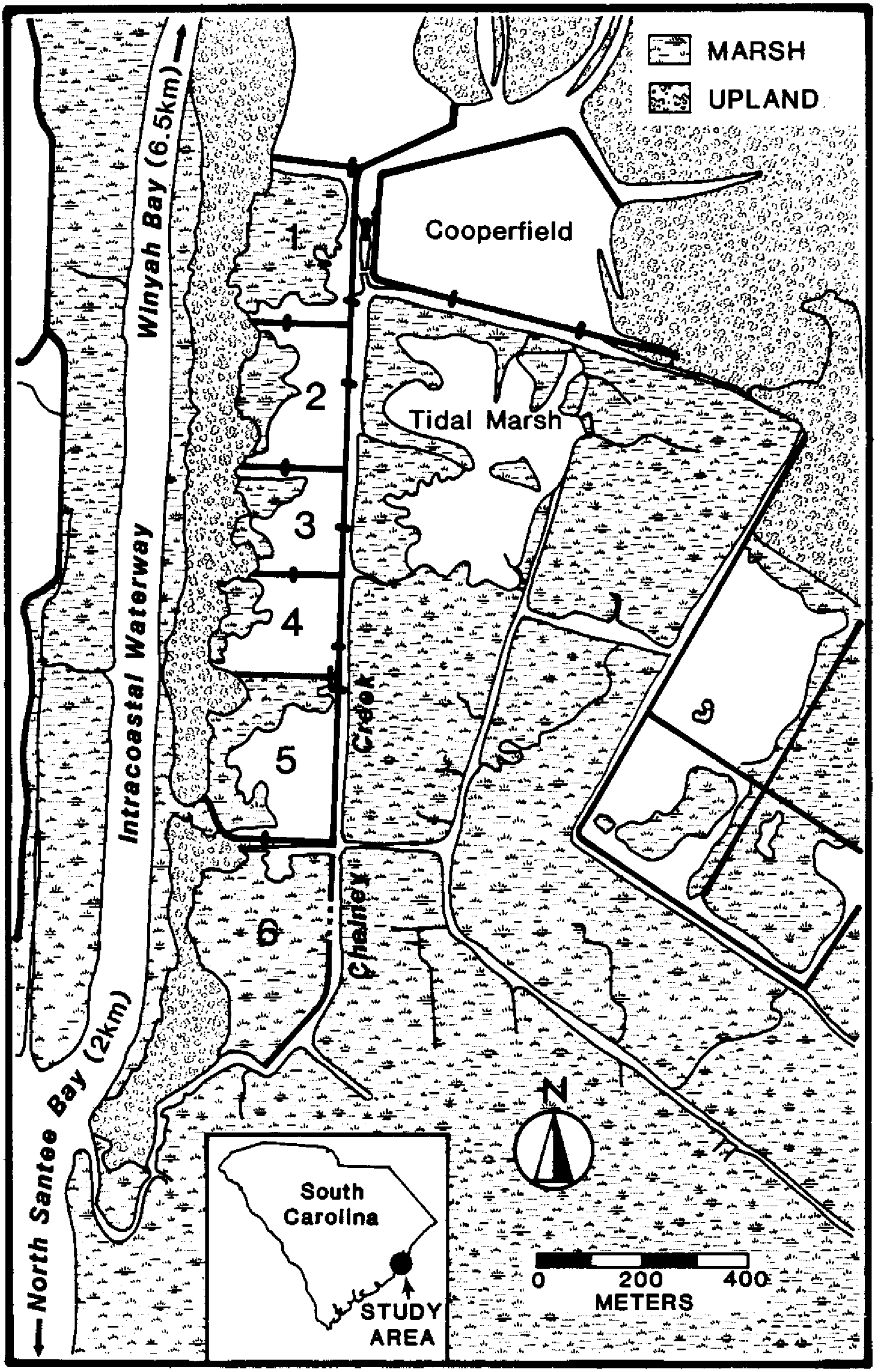

Figure 4.2 Schematic diagram of the study site at the Tom Yawkey Wildlife Center, Georgetown, South Carolina.

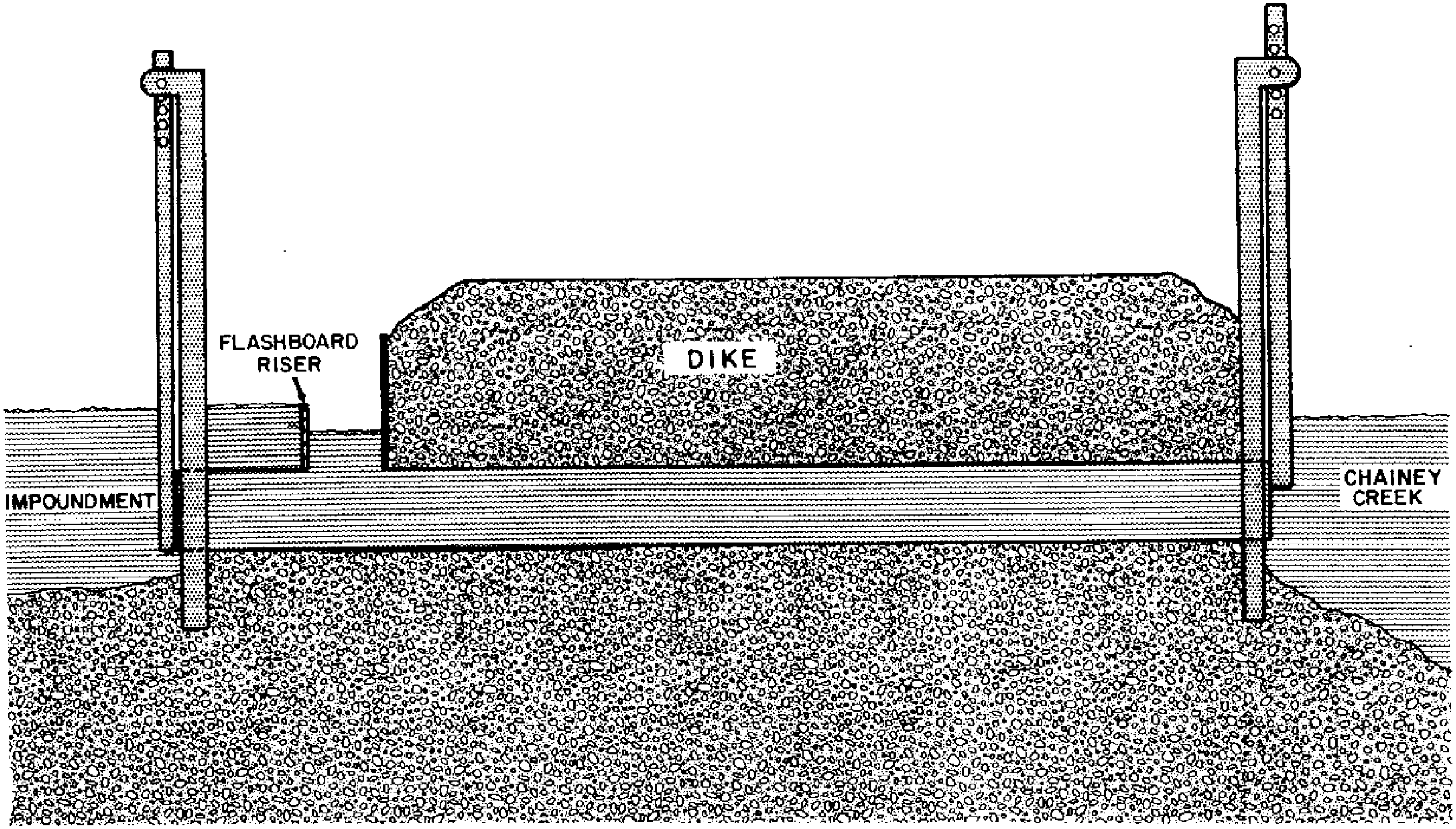

Figure 4.3 Cross-section schematic of a water control structure (ebb tide).

As a result, the five study impoundments were managed without the benefit of their full potential for water circulation. Source water to flood the impoundments originates primarily from North Santee Bay, with some input from Winyah Bay, and is supplied to the impoundment complex through Chainey Creek (Fig. 4.2).

Because of the availability of multiple units and their close association with open marsh and estuarine waters, the Paddy Field complex provides an excellent opportunity for comparative studies of impoundment and open-marsh communities. In addition, this site is owned and managed by the State of South Carolina, and, with the concurrence of the Yawkey Center Board of Trustees, was committed exclusively for use by the project team for the three years necessary to complete the study.

WATER MANAGEMENT

Controlled water-level manipulations vary with impoundment location within the estuarine tidal system and depend on the primary objectives of the resource manager (Wilkinson, 1983). During this study, water level manipulations were aimed primarily at encouraging the production of _Ruppia maritima_ and other desirable waterfowl food plants, including dwarf spikerush, _Eleocharis parvula_, and saltmarsh bulrush, _Scirpus robustus_, and secondarily at discouraging competitive undesirable emergents (e.g., _Spartina_ sp.) and algae (e.g., _Cladophoae_ sp.).

Water levels in each of the five Paddy Field impoundments, the tidal impoundment (unit 6), Cooperfield, and the adjacent salt marsh were recorded during the study (Figs. 4.4 and 4.5). The zero water level for the study impoundments was established when the impoundment beds were completely dewatered. Water level in the perimeter ditches at this time was even with the edge of the impoundment bed. Zero water level for the salt-marsh and tidal impoundment (unit 6) was established at normal low tide when no water remained on the marsh surface or mudflat habitat. Therefore, zero water level indicated similar conditions at each site. The salt-marsh and tidal impoundment were influenced by normal tidal inundation.

Water level monitoring began in January 1983 with the initiation of the wildlife portion of the study. In January and February 1983, water

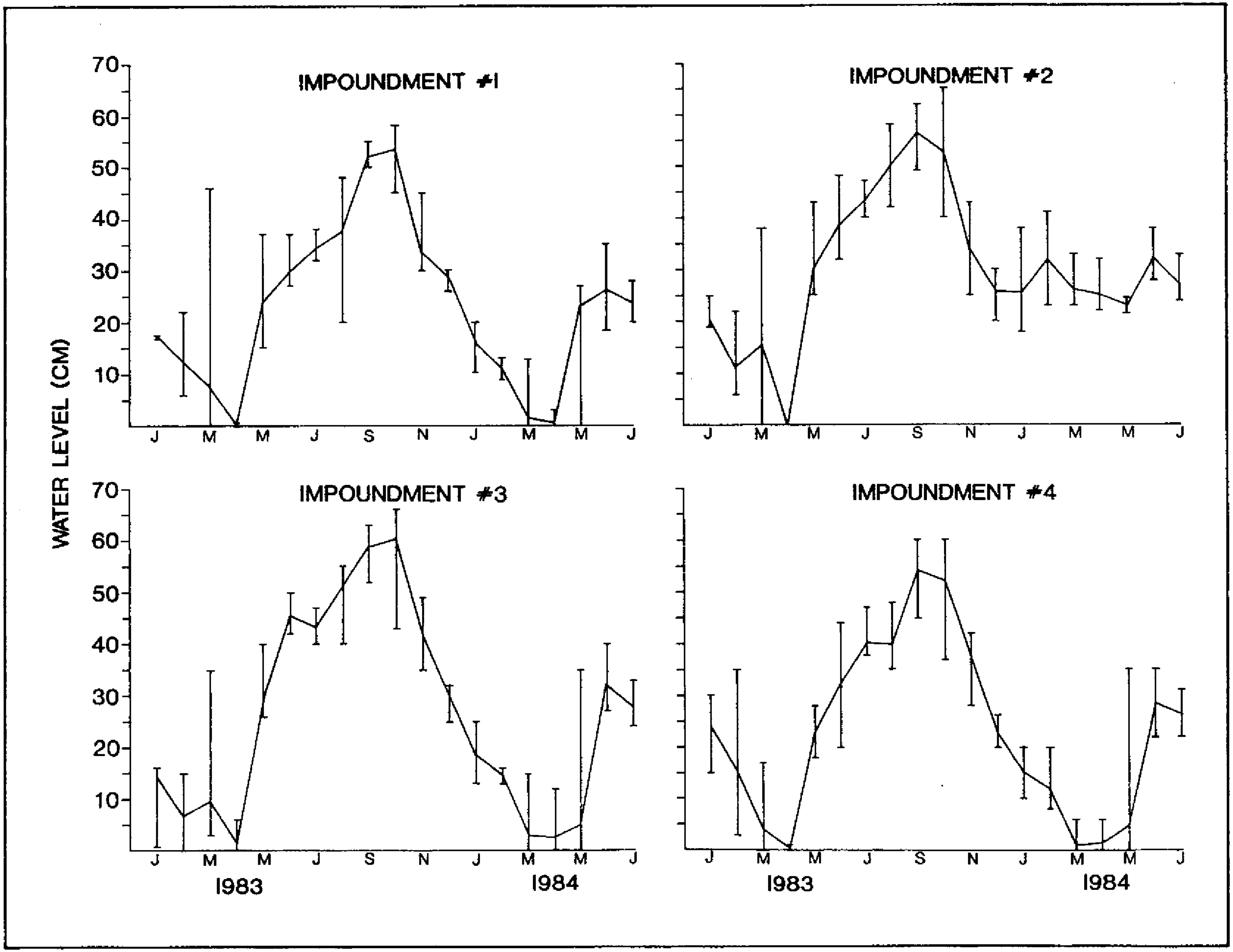

Figure 4.4 Monthly mean water levels in impoundments 1 to 4. Vertical bars indicate ranges.

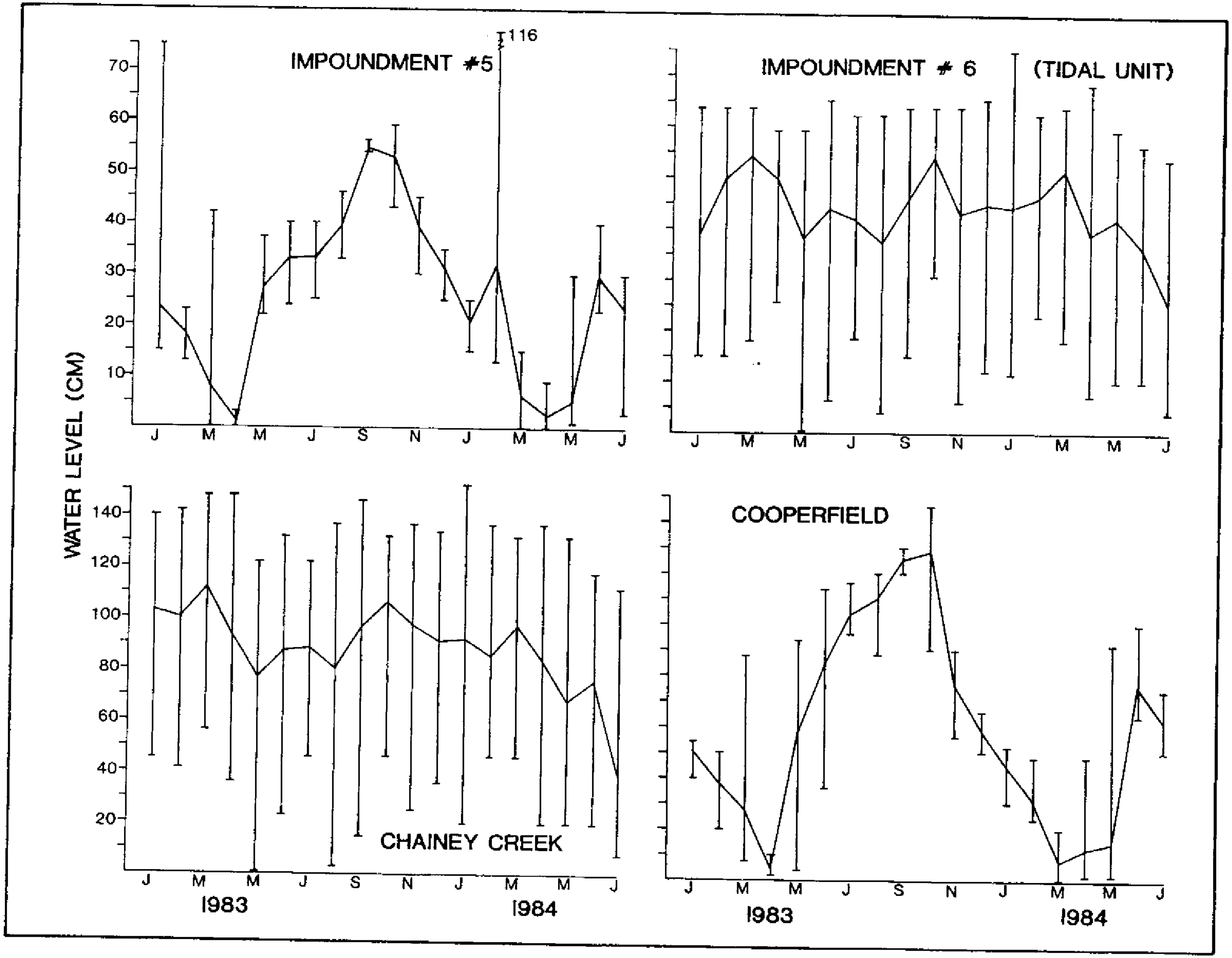

Figure 4.5 Monthly mean water levels in impoundments 5 and 6, Cooperfield and Chainey Creek. Vertical bars indicate ranges.

levels in the study impoundments were lowered by 10 cm each month to expose widgeon grass for waterfowl. Draining of the impoundments began in March 1983. Extreme high tides and above-normal rainfall reflooded some impoundments and prevented all from draining until late March. Impoundment beds were kept moist to encourage aquatic food plant production but dry enough to allow the bottom sediments time to form a firm foundation for plant growth (Joanen and Glasgow, 1965; Chaebreck, 1967).

To offset mosquito production during the spring drawdown-reflooding period, the five impoundments and Cooperfield were reflooded and quickly flushed in late-April 1983. That is, the impoundments were flooded and allowed to remain flooded (about 10 cm over highest elevations) for five days and then quickly dewatered (over approximately two tidal cycles) to remove rapidly developing mosquito larvae. After dewatering, the units were quickly reflooded to establish an initial water level of 10 to 20 cm over the beds and to prevent oviposition by mosquitos. This method was modified in 1984 to allow two rapid flushings of the perimeter ditch after the initial spring drawdown, which removed large numbers of mosquito larvae. All water used to reflood the impoundments was taken from Chainey Creek during high-tide periods.

After reflooding in early May, water-control structures were set to allow moderate tidal exchange (water circulation) by opening the outside gates and setting inside flashboards to maintain a specific water level (Fig. 4.4 and 4.5). Beginning in June 1983, water levels were gradually increased by 10 cm increments over the summer to allow growing space for the widgeon grass. On 14 June 1983, unit 4 accidently drained overnight; however, it was immediately reflooded.

By June 1983, impoundment water levels ranged from 30 to 45 cm over the beds (Figs. 4.4 and 4.5), except Cooperfield, which was covered with about 50 cm of water. In an effort to offset stressful summer conditions, extra boards were added to the water-control structures in July to retain rainfall and thus possibly reduce water salinity and temperature. However, this manipulation caused a significant reduction in total water exchange between several of the study impoundments and Chainey Creek. Water levels were slowly increased through August and September to allow for Ruppia growth. By late September, impoundment water levels ranged from 50 to 70 cm on the beds.

The gradual drawdown of impoundment water levels to expose widgeon grass for waterfowl began in late-October 1983 and coincided with the opening of the waterfowl season. Generally, water levels were reduced 10 cm every other month through March 1984, at which time the drawdown-flooding process was repeated again for the 1984 season (Table 4.1).

Impoundment manipulations were generally the same for 1984 except for the length of drawdown and the overall management of unit 2. The 1984 drawdown period was extended from 2 March until 24 May (approximately 84 days) because of above-average rainfall during this period. At the request of Task VII investigators, the water level in unit 2 was maintained at 20 cm, and the outside water-control gate was set to allow natural tidal flushing during the remainder of the 1984 field season (Table 4.1). However, as the water levels of the other units (1, 3, 4, 5 and Cooperfield) reached that of unit 2, all impoundment water levels were gradually increased by about 10 cm per month during the growing season, as was done in 1983. It should be noted that this management procedure does not substantially deviate from typical widgeon grass management; that is, managed units usually are not totally dewatered each year and may remain flooded for as long as four years (see Chapter 1).

CLIMATIC AND ENVIRONMENTAL FACTORS

Air temperatures during the project ranged from -5°to 34°C, with the lowest temperatures recorded in January, February, and March of 1983 (Fig. 4.6). High temperatures in July 1983 caused water temperatures to reach 30° to 34°C in the impoundments. These temperatures remained high through September and produced stressful conditions for many aquatic species. Similar air temperature patterns were observed for the 1984 season (Fig. 4.6).

Rainfall in this region of South Carolina averages 1.3m annually (Stuckey, 1982). At the Cat Island site the cumulative rainfall for 1983 was 1.4 m, and 1.1 m in 1984 through August (Fig. 4.7). Other sources of freshwater for the impoundments originated from the flow of the North

Table 4.1

Water-level manipulations for the Cat Island impoundments.

Date	Activity
1983	
January	Water levels dropped 10 cm
February	Water levels dropped 10 cm
March	Ponds dewatered
April	Flushing to remove mosquito larvae
May	Impoundments reflooded and flood gates set to maintain 10 to 20 cm of water over *Ruppia* beds
June	Water levels increased in 10-cm increments to allow for *Ruppia* growth
July	Water levels increased to 30 to 45 cm
September	Water levels increased to 50 to 75 cm
October	Water levels dropped 10 cm
December	Water levels dropped 10 cm
1984	
January	Water levels dropped 10 cm [*]
March	Ponds dewatered (except unit 2)
April	Ponds remained dewatered but moist
May	Ponds flushed to remove mosquito larvae reflooded
June	Water levels increased to allow for *Ruppia* growth [**]
July	Water levels increased 10 cm
September	Water levels increased 10 cm
October	Water levels dropped 10 cm
December	Water levels dropped 10 cm

[*] In 1984 Unit 2 maintained a minimum depth of 20 cm with tidal circulation.

[**] In 1984, after units 1, 3, 4, 5, and Cooperfield reached 20 cm, water levels in all units (including 2) were increased through the season as in 1983.

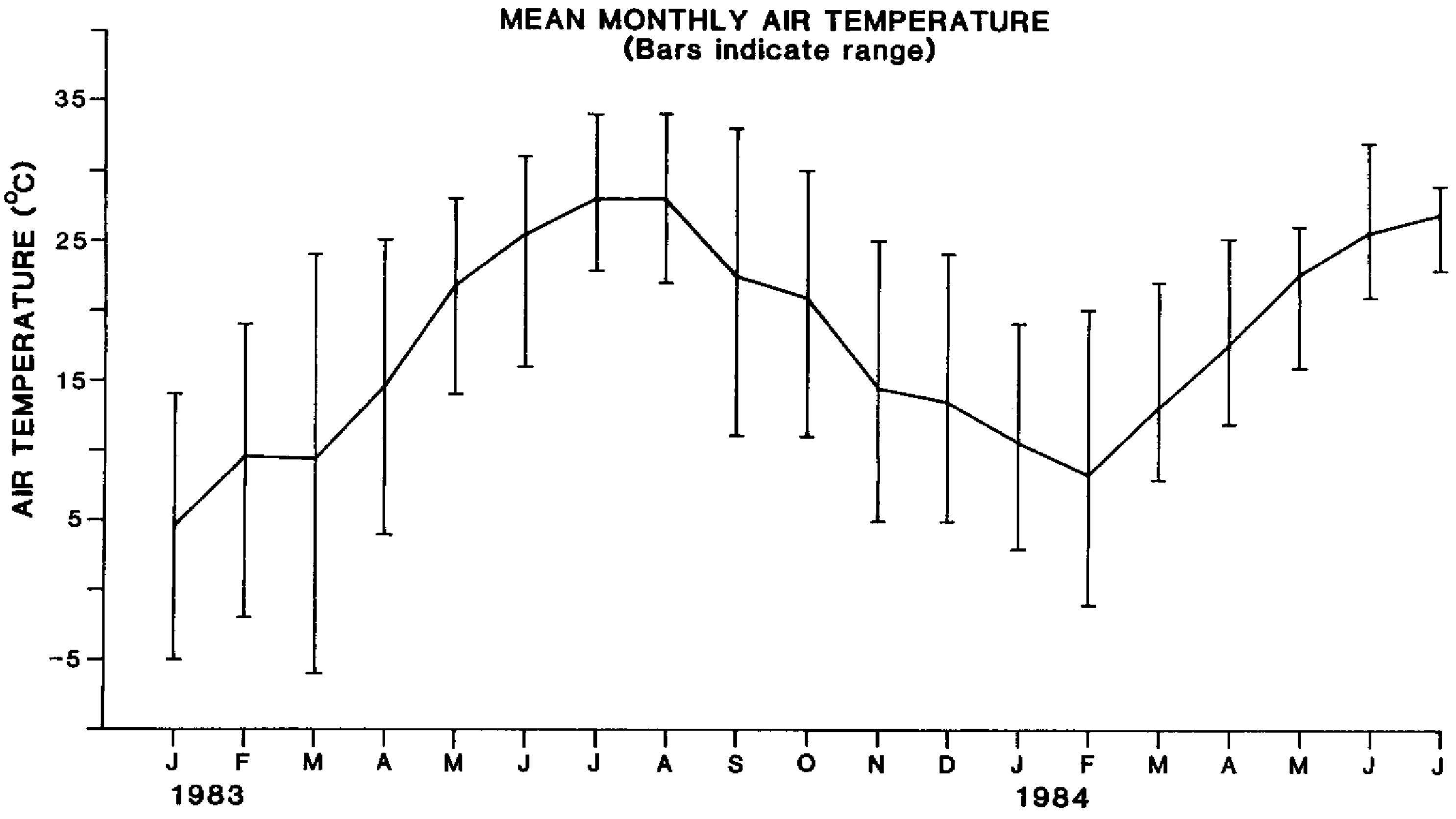

Figure 4.6 Monthly mean air temperatures for the study site at Cat Island. Vertical bars indicate ranges.

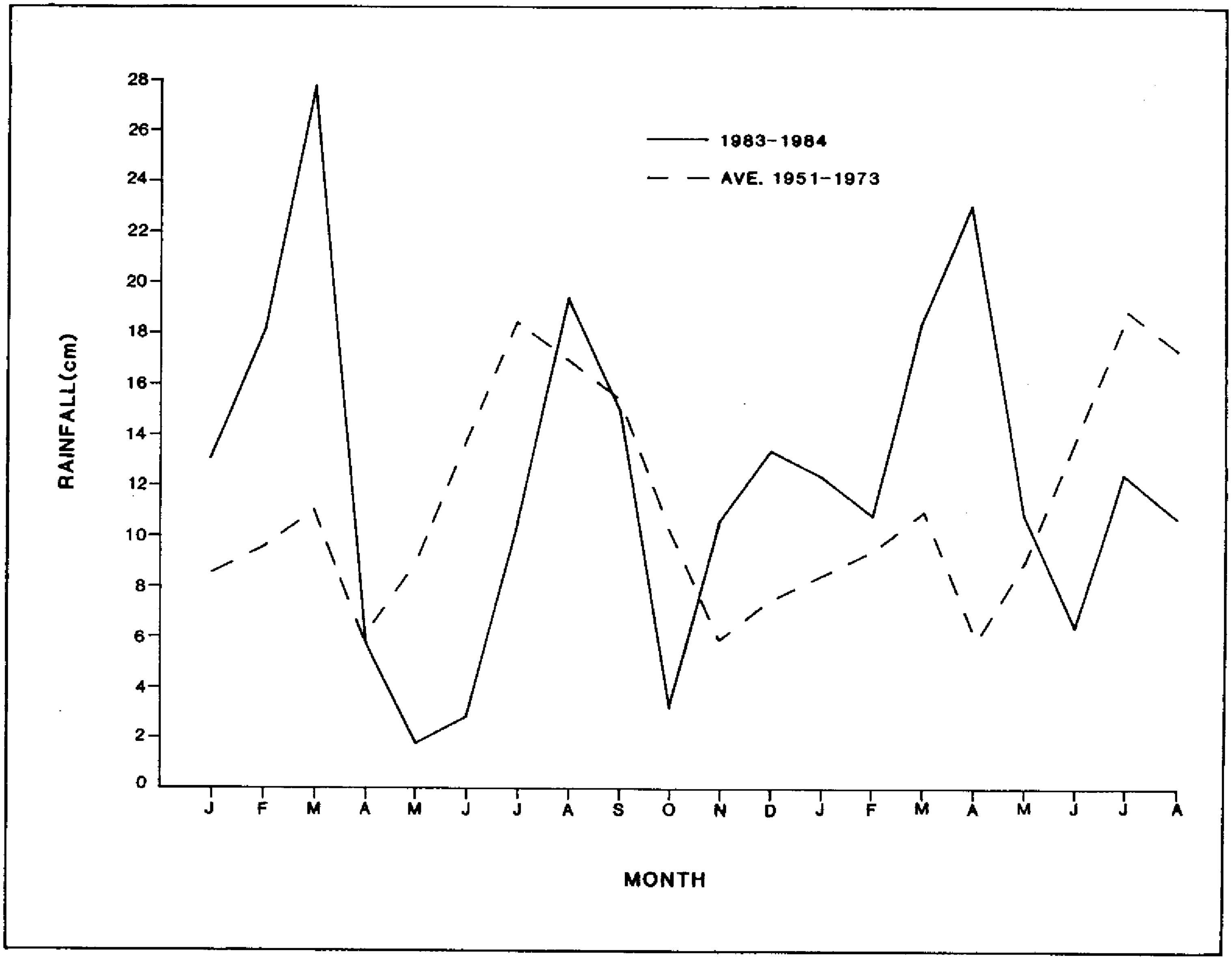

Figure 4.7 Cumulative monthly rainfall at the Cat Island impoundments in 1983 and 1984 versus that for Georgetown averaged for the years 1951 to 1973.

Santee River and a freshwater reserve pond adjacent to Cooperfield. Freshwater circulation via the reserve pond through the impoundment spillways was not provided during this study for the aforementioned reasons. Discharges from the North Santee River fluctuate during any given year and depend primarily on the amount of rainfall and the volume of water released through the Russell Dam. During the study, river discharge peaked in March-April of each year (Fig. 4.8). At a point on the river nearest the study impoundments, the mean tide range was 1.2 m, and the spring tide range was 1.4 m.

Salinity conditions at the study site exhibited a direct negative correlation with the amount of rainfall and North Santee River discharge (Fig. 4.8). The salinity for the Santee area averaged 18 to 22 ppt and ranged between 1 and 30 ppt in the study impoundments and 0 to 32 ppt in the adjacent salt-marsh and tidal impoundment during the study period (Fig. 4.9 and 4.10). Unseasonally dry conditions in the summer of 1983 caused salinities to be higher than normal in the study impoundments. Management of impoundment salinities was limited because of the temporary closure of inter-impoundment spillways (plug-trunks) during the study. The management scheme used during this study is similar to those employed for other brackish-water impoundments within the Santee Delta managed for wintering waterfowl, although salinities vary depending on impoundment location and are generally lower for sites further up the estuary.

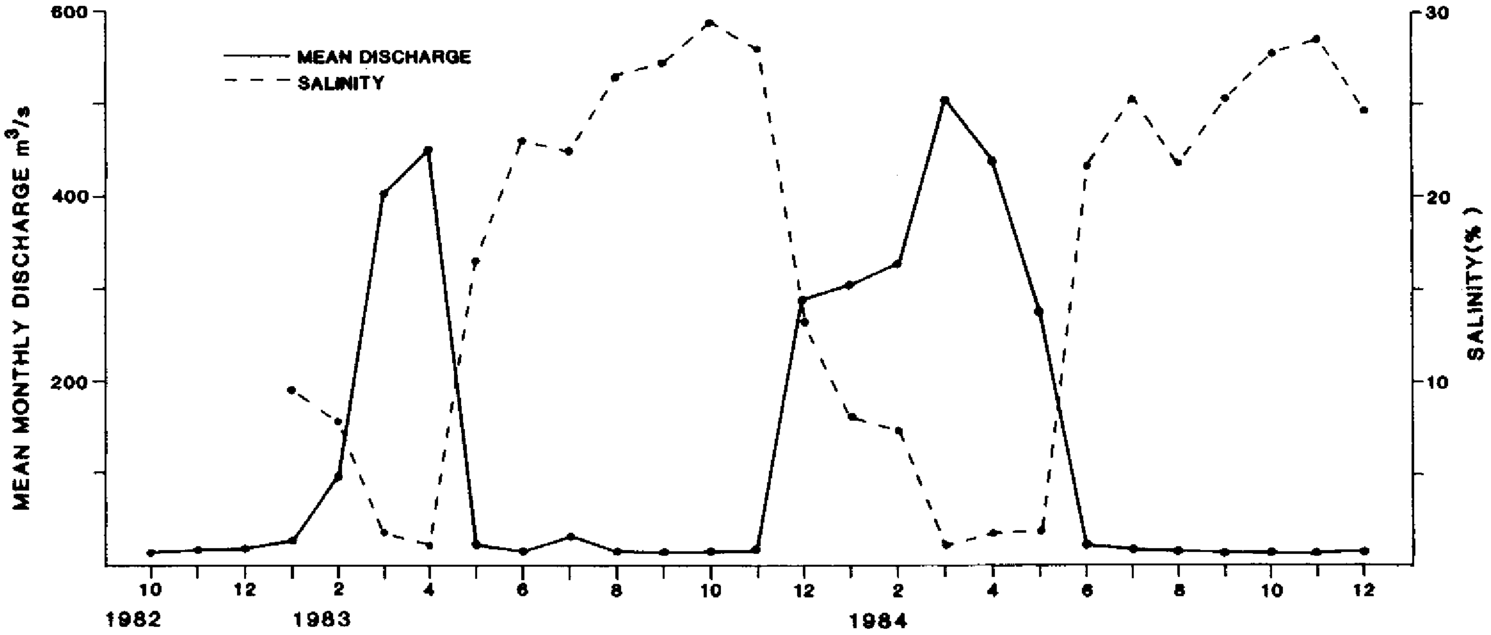

Figure 4.8 Monthly mean discharge from the North Santee River versus monthly mean salinity in Chainey Creek.

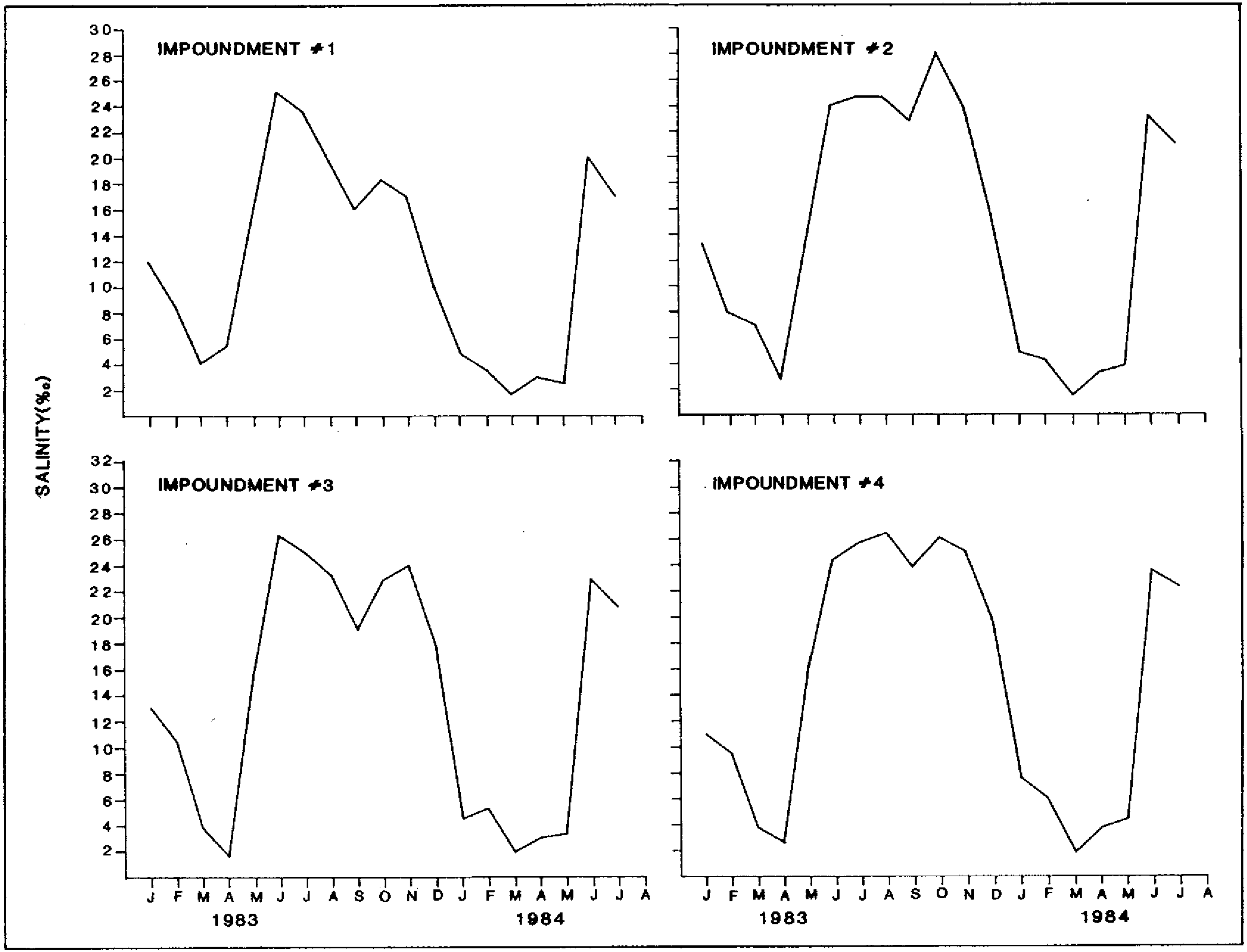

Figure 4.9 Monthly mean salinity in impoundments 1 to 4.

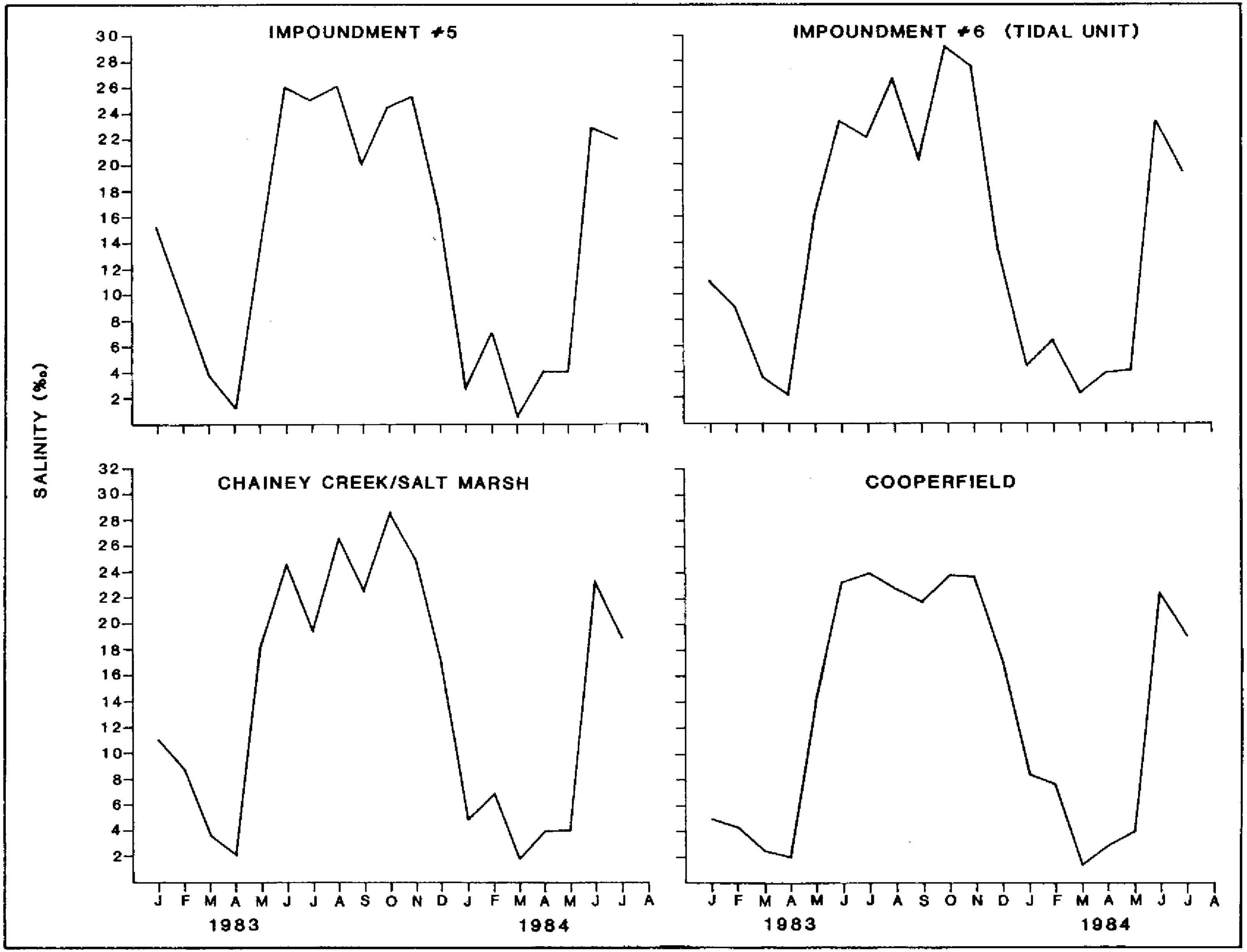

Figure 4.10 Monthly mean salinity in impoundments 5 and 6, Cooperfield and Chainey Creek.

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Chapter 5

Sedimentology, Hydrogeology and Hydrology

J. P. May and P. B. Zielinski

INTRODUCTION

Natural salt marsh originates through deposition of fine-grained sediment, which causes the buildup of the marsh surface. A thin stratum of silt and/or clay is introduced by the flood tide, deposited, and left behind by the ebb tide. Through this process, known as tidal-lag sedimentation (Postma, 1967), open bay is gradually transformed first into low marsh, then high marsh. As the surface builds up, it is covered by tidal waters less frequently. High marsh is inundated only on the spring tides.

Impoundments were constructed by partitioning portions of natural salt marsh by excavating a perimeter ditch and using that material to form dikes. The dikes, therefore, are composed of disturbed marsh-type sediments, but are separated from the underlying marsh sediments by the pre-impoundment surface. That surface is characterized by a fibrous organic layer consisting of relict root mat and stems (Fig. 5.1).

The Cat Island impoundments are located within the estuary of the North Santee River. This estuary was an open-water bay at the time the sea level rose to within a few meters of its present position some 5000 years ago. This is indicated by a sand layer located at a depth of 2 to 4 m beneath the marsh surface. The marsh sediments consist of the finer-grained silts and clays. Generally, these sediments are extensively bioturbated, because of the high level of natural biological activity in the marsh. The

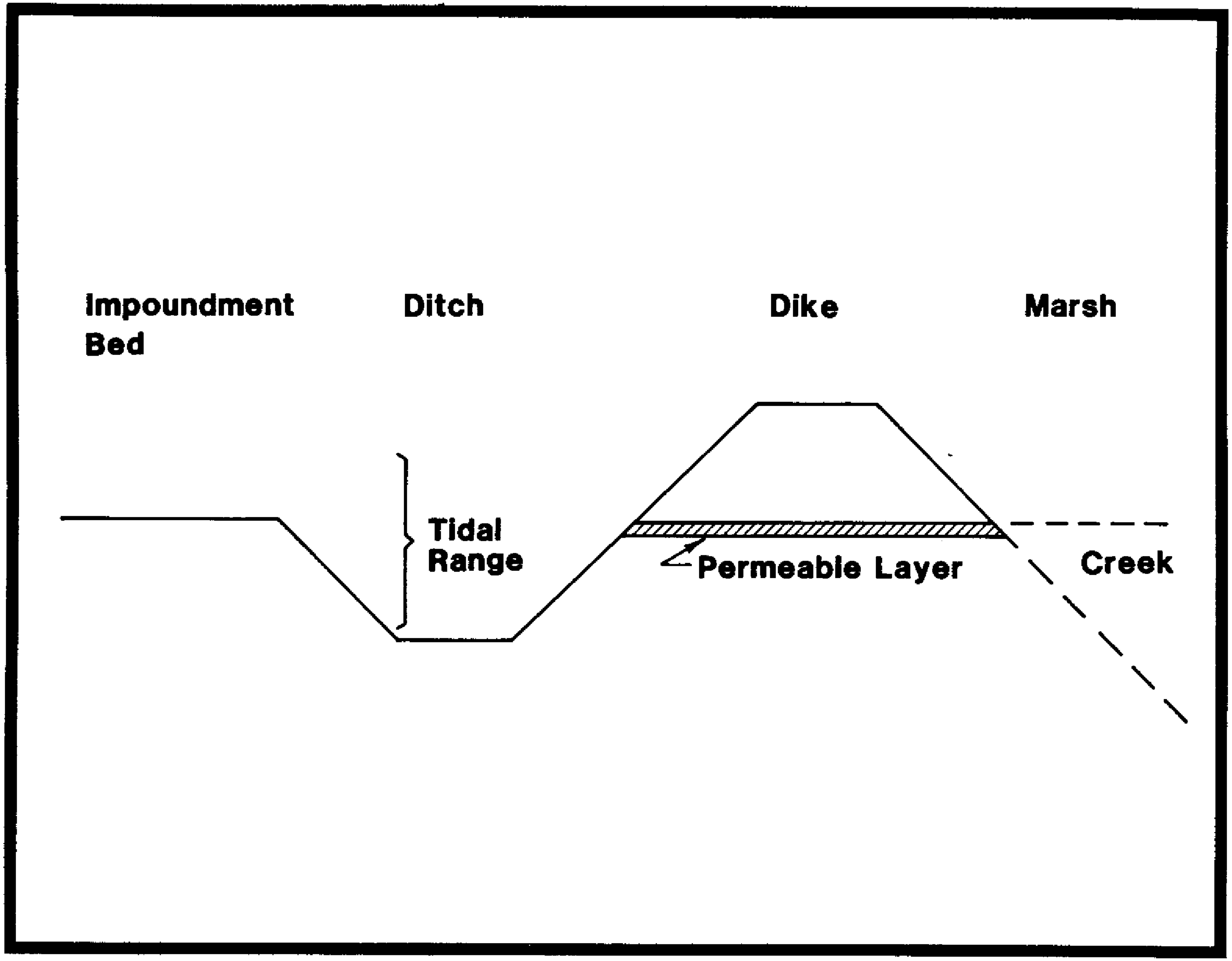

Figure 5.1 Generalized cross section through an impoundment perimeter ditch, dike, and Chainey Creek. Note that the dike was constructed from materials excavated from perimeter ditch. The original marsh surface was preserved as a fibrous organic layer of relatively high permeability.

isolation from tidal sedimentation due to diking prevents further buildup within the impoundments and causes changes in water chemistry. Agricultural activity and/or other artificial bioturbation within the impoundments has caused further disturbance of the upper layers of sediment and the addition of different types of organic materials. Because of the lack of daily flushing by the tides that would remove it, organic debris may constitute a greater percentage of the sediments than in the natural marsh.

The general biota of the impoundments, as well as the natural marsh, is influenced by the nature of the sedimentary substrate. The extent to which ground and surface water delivers and removes nutrients and debris is also important. In particular, it is of interest to determine whether nutrients are being delivered to or extracted from impoundment waters by vertical flow through the bottom or by lateral flow through the dikes. The present study was undertaken to improve our understanding of some of these processes.

The specific objectives of this study were: (1) to describe the sedimentary materials underlying the impoundment area; (2) to describe the hydrogeologic (ground water) system as it pertains to flow through the bottom to and from the impoundments; and (3) to determine the extent of lateral flow through the dikes to adjacent impoundments or to Chainey Creek.

A search of the literature revealed no previous publications on the sediments and hydrogeology of impounded coastal wetlands. In fact, geologic studies of coastal wetlands, in general, are sparse (Chapman, 1974; Frey and Basan, 1978). Studies of salt-marsh sediments by Ranwell (1972) and of estuarine sediments by Postma (1967) and Rusnak (1967) are applicable to the Cat Island marsh sediments. An unpublished report by Phillip M. Wilkinson (1970) described a study done on the Cat Island impoundments in 1967-1970 (for which purpose they were reconstructed) that included analyses of soil and water chemistry. Tim Eckard, Geology Department, University of South Carolina (personal communication, 1985), is currently studying the stratigraphy of the Santee delta region through an extensive coring program. Tom Williams, Forest Science Institute, Clemson University (personal communication, 1985), is currently studying the hydrogeology of the North Inlet region. The North Inlet marshes were also studied by May (1978). Gardner (1973) reported on hydrologic factors related to impoundments. Morgan and others (1975) investigated the characteristics and management of tidal impoundments. Studies concerning a fresh-water wetland at Madison, Wisconsin was reported by Oakes and others (1975), with a followup study by Huff and Young (1980). An unpublished report by May (1984) concerned the hydrogeology of fresh-water wetlands on Hilton Head Island, South Carolina. Several recent studies presented at the 1985 International Estuarine Research Conference (ERF, 1985) indicate a growing interest in coastal marsh sedimentology, though only one paper (May, 1985) concerned hydrogeologic factors as well. Zimmerman and others (1985) have studied ground water effect on nutrient flux in the Indian River estuary (Florida).

METHODS

Impoundment Sediments

The study of the sediments that underlie the Cat Island impoundments was based primarily on cores that ranged up to 3 m in length. Coring stations were selected quasi-randomly, being based on a desire to obtain maximum areal coverage, but limited by time constraints and accessibility (Fig. 5.2). The cores were collected with a dutch gouge corer, which resulted in reasonably good recovery in the fine-grained sediments. This corer is not capable of penetrating sand or shell layers more than a few centimeters thick. Seventeen long cores (ranging from 1 to 3 m in length) were collected from the area of the impoundments. Descriptions of the long cores are given in Appendix Table 5.1.

Sixteen short cores (10 cm) were collected from the area (Fig. 5.2) to supplement the information obtained from the long cores and to provide information on bottom conditions relevant to studies of macrobenthos and plants. Textural descriptions of the short cores are given in Appendix Table 5.2. A 4-m steel probe was used to determine the depth to the underlying sand/shell stratum (Appendix Table 5.3).

The core samples were described megascopically in the field, and subsamples were selected for further study in the Citadel Geology Lab. Lab study consisted of textural analysis based on wet sieving of the sand fraction and pipeting of the silt/clay fractions. The sediments were

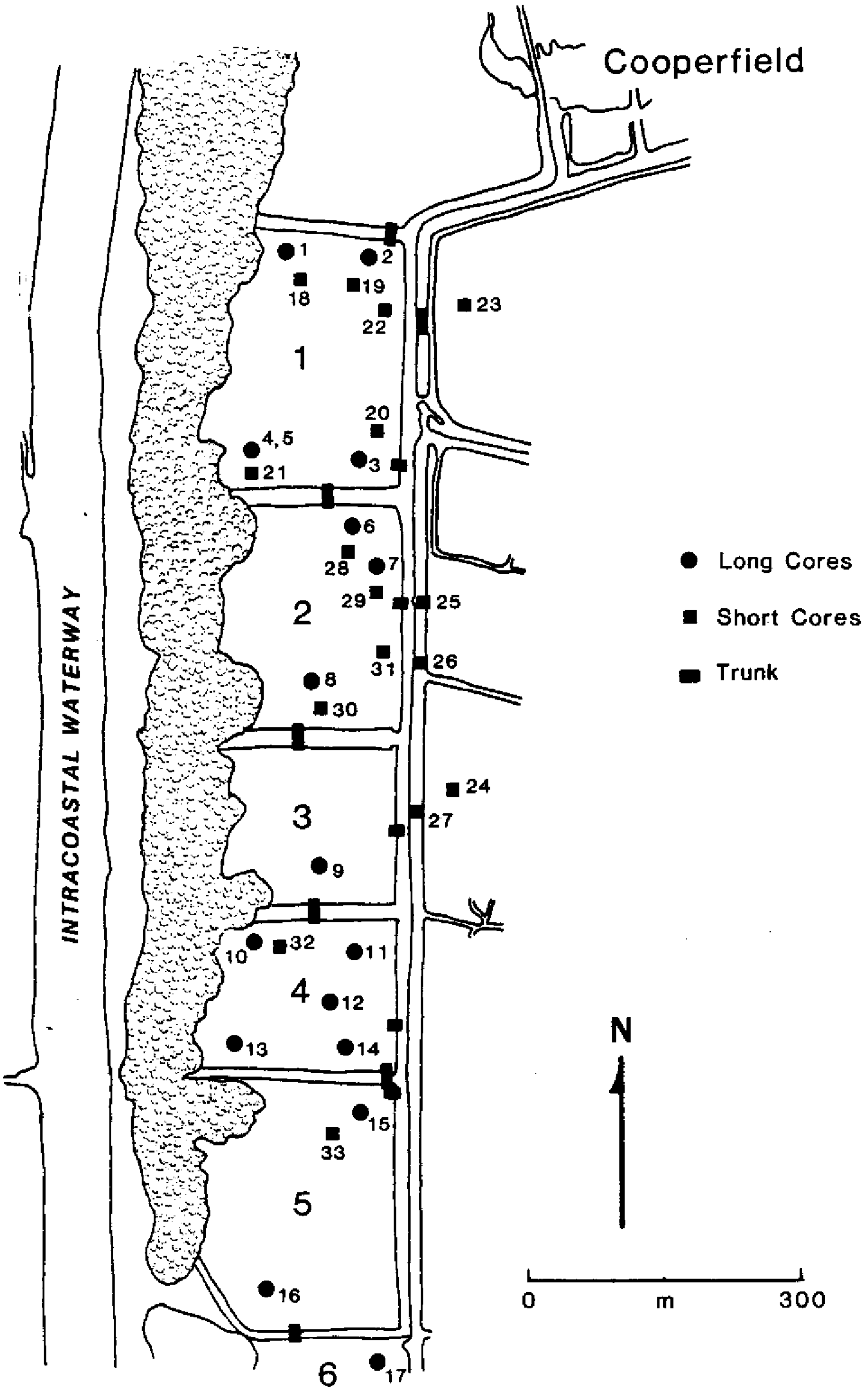

Figure 5.2 Schematic diagram of the study site showing location of sediment sampling sites.

viewed with a binocular microscope to determine their gross mineralogic characteristics. These data were interpreted and compared with sediment information from other sources in an effort to develop a synthesis that describes the general sedimentary system at the Cat Island impoundment site.

The pH and salinity of interstitial waters were measured as the cores were being taken and are listed in the core descriptions (Appendix Tables 5.1 and 5.4).

Impoundment Hydrogeology

Hydrogeological studies consisted predominantly of measuring time fluctuations of surface and groundwater levels in (1) the impoundments, (2) the adjacent salt marsh, and (3) on the adjacent Cat Island "upland." Ground-water levels were measured by emplacing piezometers at depths of 1.0 and 2.5 m beneath the ground surface (Fig. 5.3). The piezometers were emplaced by jetting and sandpacking. All stations were surveyed and all measurements converted to a common datum (mean sea level). These data were entered into the computer and plotted in time-series format.

Additional data were obtained by random percolation tests. This consisted simply of inserting a thin-walled pipe into the sediment, adding water up to the rim, and monitoring the time/decline in water level. These data were treated by the method described later as a slug test, but were less reliable because the pipe may have compacted the sediment as it was inserted and caused an artificially imposed decrease in permeability.

Water samples were collected from the piezometers and analyzed for the nutrients NH_4, NO_2-NO_3, and o-PO_4 (Chapter 6). The purpose of these analyses was to ascertain whether a relationship could be established between the ground water and the surface water in terms of nutrient content (Appendix Table 5.5). Salinities of both the ground and surface water were measured (Appendix Table 5.4).

Impoundment Dike Seepage

The study of seepage through dike structures also involved the installation of piezometers for water-level monitoring (Fig. 5.3; Appendix 5.6). Because the dikes were constructed by fill and had been compacted by road traffic, the piezometers were installed by first augering a hole (2 to

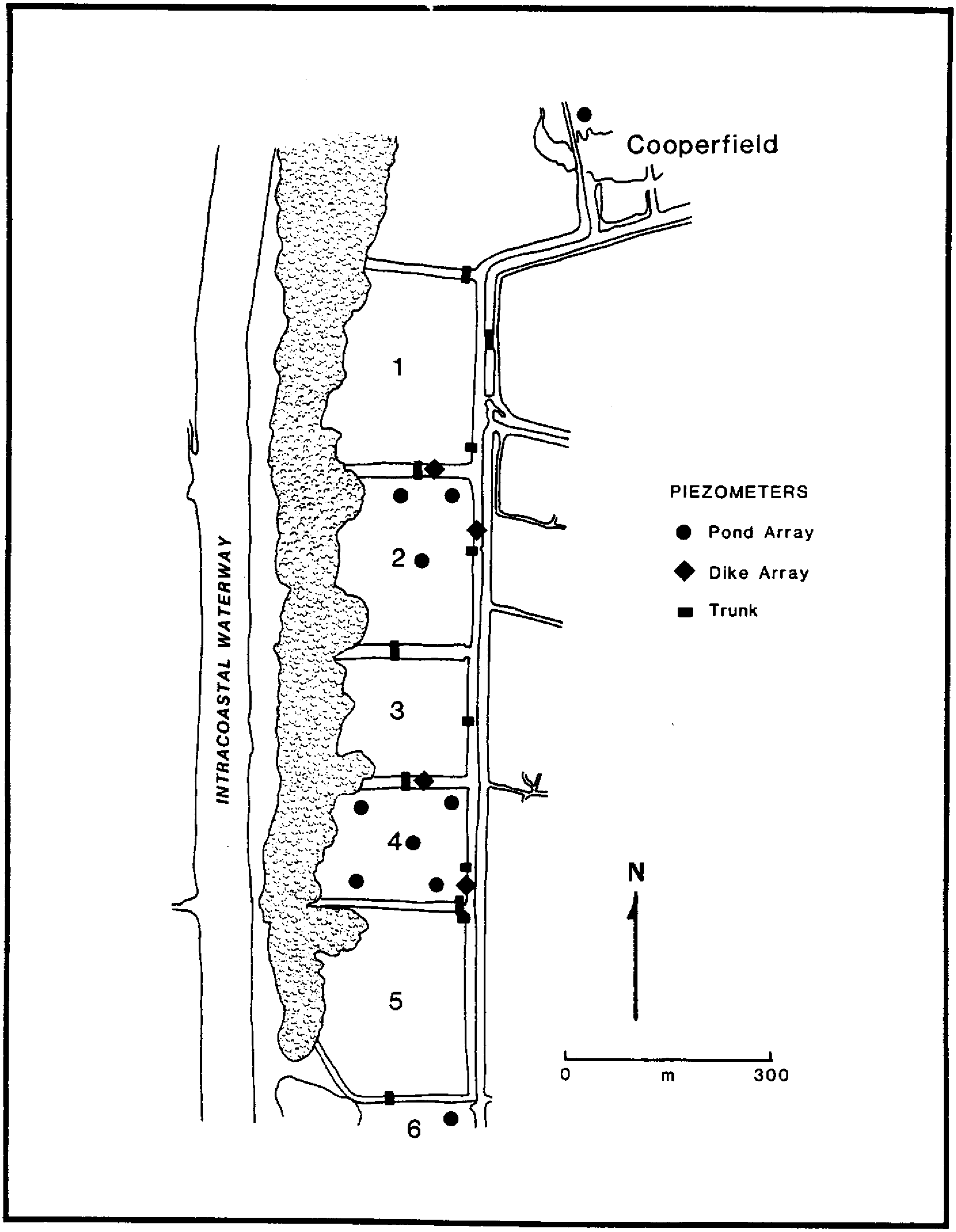

Figure 5.3 Schematic diagram of the study site showing location of piezometer sites.

3 m deep) and then emplacing a slotted and screened pipe. This method also permitted the sampling of the fill materials of which the dikes were composed (Appendix Table 5.7).

Samples of dike fill were taken to the Clemson Soils Lab for analysis, where permeability was determined by permeameter analysis. Organic content was determined by the ignition method at a temperature of 800°C (Head, 1980).

Because of the low permeability of the dike-fill materials, it was determined that the use of a "slug test" rather than the standard pump test was more appropriate. This method (Cooper et al., 1967; Papadopolas et al., 1973) is performed by either pumping the casing dry and monitoring recovery of water level or by adding a known quantity of water to the casing and monitoring water-level decline. The water-level time/decline data is plotted on semi-log paper and compared to a type curve to determine transmissivity. Transmissivity is defined as the permeability multiplied by the thickness of the permeable stratum.

Additional information on the permeability of the dikes was obtained by percolation tests. The test consisted of inserting a thin-walled, open-ended pipe into the sediment, adding a measured volume of water, and noting water-level decline. The data could have been treated as a slug test, but the results were somewhat less reliable because the lack of a screen at the bottom of the pipe may have caused compaction during insertion.

Water levels in the dike piezometers, impoundments, and creek were measured monthly (Appendix Table 5.8). Water-level recorders were deployed 5-13 December 1984 to obtain continuous data on several of the dike piezometers. Recorders were located at both the Impoundment gate and the creek gate of the trunk in impoundment 4, at the west well on the dike, and at the east well directly across from the west well (Figure 5.3).

RESULTS AND DISCUSSION

Sediments of the Impoundment Beds

The surface sediments (upper 10 cm) throughout the impoundments and adjacent "natural marsh" were characteristically fine-grained (<0.062 mm in diameter). The sand fraction (>0.062 mm in diameter) ranged from 0 to 5%

(with much of that being organic in origin). The sediment ranged from a silty clay (up to 82% clay) to clayey silt (up to 86% silt) in the upper 10-cm-thick layer. Channel sediments from the tidal creeks were much coarser, averaging 60 to 80% quartz sand, because of the significantly higher energy levels occurring in the creek as compared with the open marsh, where vegetation attenuates the tidal currents, and the impounded marsh, where diking has limited energy levels. Also, the creek may have eroded downward into an underlying sandy stratum.

Beneath the surface layer of marsh-type sediments was a layer of coarser sandy sediment that represented either the Pleistocene substrate or the earlier Holocene bay margin deposits on which the marsh sediments were deposited as a result of the Holocene rise in sea level during the past 5000 years (Fig. 5.4). When sea level reached within a few meters of its present level (4000 to 5000 years ago), the Santee estuary, as it is known today, began to form. Fine-grained sediment brought in by the Santee River was deposited in the estuary, rather than being carried farther down the valley to a site on what is now the continental shelf. Over the last 4000 to 5000 years, marsh sediment has built up to its present thickness of over 4 m.

Based on long core samples (1 to 3 m), the sediments were typically fine-grained. Sand was almost nonexistent, whereas clay content ranged from 10 to 82%. The sediments were generally poorly stratified, reflecting active bioturbation during and following deposition. Layers of root mat occasionally occurred to provide some horizontal layering.

The steel rod probe was used to determine the depth to the underlying sand (Appendix Table 5.3). In several instances, the sand layer encountered was thin enough to be broken through, and additional fine-grained sediment was encountered below. This indicates that the underlying sand layer is not continuous, but rather that it is in the form of lenses of restricted areal extent. This implies that the layers probably do not form an integrated ground water aquifer through which flow can occur for any significant distance. At a slightly deeper depth, this conclusion may not be valid, as we were only able to probe to the top of the formation.

Eckard (personal communication, 1985) drilled numerous core holes immediately south of the study area. Two of these sites, designated as

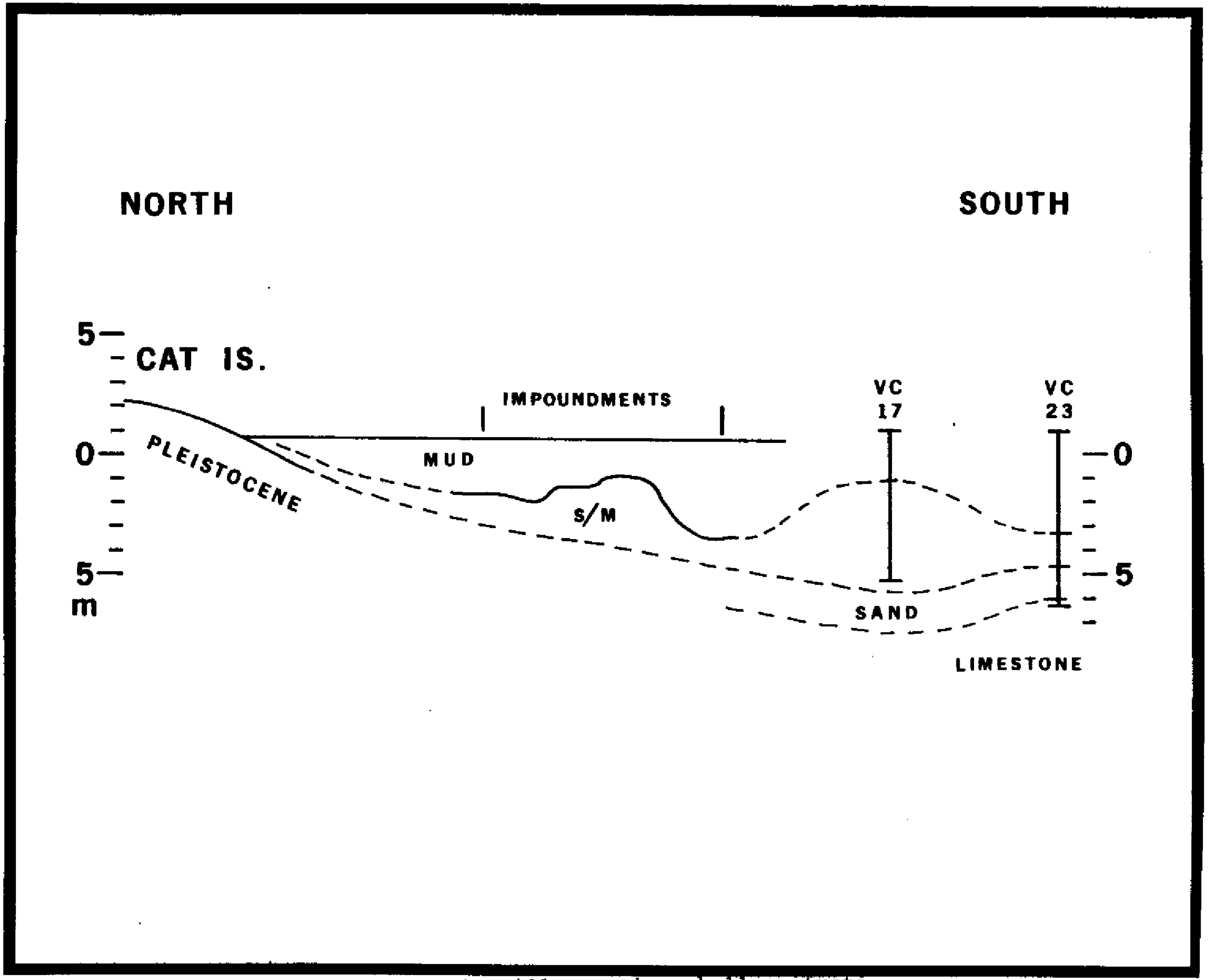

Figure 5.4 Generalized cross section illustrating shallow stratigraphy at Cat Island impoundments. "Mud" refers to fine-grained sediments ranging from silty clay to clayey silt. S/M refers to interbedded sand and mud. Sands in the S/M layer are probably lenticular.

SVC-17 and SVC-23, are pertinent to the present study. These cores were drilled with a vibracorer, which permits the penetration of sand layers, as well as those consisting of fine-grained sediments.

Core SVC-17, located 1.5 km southwest of and the closest to the Cat Island impoundments, encountered 2.15 m of mud (mixture of undifferentiated silt and clay) overlying 4.2 m of interbedded sands and muds. The upper zone corresponded with the silts and clays encountered in the area of the impoundments. The top of the deeper sandy zone was probably the sand layer that prevented deeper sampling with the dutch gouge used in the present study.

Core SVC-23, located 8 km to the southwest, indicated a similar stratigraphic sequence, with limestone bedrock being encountered at a depth of about 7 m.

The relationship of the sand layers beneath the marsh sediments to the Pleistocene sands of Cat Island cannot easily be interpreted without additional deep cores of the type collected by Eckard. It is possible that the sand layer encountered in the study area represented the underlying Pleistocene substrate beneath the Holocene marsh sediments. On the other hand, nearby vibra-cores indicated that there is a zone of interbedded sand and mud that overlies the deeper clean sands. In the former case, it is possible that a ground water aquifer, possibly even an artesian aquifer, could extend southward beneath the impoundments. In the latter case, the sand layers would be lenticular and would have little hydrologic impact. Based on hydrogeologic findings discussed later, it is suspected that the second interpretation is the more probable.

Ground Water Flow Through The Impoundment Bottom

It was of interest, from the point of view of nutrient flux, to determine whether water exchange through the bottom sediment occurred in the impoundments and adjacent marsh. Water level measurements taken in piezometers were assumed to indicate the elevation of the potentiometric surface relative to the piezometer depth.

Station 7 was located at the south margin of Cat Island (Fig. 5.3) immediately north of the study impoundments and was established to monitor the temporal fluctuation of the water table on the island. This station consisted of a single piezometer placed at a depth of 2.85 m below ground surface. The water-level elevations measured at station 7 (Fig. 5.5a) represented the potentiometric head available to cause groundwater flow through the sand layer, which lies beneath the fine-grained sediments of the adjacent marsh (and impoundments) to the south. A comparison of Fig. 5.5a to Fig. 5.6 indicates that the effect of the groundwater potentiometric head originating from Cat Island was nil.

This is in contrast to the preliminary findings of Williams (personal communication, 1985) in the North Inlet area. His study of salt-marsh hydrogeology indicated a definite relationship between the potentiometric levels measured in the salt-marsh sediments and in the adjacent upland. However, the sediments in that area are probably more permeable than those at Cat Island. This is indicated by the higher percentage of sand in the salt-marsh sediments there (May, 1978). It appears probable that the ground-water system at the North Inlet marsh area is distinctly different from that existing at Cat Island.

Figure 5.5b shows groundwater levels for the 2.5-m and 1.0-m piezometers at the tidal impoundment (unit 6) site (Fig. 5.3). This area is covered by water only at high tide. For accessibility reasons, the measurements were taken at times when the tide level was at mid to low stage. These measurements probably reflect only the maximum height of and the elapsed time since the last high tide. They would be expected to bear little resemblance to the water levels measured inside the impoundments, where surface water was controlled. There was generally a close correspondence between the levels measured in the 2.5-m piezometer and the 1.0-m piezometer. This indicates that either the two levels were in hydraulic communication or that they were both controlled by the same effects. It is concluded that, as the permeability of the sediments was found to be low, the latter is more probable. The two water levels probably responded to variations in hydrostatic pressure due to tidal fluctuations. Unfortunately, a water-level recorder was not available to monitor these levels continuously.

Water levels in impoundment 4 and 2 are shown in Figs. 5.6 and 5.7, respectively, with the surface water levels superimposed above the groundwater levels. The close correspondence between surface water and groundwater levels is obvious. This is to be expected, at least at those times when the sediment surface is covered by surface water. As was

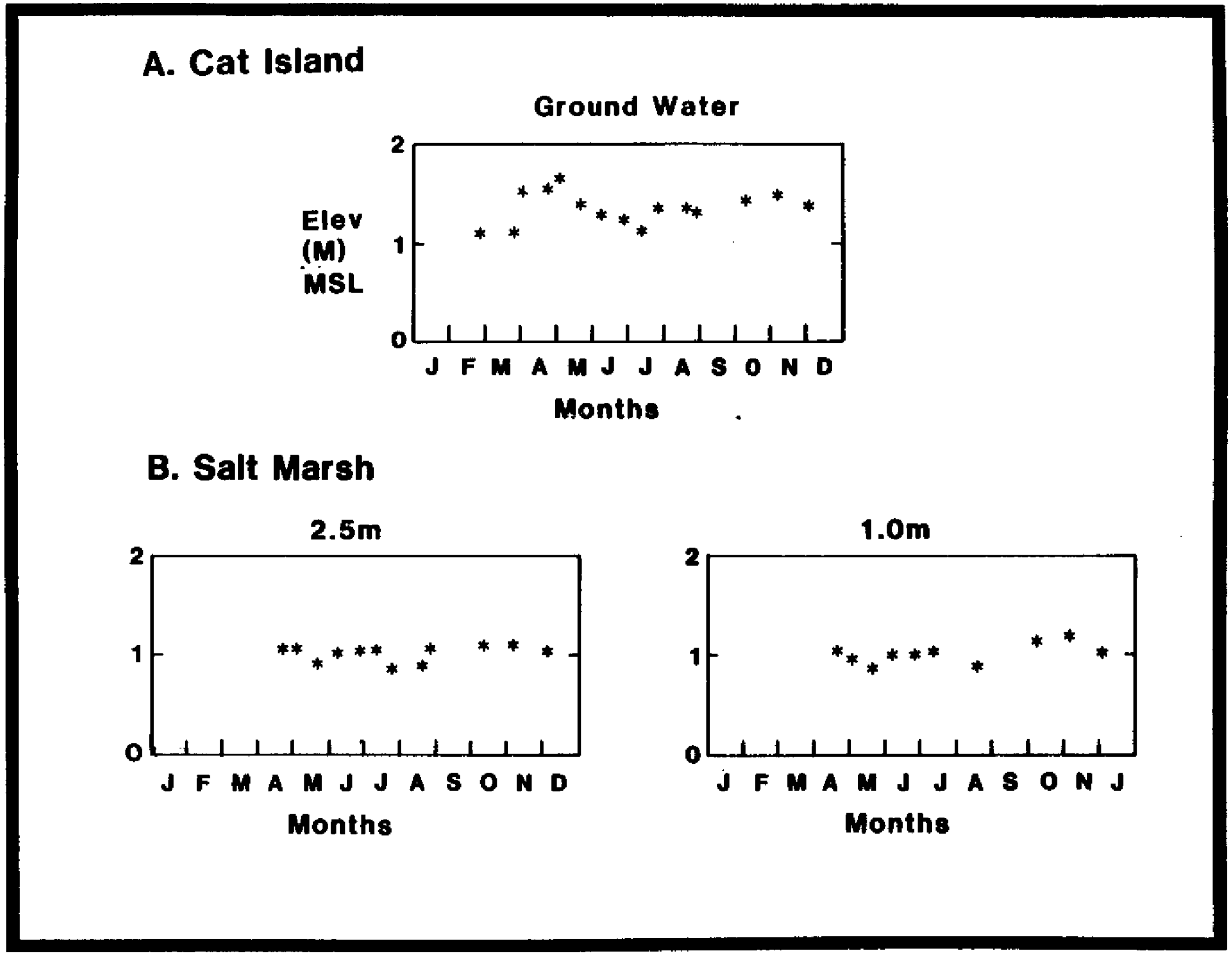

Figure 5.5 (A) Plot of ground water level against time for site 7: Cat Island upland site (2.5-m piezometer). (B) Plot of ground water level against time for site 6: marsh site (2.5-m and 1.0-m piezometers).

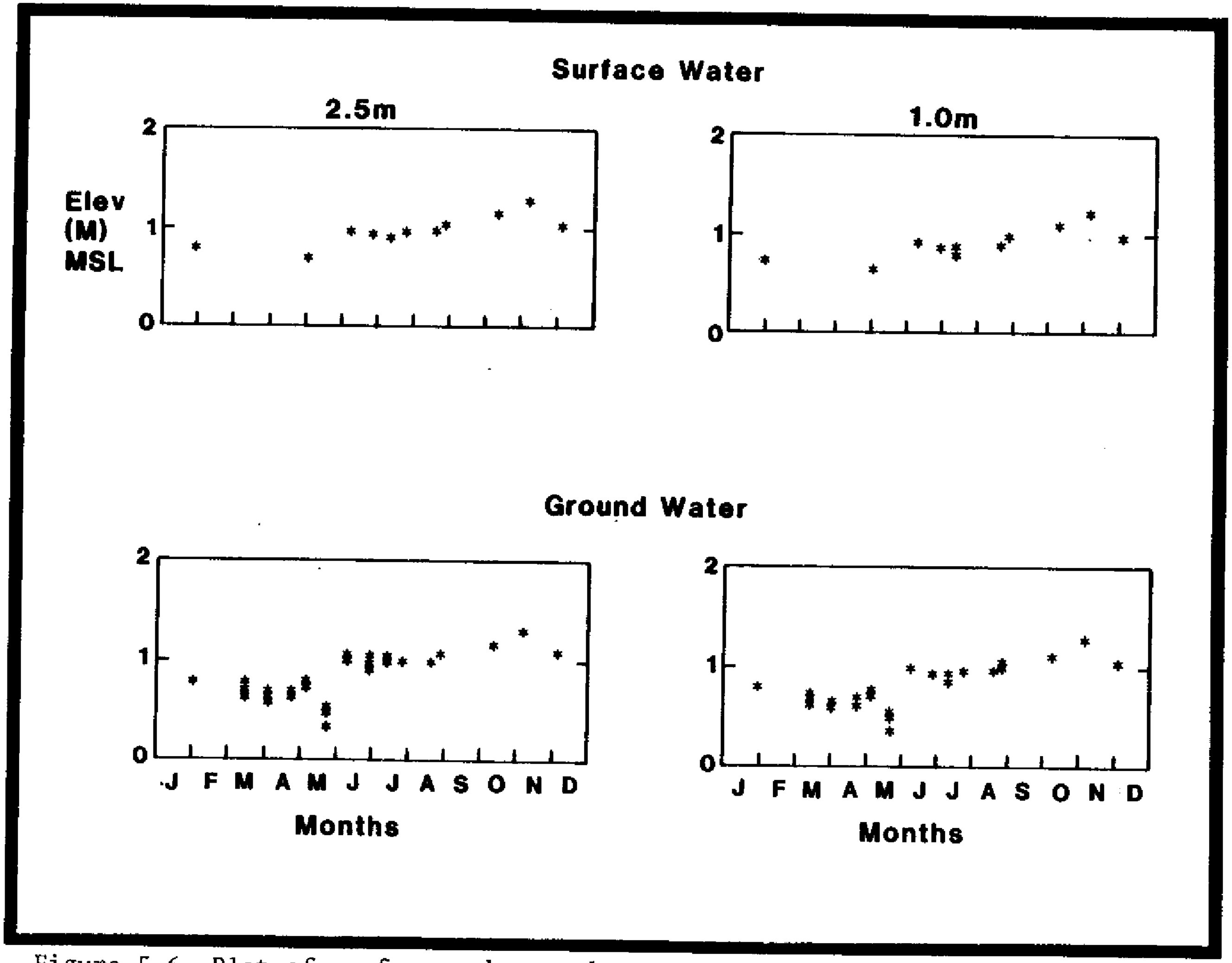

Figure 5.6 Plot of surface and ground water levels against time for site 4, the five impoundment 4 stations. Each station included a 2.5-m and a 1.0-m piezometer.

concluded in the case of the open-marsh ground water levels, the fact that the 2.5-m and 1.0-m piezometers showed such similar water levels is probably not due to any hydraulic communication between the two, but rather because they were both responding to the same force: the weight of the overlying surface-water level.

Figure 5.6 (left) shows the water levels for the 2.5-m piezometers located in impoundment 4. During the February to April interval, the surface-water level was below the sediment surface; that is, the sediments were subaerially exposed. It was during these times that the groundwater measurements displayed the most variation among stations, indicating that the primary control of water levels in the piezometers was the level of the surface water. This same relationship is shown in measurements from the 1.0 m piezometers (Fig. 5.6, right).

Water-level measurements from impoundment 2 are shown in Fig. 5.7. This pond was not dewatered during the study period. The groundwater levels show much less variability, both spatially and temporally, a further indication that water levels in the piezometers responded more to surface-water conditions than to other effects, such as artesian head from nearby Cat Island, or even the adjacent spoil areas to the west (Fig. 5.3).

The extent to which the groundwater tends to discharge upward through the pond bottom or to which surface water may tend to recharge downward through the pond bottom is not easily ascertained. A comparison to water levels measured at a single site at (1) the surface, (2) 1.0-m depth, and (3) 2.5-m depth indicated a vertical potential gradient. That is, if (1) > (2) > (3), then there is a potential for recharge, because surface pressure is greater than at depth. Conversely, discharge is indicated when pressures at depth exceed those nearer the surface. These potentials are summarized in Table 5.1. Differences in measurements of less than 10 mm may be subject to measurement error. Using only those measurements for which the difference was over 10 mm, the net recharge/discharge potentials can be summarized as shown in parentheses in Table 5.1.

The data from impoundment 2 (which was not dewatered during the study period) indicated a definite potential for groundwater discharge. This impoundment is closer to the Cat Island upland and, perhaps, there was some artesian effect. Data from impoundment 4, which was dewatered, indicated that there was no tendency toward either recharge or discharge. If

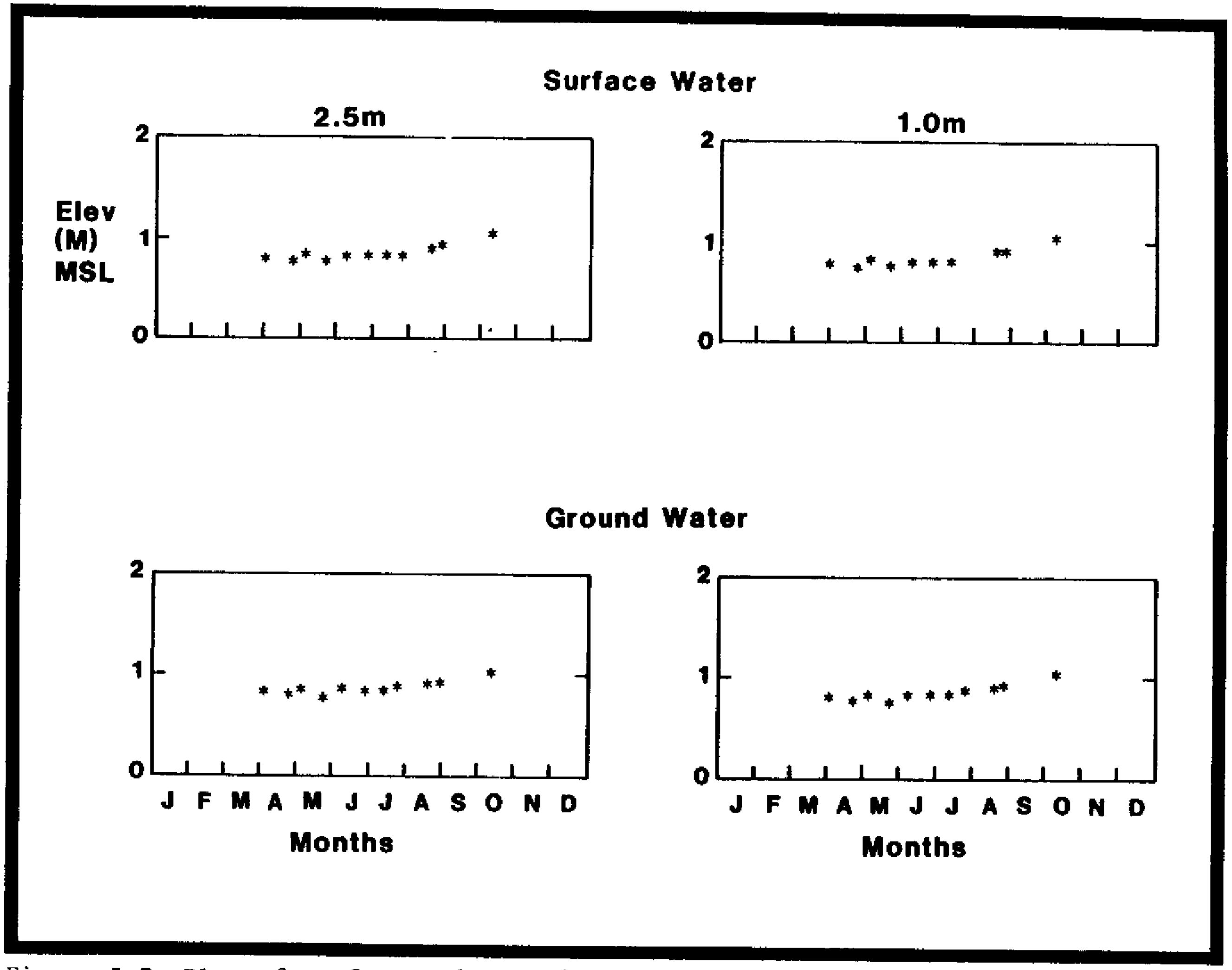

Figure 5.7 Plot of surface and ground water levels against time for site 2, the three impoundment 2 stations. Each station included a 2.5-m and a 1.0-m piezometer.

artesian conditions existed, the impoundment that was dewatered, impoundment 4, should have shown a stronger discharge potential than the impoundment that was not dewatered, impoundment 2. The values just discussed indicate only a potential for water flow through the impoundment bottom; they did not prove that such a flow, whether upward or downward, actually existed.

Limited chemical analyses were performed in both the field and the lab to characterize the ground water and to be able to compare it to the surface water. The pH of interstitial waters from some cores was measured as the cores were being taken (Appendix Table 5.1). Values of pH ranged from 6.0 to 7.0. No areas of low pH were encountered that would indicate cat clay development; however, these measurements were few and cursory. A more exhaustive analysis may well have found some cat clays. Wilkinson (1970) found that the pH frequently was as low as 3.0 or 4.0, especially in the impoundments that had been drained and exposed to air for some months.

Table 5.1

Summary of number of water-level measurements showing potential for ground-water recharge and discharge. Values expressed in parentheses include only those cases in which differences were greater than 10 mm.

Station Number (Location)	Recharge		Discharge	
2 NW	2	(0)	28	(21)
2 NE	1	(0)	26	(19)
2 C	3	(0)	25	(13)
4 NW	13	(3)	18	(4)
4 NE	25	(5)	11	(3)
4 C	11	(6)	17	(5)
4 SE	9	(3)	27	(12)
4 SW	16	(6)	16	(4)

Salinities of both the ground and surface water were measured (Appendix Table 5.4). The ground water was commonly saline, ranging from 10 to 30 ppt. This suggests that there was no significant flushing action by discharging fresh ground water. The lack of correlation of surface-water salinity to ground-water salinity indicates that any vertical flow through the impoundment bottom was probably too slow to significantly affect the chemistry of the surface water.

Water samples were analyzed for the nutrients NH_4, NO_2-NO_3, and o-PO_4 (Appendix Table 5.5). The purpose of these analyses was to determine whether a relationship could be established between the ground water and the surface water in terms of nutrient content. The results of the analyses indicated that such was not the case. The data appeared erratic. It is also possible that, even though the piezometers were repeatedly pumped out for several months prior to sampling, the groundwater samples were reflecting contamination introduced by the piezometer installation procedure (jetting).

Impoundment Dike Sediments

Dike fill materials generally consisted of impermeable, gray clay (Appendix Table 5.6). At a depth approximately equal to the elevation of the floor of the impoundments, a zone of organics-rich, friable soil was encountered. The zone was always wet, suggesting that water was able to flow through it. This was substantiated by laboratory permeability tests (Table 5.2).

The measured organics content of the permeable layer averaged 37%, as compared to about 18% in the overlying sediments. This layer probably represents the former surface of the salt marsh before dike construction. It may be slightly deeper now than it was originally, because of compaction resulting from the overburden placed on it.

Table 5.2

Permeabilities of dike sediments.

Depth (m)	Permeability (cm/day)
0.3	0.0
0.7	0.0
0.8	0.0
1.1	6.6
1.2	19.8
1.8	0.0

Impoundment Dike Seepage

The relative levels of the impoundments, dike piezometers, and Chainey Creek indicated that there existed a general negative gradient from impoundment to creek. The average head difference at impoundment 4 was about 1.2 m at low tide and about -0.3 m at high tide, for an average head difference of approximately 0.75 m between the impoundment and creek.

At the station located on the dike between impoundment 4 and Chainey Creek, continuous water-level recording in the east well showed an attenuated tidal fluctuation, indicating direct hydraulic communication with the creek (Fig. 5.8). The west well showed no tidal fluctuations, but rather a gradual decline in water level during the December 1984 study period, which corresponded with a similar decline in water level within impoundment 4. The water level within the impoundment averaged about 1.5 cm higher than the level in the west well, which averaged about 14 cm higher than the level in the east well. These results illustrate a negative gradient from impoundment to creek and are indicative of the low permeability of the dike materials.

Slug test analyses for the impoundment 2/Chainey Creek dike yielded transmissivity values of 0.0179 and 0.0239 m^2/day for duplicate tests at the east well, for an average value of 0.0209 m^2/day. At the west well, transmissivity was determined to be 0.0295 m^2/day.

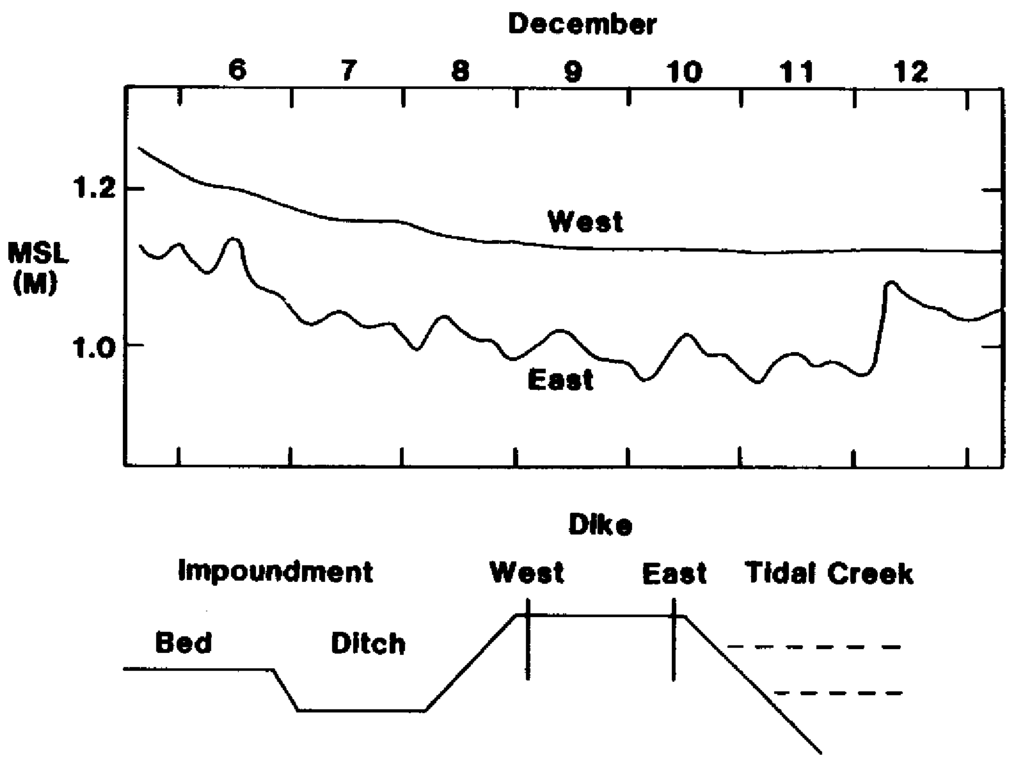

Figure 5.8 Plot of stage record at impoundment 4 for the period 5-13 December, 1984. The west piezometer was located on the impoundment side of the dike and the east piezometer was located on the tidal creek side of the dike. Note that the permeable layer did not transmit tidal water level fluctuations to the impoundment side.

Assuming an overall average transmissivity for the dike of 0.0252 m^2/day, the seepage rate through the dike was computed as follows:

$$q = 0.0252 \times 0.762/6.1 = 0.00314 \text{ m}^3\text{/day per m of dike length}$$

where 0.762 m is the average head difference between the impoundment and the creek and 6.1 m is the dike width. The thickness of the permeable layer was assumed to be 0.305 m. Based on a dike length of 244 m for impoundment 2, this flow rate indicated a volume discharge of 0.77 m^3/day. Based on a dike length of 137 m for impoundment 4, the discharge was computed to be 0.43 m^3/day. These values would vary, depending on changes in gradient due to fluctuations in creek and impoundment water levels.

An independent approach to the determination of seepage through the dikes can be made by using the lab determinations of the permeability of samples taken from the impoundment 4/5 dike (Table 5.2). Using these results, the average value was 0.13 m^3/day. A comparison to the previously calculated seepage value through the impoundment 4/Chainey Creek dike can be made by using the Darcy equation:

$$q = K\ h\ W\ dh/dx$$

or

$$q = 0.13 \times 0.305 \times 1.0 \times 0.762/6.1 = .00496 \text{ m}^3\text{/day per m of dike length.}$$

This result was the same order of magnitude as that computed earlier based on slug test data.

CONCLUSIONS

The results of this study suggest that no significant vertical flow exists through the impoundment bottoms. This conclusion was based on (1) the impermeable nature of the sediments that floor the impoundments; (2) the very low and variable (spatially and temporally) vertical hydrostatic gradients occurring beneath the impoundments; and (3) the general lack of a demonstrable causal relationship between ground and surface water based on water chemistry. Any vertical flow was almost certainly too slow to be of any significance with respect to nutrient flux to and from the impoundment system.

There was ground water communication through the dikes from impoundment to impoundment or from impoundment to creek, and the rate was approximately 0.003 to 0.005 m^3/day per meter of dike length. This rate translated to generally less than 1 m^3/day and probably did not significantly affect the general nutrient flux to and from the impoundments. It is concluded, therefore, that the nutrient flux to and from the impoundments operated independently of any water flux through the bottom and probably through any see page through the dikes. Nutrients entered and left the impoundments principally through the trunks and possibly via the animals.

ACKNOWLEDGEMENTS

The present study was supported by Grants No. NA83AA-D-00057 and NA84AA-D-00057 from the South Carolina Sea Grant Consortium (JPM and PBZ) and by 1983-1984 and 1984-1985 grants from the Citadel Development Foundation (JPM). The senior author (JPM) was assisted by Mark Epstein, Benny Maresco, Coral May, and Jimmy May. Tom Williams (Clemson University) and Tim Eckard (University of South Carolina) generously provided preliminary results of their studies in the region, for which we are most appreciative. The junior author (PBZ) was assisted by Chris Aas, Abhinav Gandhi, Rajababu Veeramachaneni, Greg Zielinski, and Mike Nussman.

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Chapter 6

Tidal Nutrient Exchanges

H. N. McKellar

INTRODUCTION

Open intertidal salt marshes are believed to be important in maintaining nutrient balances in the coastal zone by exporting critical fractions of carbon, nitrogen, and phosphorus. Odum (1968, 1980) proposed that this "outwelling" of nutrients from fertile marsh lands may support higher productivities in adjacent coastal environments. Although the magnitudes of outwelling may vary considerably from site to site, most marshes have been found to export dissolved inorganic phosphorus, ammonium nitrogen, and organic carbon (see review by Nixon, 1980; Jordan et al., 1983). The same export trends have also been documented for the salt marshes of South Carolina (Gardner, 1975; Kjerfve and McKellar, 1980; Chrzanowski et al., 1982, 1983; Dame, 1982; Whiting et al., 1985; Whiting et al., in review).

At present, there is little information on nutrient dynamics and exchange in coastal impoundments. In comparison with adjacent estuarine waters, Anderson (1979) found impoundment waters on Wadmalaw Island, South Carolina to be enriched with phytoplankton biomass and carbohydrates but relatively depleted in inorganic nutrients. However, no studies have been conducted on the net transport of nutrients via tidal exchange in such coastal impoundments. In this study, we examine aspects of the tidal exchange of water and several critical fractions of carbon, nitrogen, and phosphorus. We focused on two fractions of dissolved inorganic nutrients (ammonium and ortho-phosphate), chlorophyll-a (as an indicator of phytoplankton biomass), as well as particulate and dissolved organic carbon. The major objectives of this part of the impoundment characterization were, therefore, (1) to examine tidal patterns in the concentrations of these nutrient fractions and to compute the net tidal exchange of nutrients between the impoundments and the adjacent estuarine waters, and (2) to compare seasonal patterns in nutrient concentrations and tidal exchange of water and nutrients in the impoundments with trends in an adjacent tidal marsh system.

METHODS

Studies on water and nutrient exchange were conducted in each impoundment on a monthly basis, usually within two or three days of spring tide. During each sampling period, water flow through the control structures was measured (Marsh-McBirney electromagnetic flow meter) at approximately three-hr intervals for two complete tidal cycles (approximately 25 hr). Water samples were collected at the same time in acid-washed glass bottles by manually rinsing and filling the bottles with water directly from the tidal flow (ebb or flood) within the water-control structures. Because tidal flow through these structures was shallow (<20 cm) and/or turbulent, vertical variability in nutrient concentration and water flow was not considered.

Samples were taken immediately to a field laboratory, where they were filtered through prerinsed GF/F filters and preserved for later analysis. Aliquots of filtrate were preserved with $HgCl_2$ for later analysis of o-PO_4 by the acid molybdate method of Murphy and Riley (1962). NH_4 was analyzed by the hypochlorite method of Solarzano (1969) after preservation of filtrate with phenol (Degobbis, 1973). Particulate organic carbon was determined by dry combustion of particulate matter on precombusted GF/F filters (Whatman) and IR analysis on an Oceanography International analyzer. Dissolved organic carbon was determined on filtrate after persulfate oxidation (Menzel and Vaccaro, 1964). Chlorophyll-a was determined by modifications of the standard fluorometric analysis (APHA, 1976) using a freeze-thaw acetone extraction procedure (Glover and Morris, 1979).

For direct comparison with trends in a tidal marsh, concurrent measurements of water flow and nutrient concentration were made at the inlet creek to the marsh within a breached impoundment (impoundment no. 6, see Fig. 4.2). Remnant dikes surrounded most of the marsh, thereby limiting broad-scale sheet flow which may be more characteristic of more open, natural marshes. Because of the absence of a water-control structure, however, the marsh within this area was completely intertidal and exposed to semidiurnal tidal flushing. There was no impounded water in the marsh, and the vegetation was dominated by intertidal stands of Spartina alterniflora, S. cynosuroides, and Scirpus robustus (see: Chapter 7). Although this marsh may not have been completely representative of nonimpounded tidal marshes in the area, it represented a common situation for many former rice fields in South Carolina and was used for comparison in this study.

Water volume in the impoundments was determined from hypsographic curves for each impoundment (Figs. 6.1 and 6.2) and water-level recordings during each sampling. The volume of tidal exchange in the tidal marsh and in the impoundments was calculated from time-series plots of instantaneous water flow integrated over the two complete tidal cycles during each sampling period. The corresponding water residence time was calculated as the water volume divided by the volume of tidal exchange per tide. Water residence times were converted to a daily basis by assuming a 12.42-hr tidal cycle.

The instantaneous flow rate (mass flow per second) for each constituent in the water was computed as the cross-product of water flow and concentration. Time-series plots of instantaneous mass flow were also integrated over two complete tidal cycles for each sampling period to compute the flow-weighted mean concentrations of each constituent for both ebb and flood tides. For the time interval between monthly sampling dates, the mean net tidal exchange (F_1, mass flow per tide) for each nutrient was computed as

$$F_1 = V_T (C_f - C_e) \qquad (1)$$

where V_T = mean tidal volume (l) for the interval, taken as the average of the flood and ebb tide volumes for the four tidal cycles sampled before

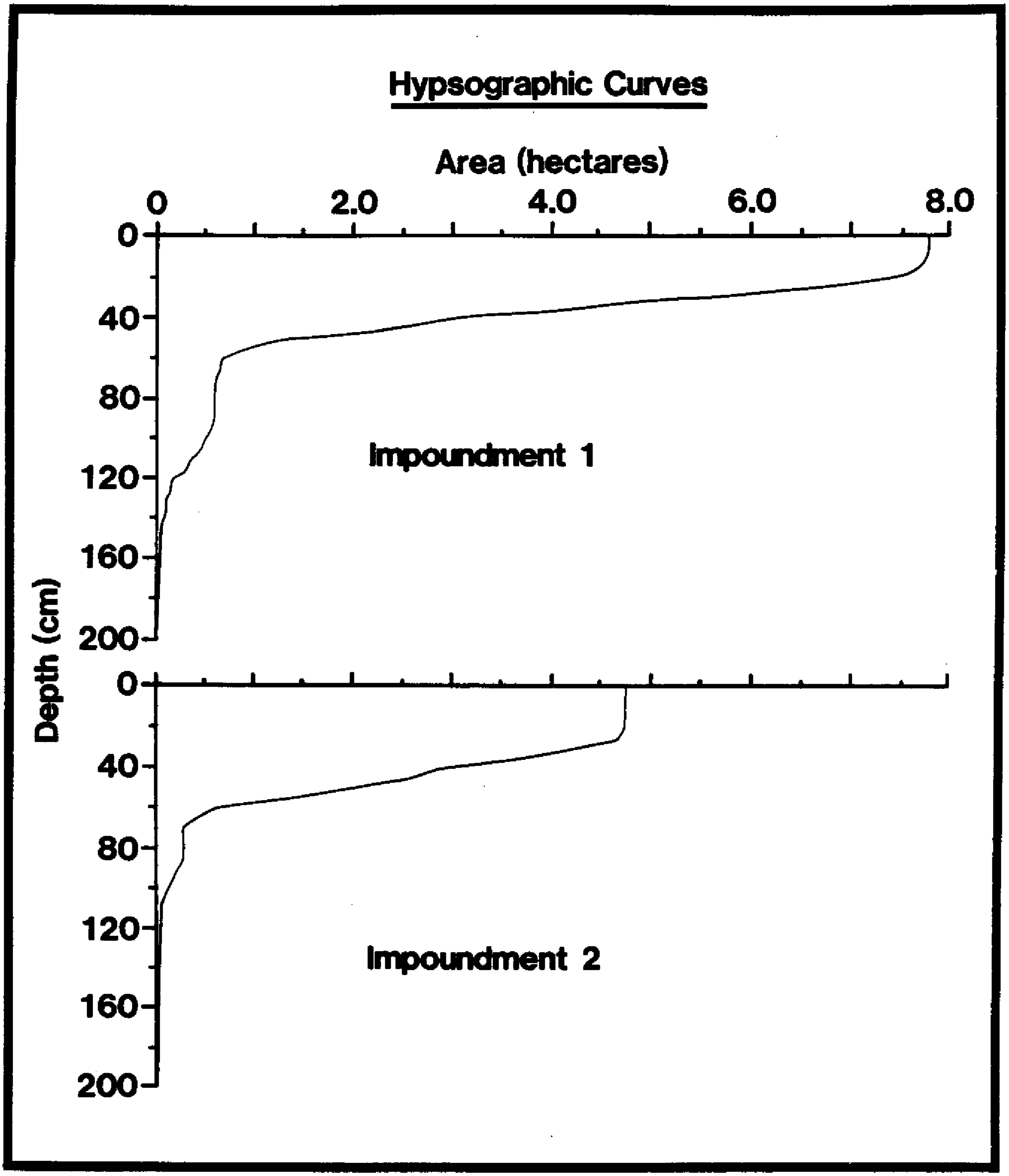

Figure 6.1 Hypsographic curves for impoundments 1 and 2 showing depth and area relationships at various water levels.

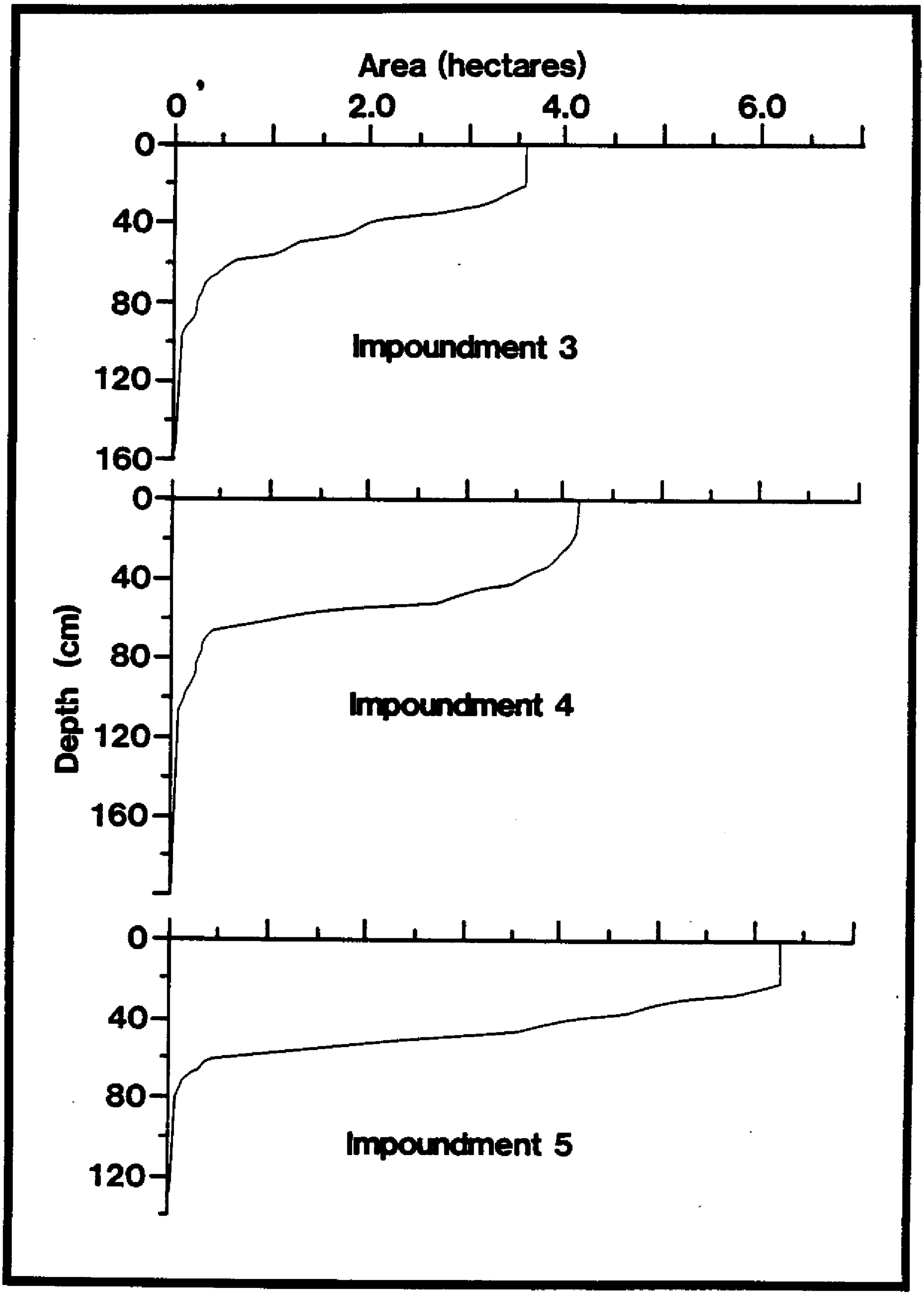

Figure 6.2 Hypsographic curves for impoundments 3, 4, and 5 showing depth and area relationships at various water levels.

and after each monthly interval; C_f = mean flow-weighted concentration for the four flood tides sampled; and C_e = mean flow-weighted concentration for the four ebb tides sampled.

These calculations estimated net nutrient flow associated with daily tidal exchange without regard for net monthly accumulations or losses of water volume. On a monthly time interval, these estimates were considered adequate for the tidal marsh, which completely drained after each tide and exhibited no net change in water volume. For the impoundments, however, additional terms were needed to account for nutrient flows associated with both net changes in water volume over the monthly time intervals and large water flows during impoundment drainage and reflooding. For net changes in water volume over monthly sampling intervals, the additional nutrient flow (F_2) was computed as

$$F_2 = (V_{net})\ (C_t) \qquad (2)$$

where V_{net} = accumulation or loss of water over the monthly time interval, determined from changes in water level and the corresponding hypsographic curves for each impoundment (Fig. 6.1 and 6.2;) C_t = the flow-weighted flood tide concentration (C_f) when there was net water accumulation or C_t = the flow-weighted ebb tide concentration (C_e) when there was a net loss of water. In addition, the net flux of nutrients during major events of impoundment draining or flooding (F_3) was calculated directly from the integrated time-series plots of instantaneous flux rates during these periods. The major flood-drain-reflood events (designed for mosquito control) occurred over a 1-week period in the spring (April/May) and accounted for a considerable portion of the net annual flux of water and nutrients in the impoundments. The net annual nutrient exchange for the 1982-1983 year was computed as the sum of these fluxes, ($F_1 + F_2 + F_3$) integrated over the 12-month period. All fluxes were divided by total surface area to yield area-based exchange values.

RESULTS AND DISCUSSION

Water Exchange

Patterns of nutrient exchange in coastal wetlands are controlled by complex interactions of biology, geochemistry, and hydrology (Gosselink and Turner, 1978). Fig. 6.3 summarizes some key aspects of the tidal hydrology of these systems in terms of changes in the impounded water volumes, volumes of tidal exchange, and corresponding water residence times.

The volume of impounded water in the tidal marsh was considered negligible, although there were small quantities remaining in the bottom of the drainage creeks at low tide and perhaps some residual water left in localized depressions on the marsh surface. The water volume in the impoundments (Fig. 6.3, top panel) reflected the basic water-management scheme used during the study, with minimum volumes (2.1 ± 0.5 million liters) after the winter drawdown, and maximum volumes (24 ± 3 million liters) in the fall. Drawdown was initiated in October, and the volume of water in the impoundments had declined to about 10 million liters by the end of the year.

The volume of tidal exchange varied considerably during the year in both the tidal marsh and the impoundments (Fig. 6.3, middle panel). Although most sampling dates were within two or three days of the astronomical spring tides, the actual tidal height (and tidal volume) were affected largely by local hydrography and meteorology. Tidal exchange in the marsh varied from about 1 to 5 million liters per tide, with an annual average for the eight sampling dates in 1983 (16 tidal cycles) of 2.8 ± 0.5 million liters per tide. Because the marsh was essentially drained at each low tide, the turnover rate for water in the marsh was once per tide. The corresponding water residence time in the marsh was, therefore, one tide (12.42 hr or 0.52 day).

In the impoundments, the volume of tidal exchange varied mainly as a function of the water-management scheme used during the study. During the spring flushing sequence, the tidal flow reached maximum rates of 3 to 4.5 million liters per tide (Fig. 6.3, middle panel), with corresponding water residence times of less than a day (Fig. 6.3, bottom panel). During the

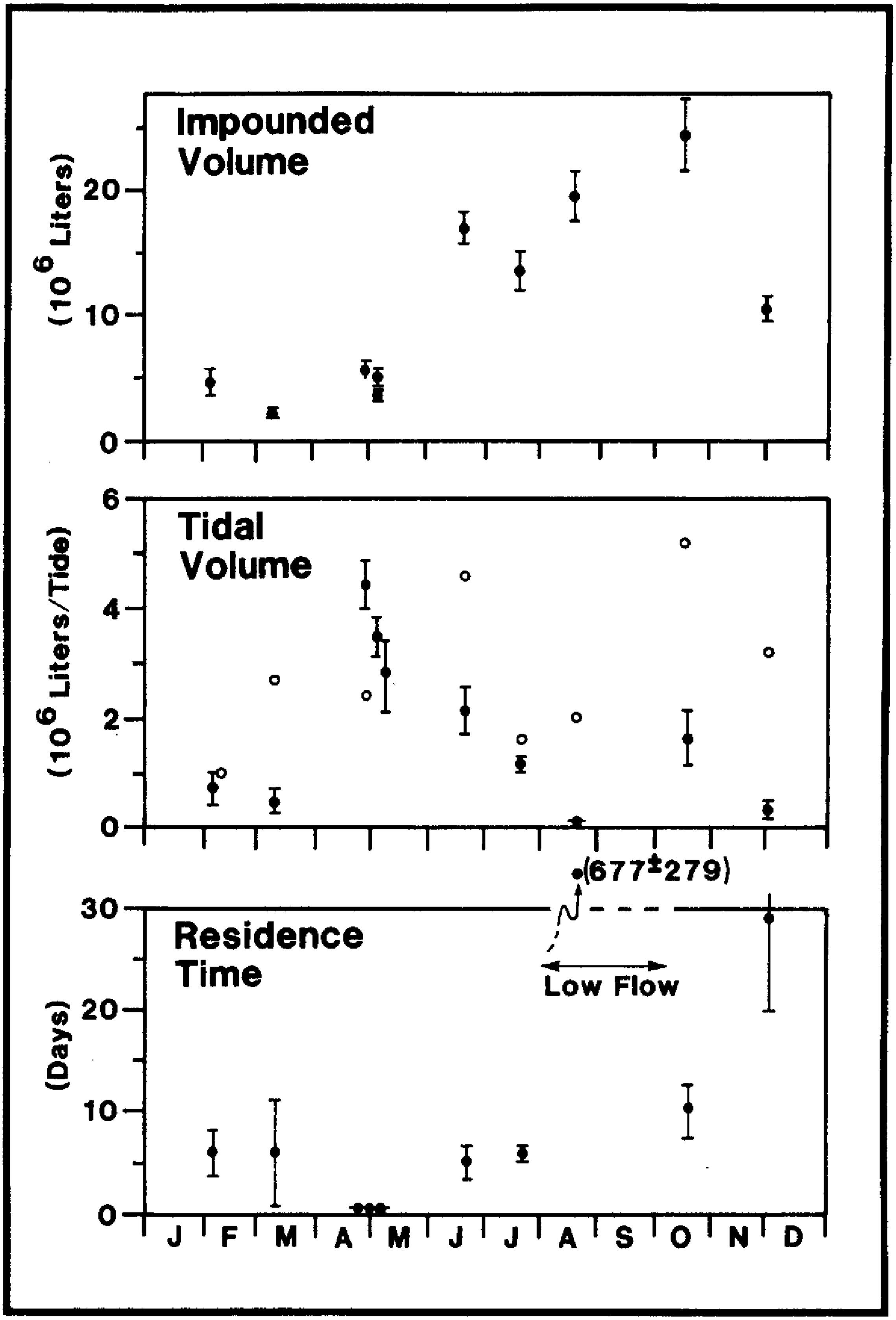

Figure 6.3 Tidal hydrology for 1983 (averaged over two tidal cycles). Solid data points represent the means (± standard errors) for all five impoundments. Open circles (middle panel) represent the mean tidal water volume in the tidal marsh.

late summer and early fall, when the impoundments were at their maximum water levels, tidal water exchange dropped to a minimal rate (0.02 ± .01 million liters per tide) with corresponding water residence times of greater than a year. Outside of these periods of maximum and minimum flushing, the mean volume of tidal exchange in the impoundments (1.1 ± 0.3 million liters per tide) was less than half (39%) of the mean flushing rate of the tidal marsh. Corresponding mean residence times for water in the impoundments (5 to 10 days) was 10 to 20 times longer than the 0.52-day residence time in the tidal marsh.

Other potential pathways of water movement include groundwater seepage through the bottoms of the impoundments and through the impoundment dikes. However, May and Zielinski (Chapter 5) found that there was no significant vertical flow of groundwater through the impoundment bottoms because of the impermeability of the bottom sediments and the low vertical hydrostatic gradients. There was, however, some seepage through a fibrous organic layer in the impoundment dikes. But even with maximum hydraulic gradients through the dikes when the impoundments were at maximum stage during the summer, the computed seepage rate amounted to less than 0.001 million liters per day. This water flow was less than 5% of the tidal water flow even during this late summer period of low tidal exchange. Therefore, we consider that the most significant pathways of aqueous nutrient transport occurred through tidal exchange of surface waters.

Ortho-Phosphate

For the tidal marsh, mean flood tide concentrations of o-PO_4 varied between 0.5 and 1.5 ug-at/liter, with no apparent seasonal trend (Fig. 6.4). Mean ebb-tide concentrations were consistently higher than on flood tides. These differences were particularly evident during the spring and summer, when concentrations during the ebb flow (almost 4 ug-at/liter) were 2 to 3 times those during flood flow. The highest concentrations observed during ebb flow (5 to 6 ug-at/liter) occurred during low-tide drainage of the marsh (May and August, Fig. 6.4).

These concentration differences led to a considerable net export of o-PO_4 from the marsh during the spring, summer, and fall (Fig. 6.5) culminating in a net annual export of 0.32 g o-PO_4 $m^{-2} yr^{-1}$.

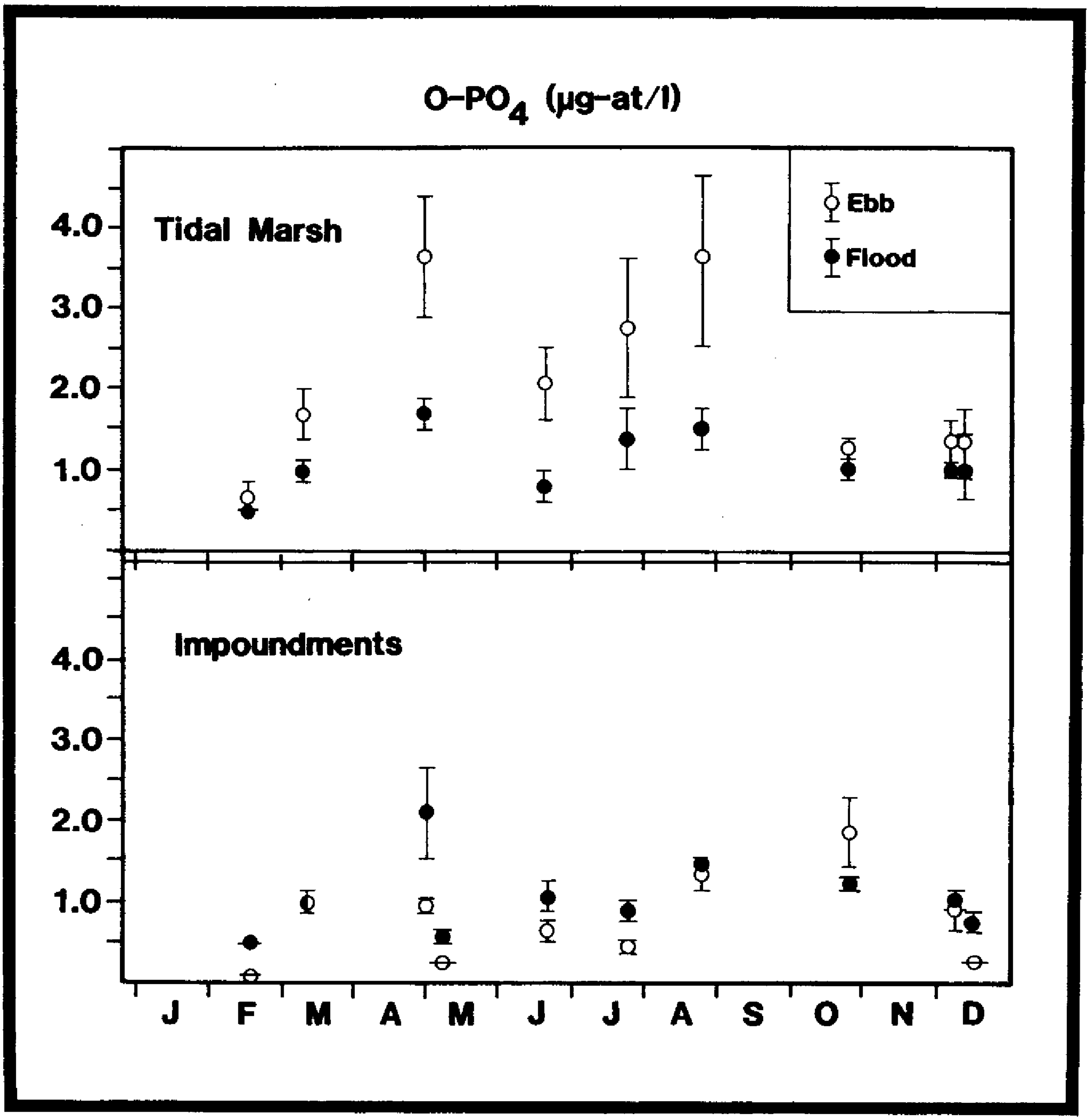

Figure 6.4 Ebb vs. flood tide concentrations of dissolved orthophosphate (o-PO_4) in the tidal waters of the open marsh and the study impoundments, 1983. Each pair of ebb/flood data points was computed from monthly, 25-hr. studies with an n=9 for the open marsh means and an n=45 for the impoundment means.

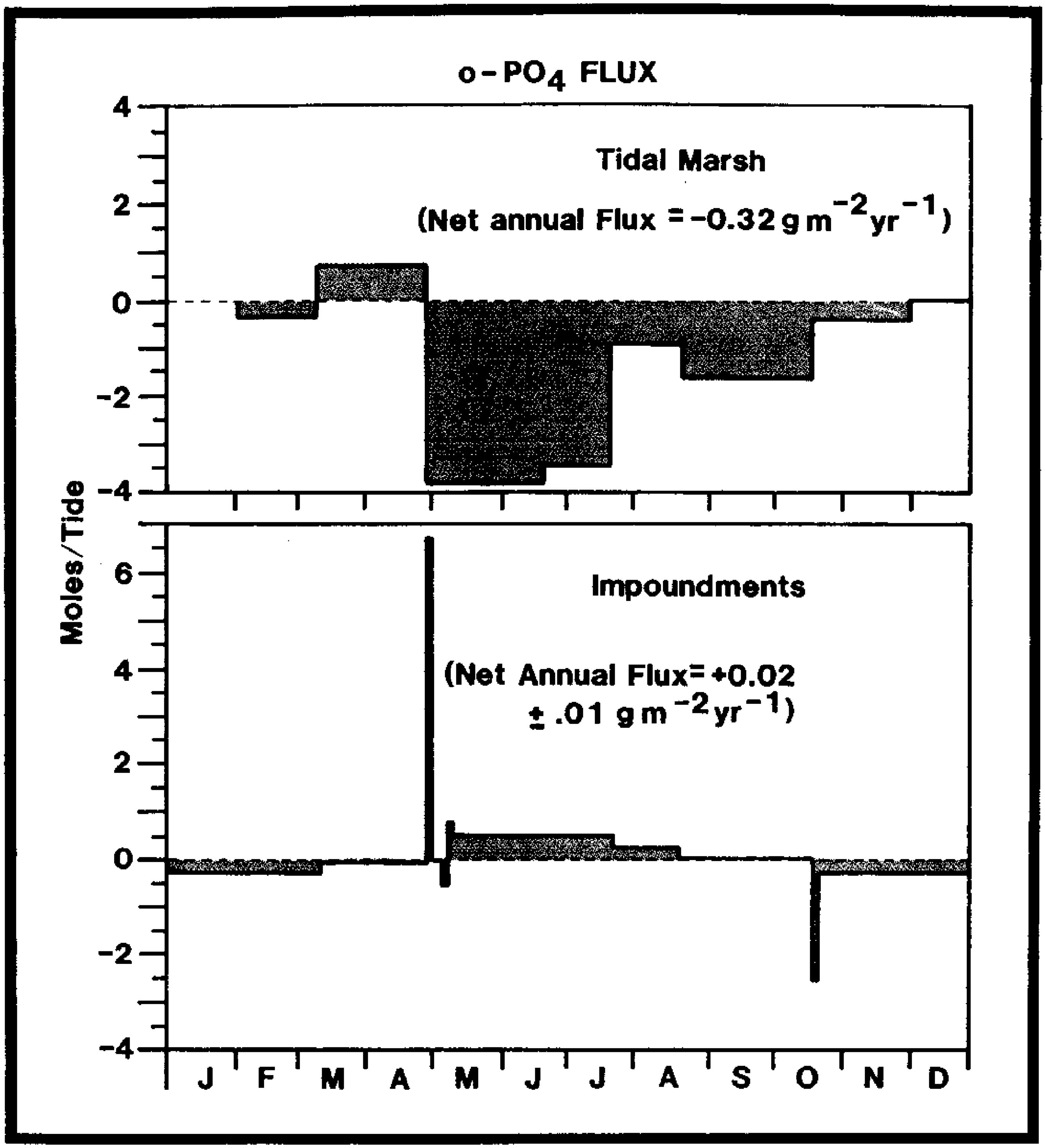

Figure 6.5 Net tidal flux of ortho-Phosphate (o-PO_4) for the tidal marsh and impoundments. The curve for the impoundments represents the mean flux for all five impoundments. Values for individual impoundments are shown in Table 6.1.

In the impoundments, flood-tide concentrations of o-PO_4 were similar to those found in the tidal marsh (Fig. 6.4). This was expected, because Chainey Creek is the tidal-water source for both systems. In contrast to the tidal marsh, however, ebbing water from the impoundments was usually 1.5 to 3 times lower in concentration than flood-tide waters. This trend was especially consistent through most of the growing season (April to July). The major flushing events in late April/May culminated in considerable net import of o-PO_4 to the impoundment (Fig. 6.5) which was followed by consistent import through the summer. Concentration differences became ebb dominated in October, beginning with the initial stages of the fall-winter drawdown in the impoundments. Through the fall and winter the impoundments exported o-PO_4 with the net outflow of water during this time. The mean net annual exchange of o-PO_4 in the impoundments yielded a small net import ($+ 0.02 \pm 0.01$ g $m^{-2}yr^{-1}$), although two of the five impoundments showed a small net annual export (Table 6.1). Regardless of the net direction of o-PO_4 flow, the magnitude of exchange was more than an order of magnitude lower than the o-PO_4 export found for the tidal marsh.

Ammonium

As for o-PO_4, flood-tide concentrations of NH_4 in the tidal marsh were similar to those in the impoundments (Fig. 6.6). Flooding waters from Chainey Creek typically averaged around 5 ug-at/liter or less and exhibited no apparent seasonal trend. Also, as for o-PO_4, NH_4 concentrations during ebb flow from the tidal marsh were consistently higher than during flood flows, with maximum spring and summer differences of three to sevenfold. Again, peak ebb-tide concentrations up to 80 ug-at/liter occurred during low-tide drainage of the tidal marsh (May and July). Then patterns culminated in a net export of NH_4 from the tidal marsh during the spring, summer, and fall, with a net annual export of 0.4 g $m^{-2}yr^{-1}$ (Fig. 6.7).

For the impoundments, difference between ebb- and flood-tide concentrations were usually small, with concentrations near the lower limits of detection (Fig. 6.6). However, these slight differences were flood dominated during summer and fall, yielding a small net tidal import

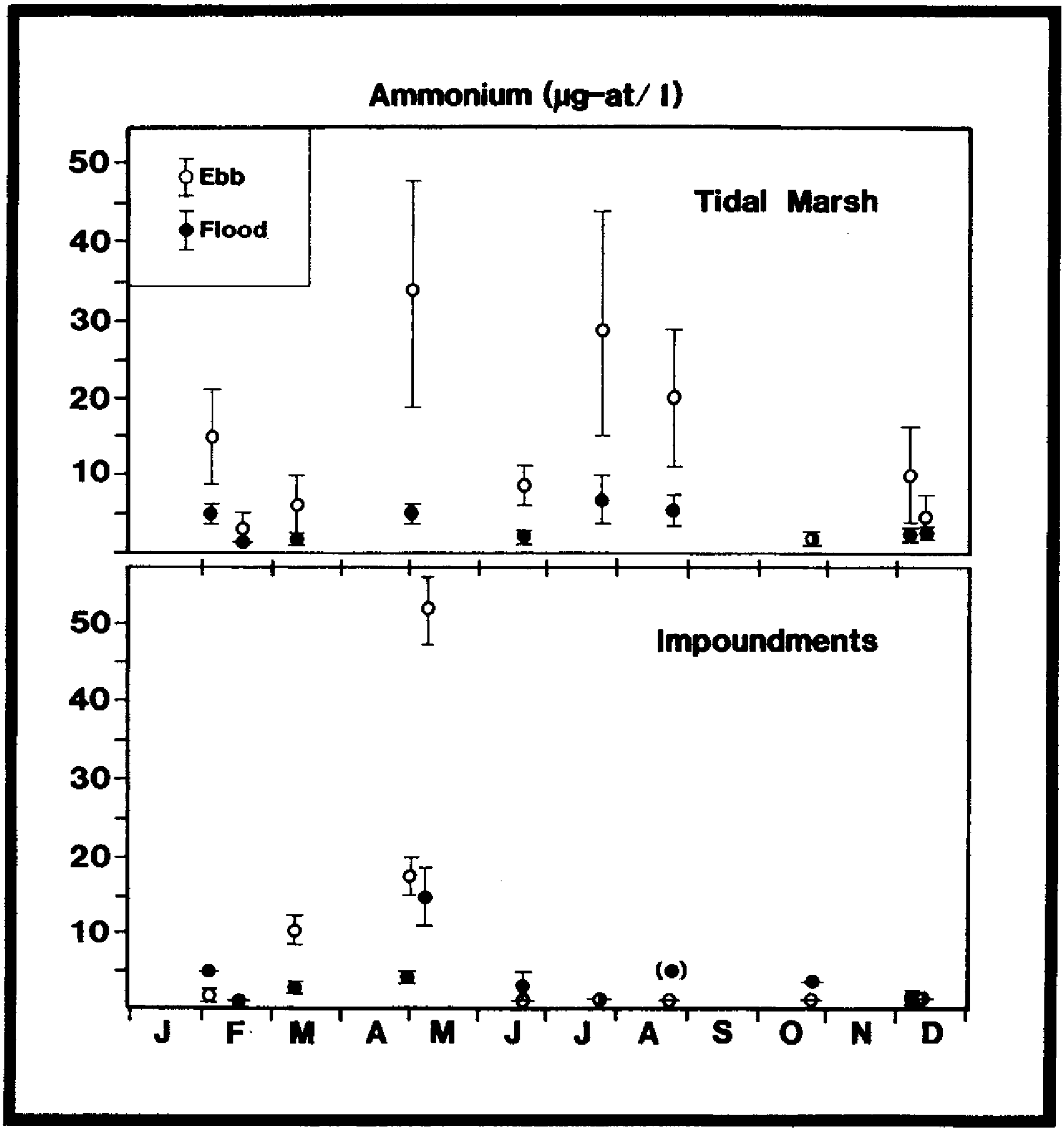

Figure 6.6 Ebb vs. flood tide concentrations of dissolved ammonium (NH_4) in the tidal waters of the open marsh and the impoundments, 1983. (n for each pair of data points was the same as for Figure 6.4).

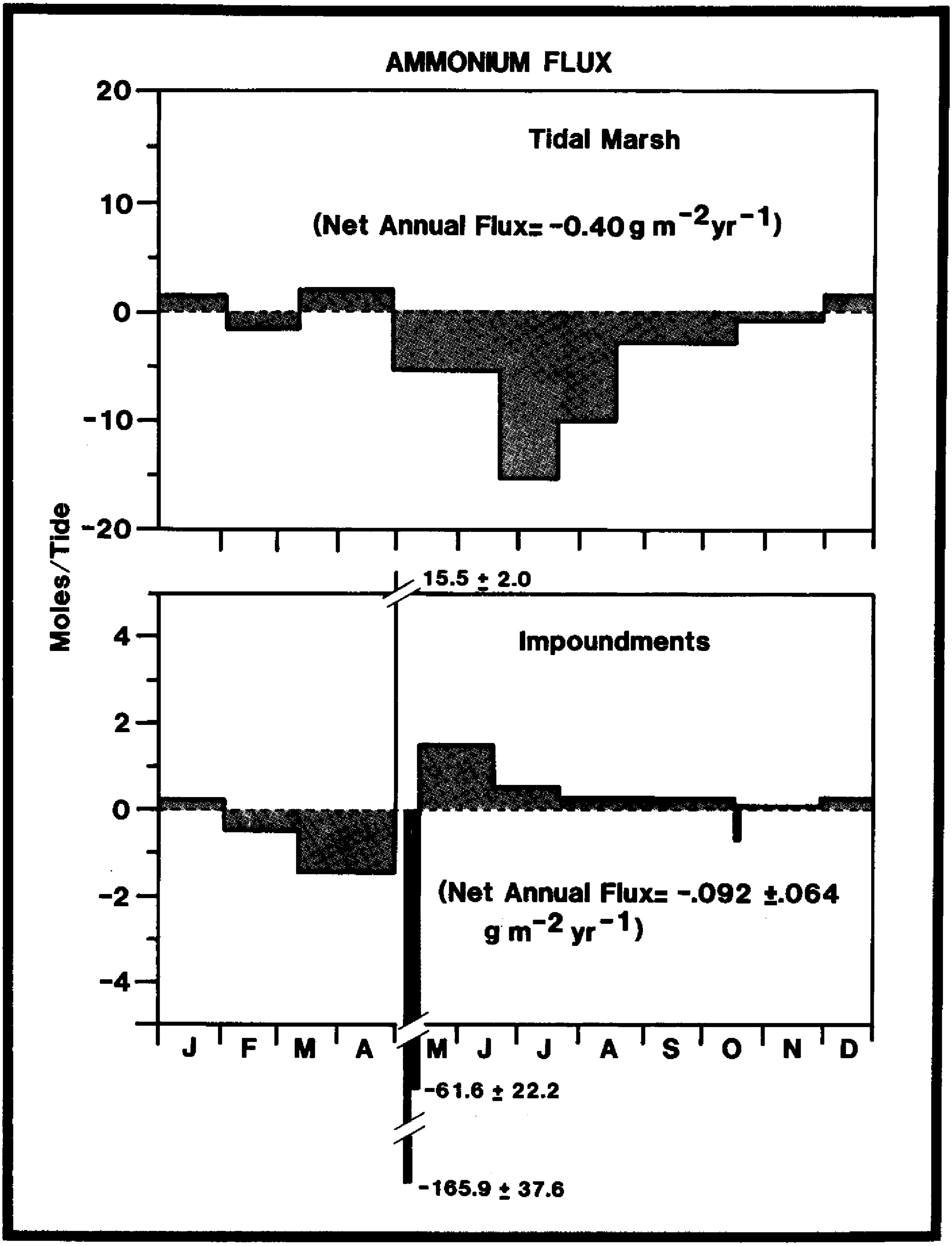

Figure 6.7 Net tidal flux of ammonium (NH_4) for the tidal marsh and impoundments. The curve for the impoundments represents the mean flux for all five impoundments. Values for individual impoundments are shown in Table 6.1.

Table 6.1

Net annual nutrient flux via tidal exchange

(g m^{-2} yr^{-1}; + = import, - = export).

Dissolved Nutrient Fractions			Phytoplankton Biomass		
(Site)	(oPO_4)	(NH_4)	(Chlorophyll-a)	(P*)	(N*)
Tidal marsh	-0.322	-0.405	+0.209	+0.255	+1.340
Impoundments					
1	+0.027	-0.042	-0.054	-0.066	-0.475
2	-0.014	+0.077	-0.172	-0.210	-1.514
3	+0.036	-0.137	-0.210	-0.256	-1.849
4	+0.044	-0.051	-0.037	-0.045	-0.325
5	-0.010	-0.309	-0.042	-0.051	-0.370
Impoundment mean					
$\bar{X}$	+0.017	-0.092	-.103	-0.126	-0.907
± SE	±0.012	±0.064	±.037	±0.045	±0.322

*Phosphorus (P) and nitrogen (N) components of phytoplankton biomass were calculated from chlorophyll-a measurements assuming a 50:1 ratio of phytoplankton carbon to chlorphyll-a (Strickland, 1965) and a Redfield ratio of 106:16:1 for C:N:P in phytoplankton biomass.

(Fig. 6.7) along with a net input due to water accumulation during this time. The largest differences in tidal concentrations and NH_4 exchange in the impoundments occurred during the end of the winter/spring drawdown (March) and during the flood-drain-reflood events of April and May. During these times, ebb-tide NH_4 concentrations were consistently three to five times higher than in flood-tide waters (Fig. 6.6). The April/May flushing events clearly resulted in a net export of NH_4 from the impoundments which dominated the mean net annual export from the impoundments of about 0.1 g NH_4 $m^{-2}yr^{-1}$ (Fig. 6.7).

This trend contrasted with those of o-PO_4 taken up by the impoundments during this time. Perhaps the exposed and shallow flooded substrates during the drawdown and flushing of the impoundments provided favorable conditions for nitrogen fixation with subsequent release of NH_4 into impoundment waters. Also, because early spring was a period of high river discharge, with potentially high NO_3 inputs, there could have been rapid NO_3 uptake and subsequent ammonification by the benthos and water column. Clearly, this period represented a very dynamic interval for N transformation in the impoundments. Even with these dramatic export events in the spring, however, the mean net annual export from the impoundments was still considerably less than the observed export from the tidal marsh (Fig. 6.7; Table 6.1).

Phytoplankton Biomass

Nutrients are also transported in the biomass of planktonic organisms entrained in the tidal waters. Measurements of chlorophyll-a were taken as an indicator of phytoplankton biomass. For the tidal marsh, the actual differences in chlorophyll-a concentrations between ebb and flood tides were small and variable (Fig. 6.8). However, the flow-weighted mean concentrations were almost all flood dominated throughout most of the year, suggesting a consistent import of phytoplankton biomass to the marsh surface via daily tidal exchange (Fig. 6.9). These data indicated a net annual import of chlorophyll-a to the marsh of 0.2 g $m^{-2}yr^{-1}$ (Fig. 6.9; Table 6.1).

In obvious contrast, ebb-tide concentrations of chlorophyll-a in the impoundments consistently exceeded those in flood-tide water (Fig. 6.8). The impoundment environment was apparently favorable for phytoplankton growth during most of the year. Summer phytoplankton blooms in the impoundments yielded mean ebb-tide chlorophyll-a levels of 45 to 55 ug/liter (July and August) which exceeded flood-tide concentrations by three to fourfold. These patterns yielded a considerable net export of chlorophyll-a from the impoundments during the summer, dominating a net annual export of 0.1 ± 0.04 g m^{-2} yr^{-1} (Fig. 6.9; Table 6.1).

In addition to the flux values for chlorophyll-a, Table 6.1 also lists estimates for nitrogen and phosphorus flux bound in the phytoplankton biomass. To estimate the nutrient exchange associated with phytoplankton transport we used a 50:1 ratio of phytoplankton carbon to chlorophyll-a (Strickland, 1965) and the standard Redfield ratio of 106:16:1 for C:N:P in plankton biomass. According to these estimates, the tidal nutrient exchange via phytoplankton biomass was considerable for both the tidal marsh and the impoundments. The tidal marsh imported four

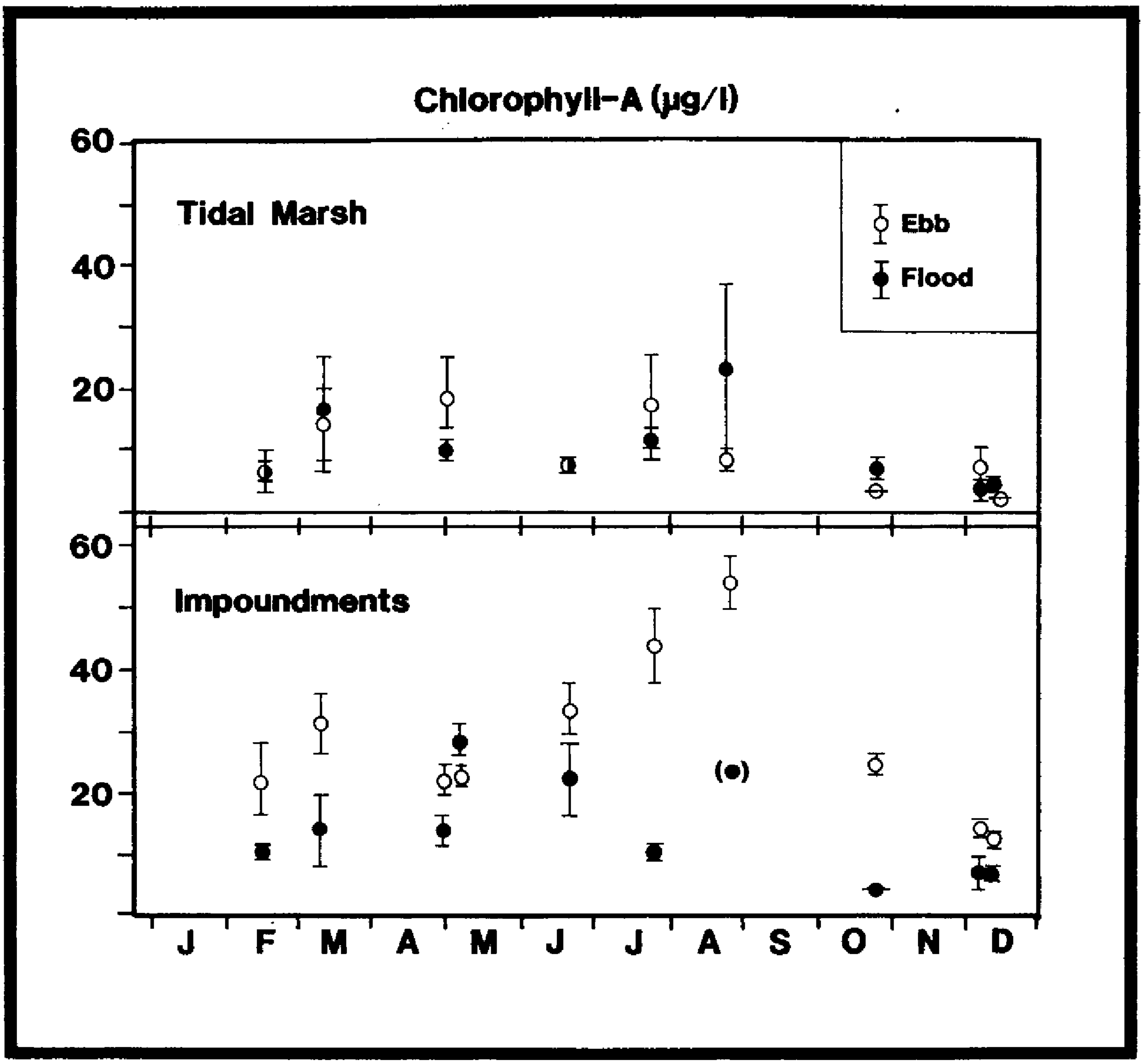

Figure 6.8 Ebb vs. flood tide concentrations of chlorophyll-a in the tidal waters of the open marsh and the impoundments, 1983. (n for each pair of data points was the same as for Figure 6.4.)

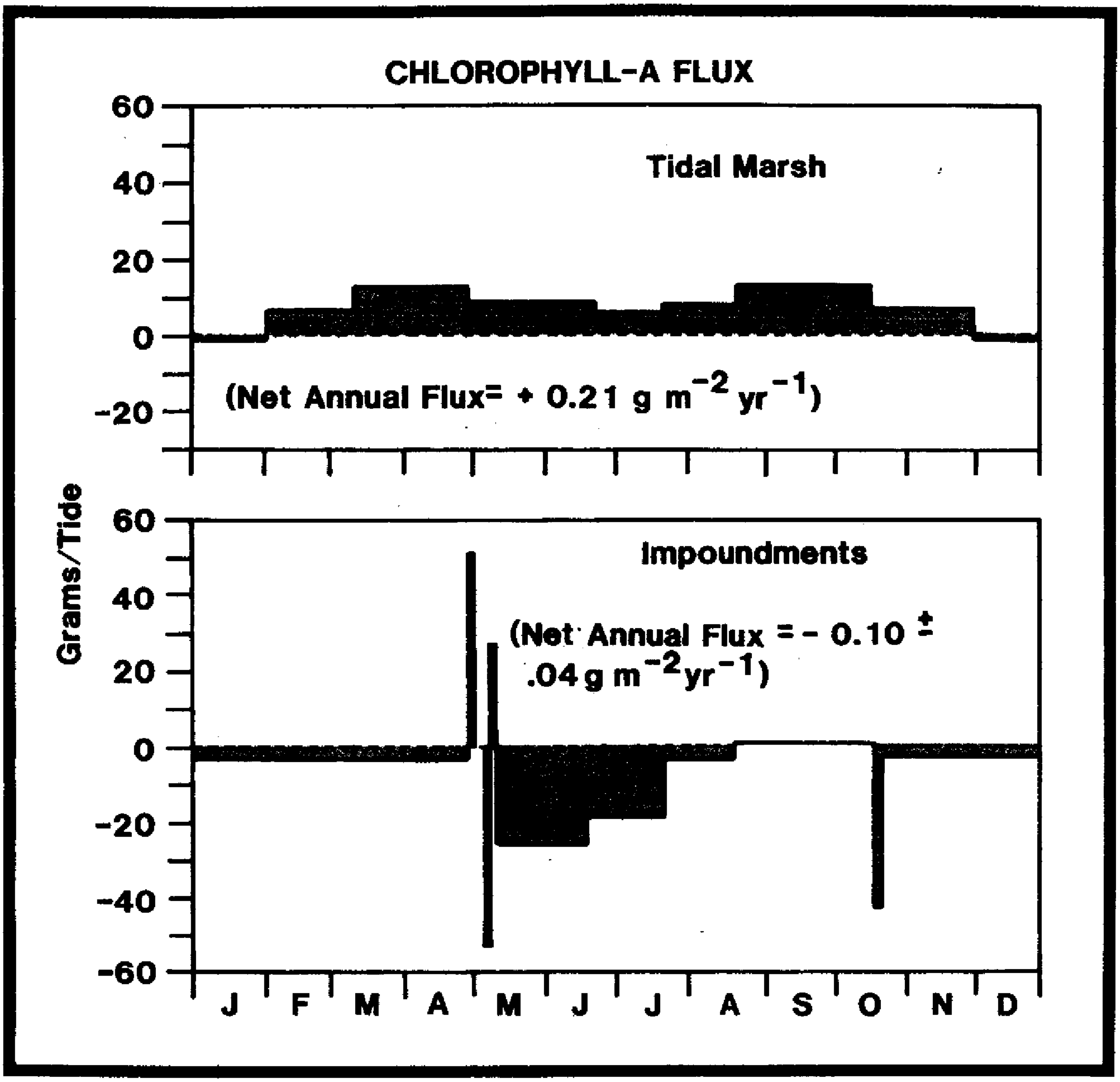

Figure 6.9 Net tidal flux of chlorophyll-a for the tidal marsh and impoundments. The curve for the impoundments represents the mean flux for all five impoundments. Values for individual impoundments are shown in Table 6.1.

times as much nitrogen as phytoplankton biomass as it exported in the form of dissolved ammonium. For the impoundments, tidal exchange of both nitrogen and phosphorus in phytoplankton biomass was much higher than in dissolved inorganic forms. In fact, the impoundments may have exported more nitrogen as phytoplankton biomass than the tidal marsh did in the form of ammonium. Therefore, in terms of total nutrient exchange, the high production and export of phytoplankton biomass from the impoundments may have partly compensated for the limited tidal exchange of water and dissolved nutrients.

Organic Carbon

The computation of net tidal flux of nutrients depends heavily on complete data sets for each monthly sampling period. Data sets for organic carbon were less complete than for the other constituents because of lower sampling frequency and higher rates of sample loss in the analytical phase. Therefore, we focused mainly on the mean concentration differences between ebb and flood tides, which suggested some differences and similarities between the tidal marsh and the impoundments.

Total organic carbon was dominated by dissolved fractions in both the tidal marsh and the impoundments (Fig. 6.10). Concentration peaks (40 to 60 mg/liter) were noted in June for both systems (Fig. 6.10). In the tidal marsh, dissolved organic carbon (DOC) was consistently higher on ebb tides throughout the year. Although there was considerable variability in concentrations through individual sampling dates, this seasonal trend suggests DOC export from the marsh. In the impoundments, ebb-tide concentrations were similar to flood-tide values throughout the spring. However, ebb-tide concentrations were markedly higher by as much as three fold from late summer through the fall. This pattern suggests a consistent DOC export from the impoundments at this time, perhaps related to the senescence and decomposition of macrophyte and phytoplankton populations.

Particulate organic carbon (POC) concentrations showed similar seasonal patterns in both the tidal marsh and the impoundments (Fig. 6.11) with higher concentrations (5 to 10 mg/liter) during the spring and summer. In the tidal marsh, POC concentrations were highly variable on individual sampling dates. However, mean ebb-tide concentrations were

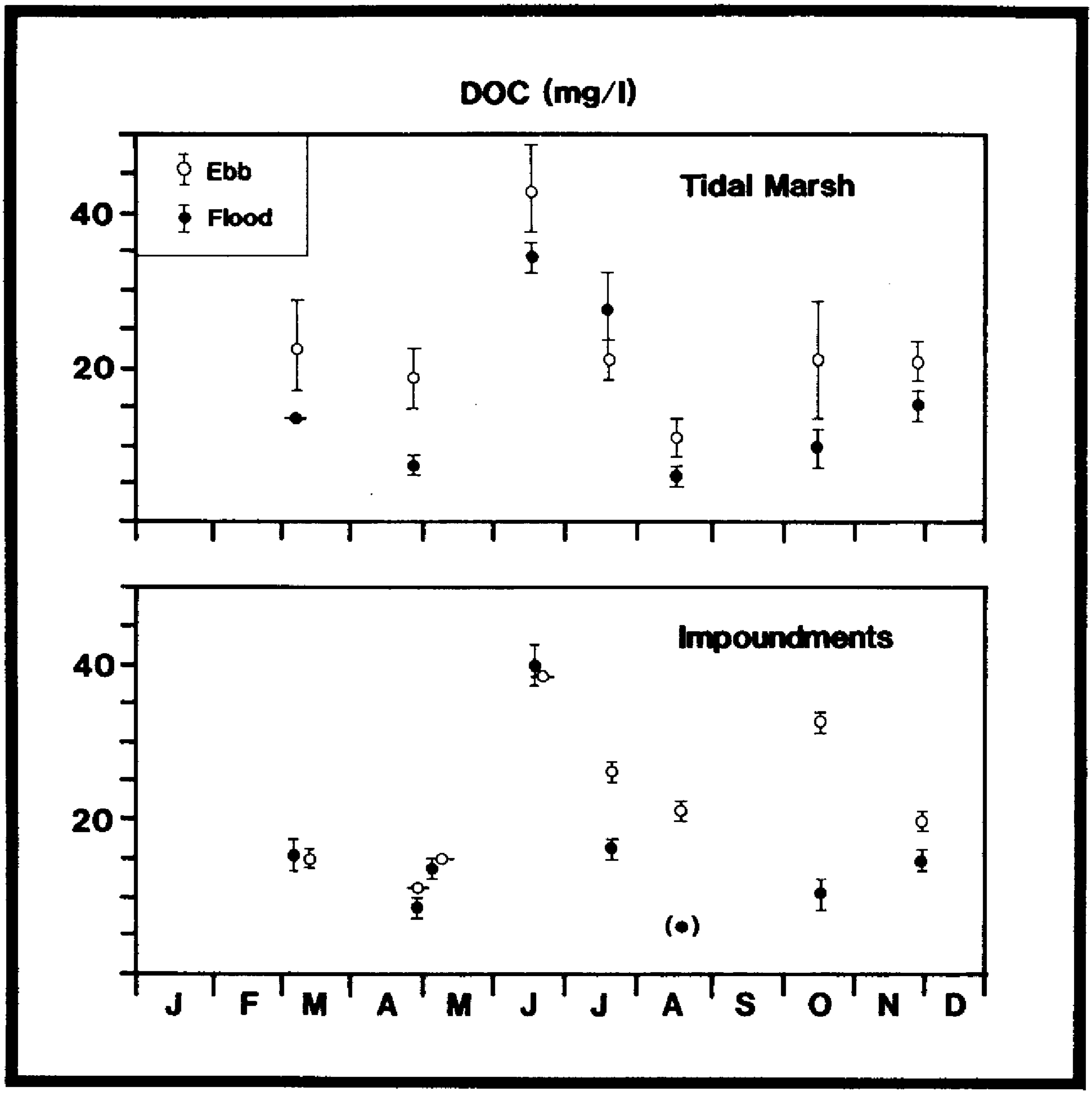

Figure 6.10 Ebb vs. flood tide concentrations of dissolved organic carbon (DOC) in the tidal waters of the open marsh and the study impoundments, 1983. (n for each pair of data points was the same as for Figure 6.4.)

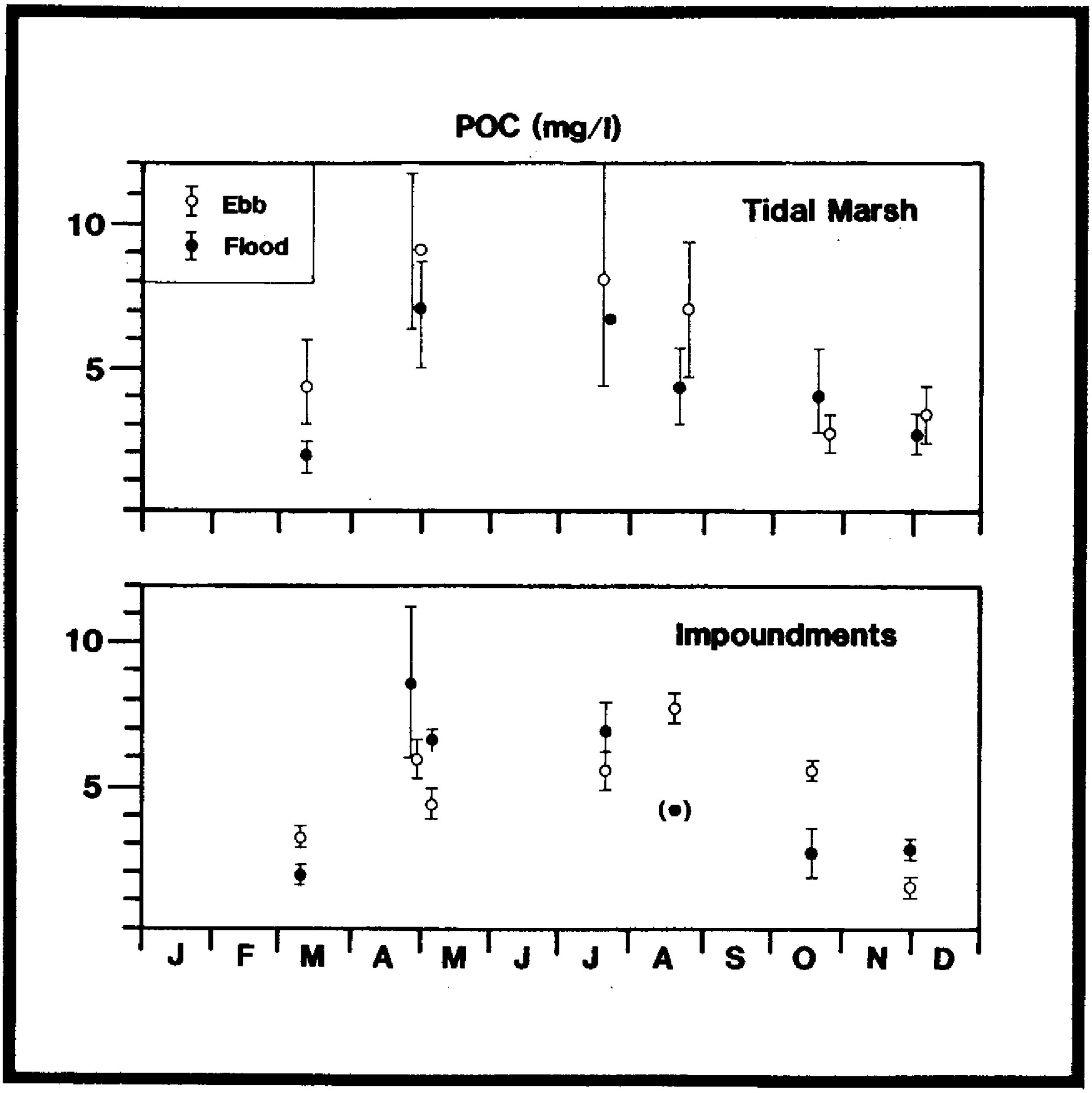

Figure 6.11 Ebb vs. flood tide concentrations of particulate organic carbon (DOC) in the tidal waters of the open marsh and the study impoundments, 1983. (n for each pair of data points was the same as Figure 6.4.)

consistently higher than mean flood-tide values, suggesting some export of POC throughout the year. In contrast, the impoundments showed no clear seasonal patterns in ebb and flood differences, even though sample variability on individual dates was smaller. The higher ebb-tide concentrations in the impoundments in August and October (Fig. 6.11) could have been related to the dense phytoplankton stocks during the late summer and early fall (see Fig. 6.8).

CONCLUSIONS

Nutrient cycling and productivity in wetland ecosystems are controlled by complex interactions of biology, geochemistry, and hydrology (Gosselink and Turner, 1978). It is not surprising, therefore, that the magnitude of nutrient and organic flux in whole-marsh ecosystems varies considerably (see review by Nixon, 1980). However, there is clearly some agreement in the literature on the direction of net flux (import or export) of several critical nutrients. Most salt and brackish marsh systems tend to export o-PO_4 and NH_4 in tidal waters (Valiela et al., 1978; Woodwell and Whitney, 1977; Woodwell et al., 1979; Jordan et al., 1983). Recent studies of the North Inlet salt marsh in South Carolina indicate that trends of nutrient export are particularly evident even on the large scale of a 34-km^2 marsh ecosystem (Kjerfve and McKellar, 1980; Whiting et al., 1985; Whiting et al., in review). Mechanisms controlling this export are probably related to the nutrient dynamics of the dominant vegetation (Hopkinson and Schubauer, 1984) and high rates of decomposition and remineralization in marsh substrates (Pomeroy and Wiegert, 1981; Good et al., 1982), coupled with the diffusion and drainage of substrate pore waters during low-tide exposure (Gardner, 1975; Wolaver et al., 1980, 1983). However, Jordon and Correll (1985) have demonstrated that low-tide drainage accounted for only a small portion of the total tidal export of dissolved nutrients from a mesohaline *Typha* marsh.

Many of the same mechanisms that characterize natural open marshes are probably similar in the former rice fields in South Carolina that are now open to semi-diurnal tidal flushing and that have succeeded to intertidal marshlands. Data for a tidal marsh in a breached impoundment have been presented here. Ebb-tide concentrations of both o-PO_4 and

NH_4 were consistently higher than flood-tide concentrations (Figs. 6.4 and 6.6). This trend suggested a tendency for the tidal marsh to indeed export these nutrients, especially during low-tide drainage. Calculations of seasonal and net annual exchange indicated consistent export of both o-PO_4 and NH_4 during the summer and fall, culminating in a net annual export of 0.3 and 0.4 g $m^{-2}yr^{-1}$, respectively (Figs. 6.5 and 6.7). These estimates are within the range of values reported for o-PO_4 and NH_4 export from other coastal marshes on the East Coast (see review by Nixon, 1980).

In contrast to the tidal marsh, impounded wetlands examined in this study exhibited different trends of tidal transport of o-PO_4 and NH_4. In the impoundments, o-PO_4 was imported during the spring and summer and was exported during the fall and winter, culminating in a mean net annual exchange near zero (+ 0.02 ± 0.01 g $m^{-2}yr^{-1}$, Fig. 6.5).

Ammonium was strongly exported from the impoundments at the end of the spring drawdown and during the rapid flushing events. Even with consistent NH_4 import to the impoundments over the summer, the spring exports dominated the annual net flow (- 0.09 ± 0.06 g $m^{-2}yr^{-1}$, Fig. 6.7). However, the net annual NH_4 export from the impoundments as a whole was considerably less than for the tidal marsh.

Data on other fractions of dissolved inorganic nutrients, especially NO_3 and NO_2, would clearly contribute to the discussion of nutrient exchange in these impoundments. Continuing work on South Carolina impoundments includes analyses of these fractions of nitrogen as well as other fractions of dissolved and particulate carbon, nitrogen, and phosphorus.

Typically low concentrations of NO_3-NO_2 and corresponding low N:P ratios in coastal waters are attributed largely to high rates of NO_3 reduction and denitrification in the anaerobic coastal sediments (Nixon, 1980; Hopkinson and Wetzel, 1982). However, in river-influenced coastal areas, such as the Santee Delta region, distributions of NH_4 and NO_3 may vary considerably during periods of high river discharge. In other ongoing work, Osemene (1985) found that during some periods of high discharge of the Santee River (March and April, 1983), concentrations of NO_3-NO_2 entering the delta region (2.8 to 4.4 ug-at/liter) were substantially higher than NH_4 concentrations (0.4 to 1.3 ug-at/liter).

During more recent periods of high discharge (February 1984) NO_3-NO_2 in the river water reached levels as high as 20 ug-at/liter and was clearly the dominant fraction of dissolved inorganic nitrogen. In our continued work on coastal impoundments in this area, information on such differences in nitrogen fractionation will add considerably to our understanding of nutrient exchanges in these dynamic systems.

Another form of tidal nutrient transport occurs with the entrainment of planktonic organisms in tidal waters. The impoundments examined in this study were evidently favorable environments for phytoplankton growth, with maximum chlorophyll-a concentrations greater than 100 ug/liter observed in late summer. Although the tidal marsh imported phytoplankton biomass throughout most of the year, the impoundments exported phytoplankton, especially during the spring and summer (Fig. 6.9).

Using standard conversion ratios for chlorophyll and nutrients (Table 6.1), we estimated that the tidal nutrient exchange via phytoplankton biomass was probably greater than for dissolved inorganic fractions, in both the tidal marsh and the impoundments. Whereas the tidal marsh tended to export nutrients in dissolved inorganic forms (NH_4 and o-PO_4), the impoundments exported nutrients via phytoplankton biomass. These results suggest that the exchange of nutrient elements via tidal waters in impoundments and in tidal marshes may be more comparable in total quantity but were considerably very different in quality. At present, we can only speculate about the secondary effects of such differences in nutrient quality on adjacent estuarine areas; the issue needs more direct evaluation in the future.

Some of these results have potential water-management implications for coastal impoundments. Tidal patterns of nutrient exchange in the impoundments was clearly different from those observed in the tidal marsh. Some of the differences were related directly to the quantities of water movement. During summer periods of restricted water flow in the impoundments, the corresponding tidal nutrient exchange was proportionately reduced. This condition was in stark contrast to the tidal marsh, which showed maximum rates of nutrient export during the summer. If the goal of water-management alternatives is to reduce these differences, then efforts to increase water exchange during the summer may be appropriate.

Other differences in nutrient exchange, however, are related more to the basic biotic and geochemical differences that characterize an impounded environment versus an intertidal environment. As long as a wetland is dominated by submerged benthic habitats (as in impoundments), there will be considerable differences in the ways that system processes nutrients compared to an intertidal system. Until we can evaluate these differences in terms of their positive and negative impacts on the adjacent waters, it will be difficult to propose a more appropriate water-management regime.

Further research is clearly needed to effectively address the issues concerning the impact of impoundments on estuarine water quality and productivity. In this study, we were able to quantify some differences between impoundments and a tidal marsh with respect to tidal exchange of dissolved inorganic and plankton-bound forms of carbon, nitrogen, and phosphorus. We still need a better understanding of the total budget for each nutrient constituent, including the dynamic partitioning between particulate and dissolved forms as well as organic and inorganic forms.

Data on organic carbon fractions suggested that both the tidal marsh and the impoundments exported particulate and dissolved fractions. The quality of that organic export is still unknown. Because most of the organic carbon transport was in dissolved forms, we need especially to compare the differences between impoundments and marshes in the quality of DOC export. The value of DOC components can be indicated by analyzing for the low-molecular-weight, labile fractions (such as in dissolved carbohydrates which are easily utilized by estuarine microbes). These can then be compared to the higher-molecular-weight fractions which are more refractory and less easily utilized. Although both impoundments and marshes may export organic carbon, differences in the quality of the organic matter is critical in evaluating the larger-scale impacts of impoundments.

Though we now have some information on nutrient and organic exchange in a specific set of impoundments, we still need to assess the areal extent over which impoundments affect water quality in adjacent waterways. We specifically need to quantify spatial and seasonal changes in water quality throughout an estuarine area where impoundments are managed and compare trends with an area where there are few impoundments.

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SECTION IV

PRIMARY PRODUCTIVITY AND SYSTEMS METABOLISM

GENERAL INTRODUCTION

Open tidal marshes are regarded as very important to general coastal ecology in terms of their high productivity, their function as protective and nutrient-rich nursery grounds for juvenile fish and shellfish, and their role in the nutrient balances of coastal waters (de la Cruz, 1973; Greeson et al. 1978, and others). At present, we know little of how these basic ecological processes function in impounded wetlands. This study represents an initial effort to elucidate some basic properties of primary productivity and community respiration in representative impounded wetlands.

Three plant communities dominate the landscape in the Cat Island impoundments: (1) the emergent and submergent aquatic macrophytes rooted in the bottom sediments, including their attached microscopic epiphytes, (2) the suspended, unattached, microscopic phytoplankton in the water column, and (3) the benthic microscopic algae that are found growing on or among the bottom sediments, largely in the top 0.5 cm of the sediments. Although the same primary production components may be present in open-marsh, conditions may favor a different distribution of productivity among open marsh plant communities than that found in impoundment communities. A clear understanding of the comparability of primary productivity of impounded and open marshes requires, therefore, a full accounting of the contributions of all components in both systems.

In this section we present three chapters examining seasonal patterns of primary production in the major plant communities (macrophytes, phytoplankton, and microbenthic algae). Studies were conducted in the impoundments as well as in the adjacent marshes for direct comparison. Related aspects of oxygen dynamics and aquatic-community metabolism were also examined for the impoundments. A fourth chapter provides a synthesis of the component productivity results and presents summary comparisons with productivity data from other wetland sites.

Chapter 7

Macrophyte Productivity

B. J. Kelley and R. D. Porcher

INTRODUCTION

Macrophyte vegetation is a prominent feature of both fresh and salt water impoundments in coastal South Carolina. A primary objective of the majority of impoundment owners is to attract waterfowl (see Chapter 3). Edible macrophytes are encouraged; e.g., Ruppia maritima, Scirpus robustus, and Polygonum sp. and "undesirable" competitors such as Spartina alterniflora, S. cynosuroides, and Typha sp. are discouraged by a variety of management methods (Morgan et al., 1975; Joyner, personal communication). The five Cat Island impoundments used in this study were managed in a traditional saltwater management program, described in Chapter 4, which encourages the growth of widgeon grass, Ruppia maritima, dwarf spike rush, Eleocharis parvula; and salt marsh bulrush, Scirpus robustus (Joyner, personal communication). The early history of the impoundments and their vegetation is described by Wilkinson (1970). In this initial work (1967-1969), Wilkinson used different management techniques on each of the five impoundments. Different macrophyte communities developed in each system. These original community patterns may account in part for the differences in community composition observed among the impoundments in the present study.

A durable but unproven hypothesis that has influenced tideland impoundment policy in South Carolina (S.C. Coastal Council Regulations,

1978) states that primary productivity and other processes in salt-marsh ecosystems are enhanced by an energy subsidy to the system provided by daily tidal flow (Odum, 1961; 1974; Teal, 1962; Odum and Fanning, 1973; Steever et al., 1976; Hopkinson et al., 1978). Odum et al. (1983) compared net aerial primary productivity (NAPP) of impounded and unimpounded giant cutgrass, *Zizaniopsis miliacea*, in a tidal freshwater marsh and found tidal NAPP to be significantly higher than impounded NAPP. They interpreted the difference as being due to an energy supplement received by the tidal marsh. Other authors have argued for the tidal-subsidy concept by noting the greater productivity of a species when it is located along creek banks than in areas with less tidal flushing (Steever et al., 1976). If this concept is correct, impounding a tidal marsh with an interruption of the daily tidal flow should result in reduced primary productivity through loss of the energy subsidy.

To examine this possibility, we measured the NAPP of the important macrophyte species in the study impoundments and an adjacent tidal marsh so that comparisons could be made. We have used our results to discuss the following questions: (1) Were impoundment macrophytes less productive than tidal macrophytes? (2) Were impoundments sufficiently similar in their macrophyte production characteristics to be treated as replicates? (3) Were impoundment management practices used during the study period producing the macrophyte species desired and at the times they were needed?

Several features of the tidal marshes used in our study could possibly affect the general applicability of some of our results. The tidal impoundment (unit 6) used in 1983 (Fig. 7.1) was an old impoundment with breached dikes. Diurnal tidal flooding occurred, but it may have been less extensive or not typical of unaltered marsh because of remnant dikes and ditches. Tidal marsh 2 (Fig. 7.1) used in 1984 was also an old impoundment, but its dikes and ditches had so thoroughly deteriorated that little if any restriction of flow occurred. For these reasons, comparison of our tidal marsh data to unaltered tidal systems should be done cautiously.

METHODS

The measurement of net aerial primary productivity (NAPP) was conducted over two growing seasons from February 1983 to March 1985. The same field and laboratory procedures were followed both years, but with differences in sampling design. Magnified tracings (6X) of color infrared aerial transparencies of the five Cat Island impoundments and adjacent tidal marsh were made using a Wild M-5 stereomicroscope with a drawing tube. This permitted macrophyte community boundaries to be delineated and each community area to be determined by planimetry. The vegetation maps produced were ground-truthed. The macrophyte communities identified (seven in the study impoundments and three in the tidal marsh) became the strata for a stratified random sampling design used in the estimation of macrophyte productivity. The sampling pattern allowed the determination of NAPP for each community and permitted statistical comparisons by analysis of variance (ANOVA) among the various communities and between tidal marsh and impoundments. During the first growing season (February 1983 to January 1984), all five impoundments and the tidal impoundment (unit 6) were studied (Fig. 7.1). During the second growing season (February 1984 to January 1985), the number of impoundments used was reduced to three, impoundments 1, 3, and 4, to allow an increase in the number of replicates per community for impoundment-to-impoundment comparisons. The tidal study area was moved to the more thoroughly flushed marsh (tidal marsh 2, Fig. 7.1) across Chainey Creek.

Net aerial primary productivity was determined for each of the macrophyte communities identified in the impoundments and tidal marsh, using a modification of the Lomnicki method as described in Shew et al. (1981). However, two of the impoundment communities, _Distichlis_ and _Ruppia-Eleocharis_, could not be reasonably handled by this method and were studied by the Milner-Hughes (1968) procedure. The small size and density of growth of these species made the removal of fallen and standing dead material from quadrats, required by the Lomnicki method, impractical in the field. Screens used in the Lomnicki method were constructed of 1/4-in. PVC pipe and 1-mm-mesh fiberglass screen. Screening was secured to the PVC pipe using clips made from 3/4-in. PVC pipe. Quadrat size was

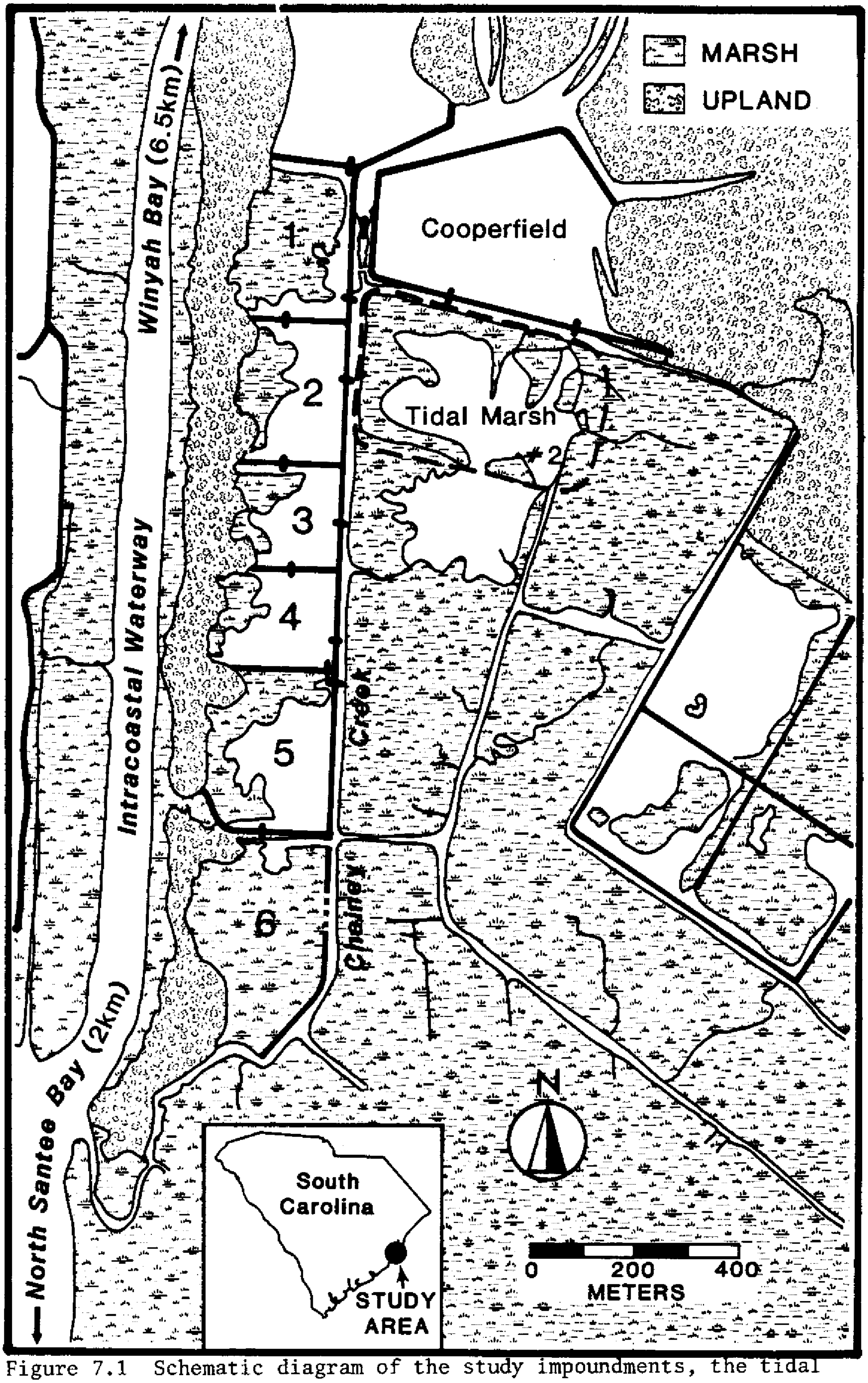

Figure 7.1 Schematic diagram of the study impoundments, the tidal impoundment (unit 6) and tidal marsh area #2.

1/4 m2 for the S. alterniflora, S. cynosuroides, Scirpus robustus, S. validus, and Typha communities and 1/25 m^2 for the Distichlis and Ruppia-Eleocharis communities.

Field samples were returned to the laboratory, sorted to species, dried in paper bags at 100° C for five days, and weighed to the nearest 0.1 g.

In the Lomnicki method estimates of annual productivity were made by summing the interval (monthly) productivities for the growing season, where NAPP interval = Δ live + Δ ADP + FD and ADP = attached dead parts; FD = fallen dead and standing dead culms. In the Milner-Hughes method annual production estimates were sums of interval (monthly) values for the growing season as in the Lomnicki method, but interval mortality was not considered. Resultant data, therefore, underestimated annual production.

Estimates of total macrophyte NAPP for individual impoundments and the tidal-marsh systems were made by summing the contributions of each community the system contained (community NAPP estimate per square meter times community area in square meters equalled total community contribution). An average square meter production estimate for each system was made by dividing the total system NAPP estimate by the system area in square meters. Statistical comparisons were made using the Human Systems Dynamics (HSD) ANOVA software with an Apple IIe microcomputer.

RESULTS AND DISCUSSION

Vegetation maps and a species list (see Appendix Chapter 7) show that the impoundment flora was more diverse than that of the adjacent tidal marsh (7 major communities vs. 3 and 19 species vs. 5, respectively). Community composition of each impoundment and the tidal marsh with area of cover and percentage of cover is given in Table 7.1. The Ruppia-Eleocharis community dominated all impoundments (average cover 53%) and was absent from tidal areas. Ruppia and Eleocharis grew on the shallow impoundment flats as submerged members of the aquatic community during times when the fields were flooded. The importance of other communities, judged by percentage of cover, varied among the impoundments. Emergent species comprised nearly 100% cover in the

Table 7.1

Macrophyte community composition, area (m^2), and the % cover of each impoundment and the tidal marsh.

IMPOUNDMENT #1

Species*	Area	% Cover
Sp. cynosuroides	9,489	16%
Sp. alterniflora	18,885	33%
Sc. robustus	7,494	13%
Distichlis	185	<1%
Ruppia-Eleocharis	21,530	37%
TOTAL	57,583	

IMPOUNDMENT #2

Species	Area	% Cover
Sp. cynosuroides	7,053	15%
Sc. robustus	15,219	32%
Typha	2,830	6%
Sp. alterniflora	209	1%
Distichlis	70	1%
Sc. validus	2,807	6%
Ruppia-Eleocharis	19,488	41%
TOTAL	47,676	

IMPOUNDMENT #3

Species	Area	% Cover
Sp. cynosuroides	3,480	10%
Sp. alterniflora	7,540	21%
Distichlis	2,065	6%
Sc. robustus	139	1%
Ruppia-Eleocharis	22,040	62%
TOTAL	35,264	

IMPOUNDMENT #4

Species	Area	% Cover
Sc. robustus	1,127	12%
Sp. alterniflora	1,926	5%
Distichlis	1,694	4%
Typha	1,392	3%
Sp. cynosuroides	3,503	9%
Ruppia-Eleocharis	27,399	67%
TOTAL	41,041	

* *Sp.* = *Spartina*, *Sc.* = *Scripus*

Table 7.1 Continued

IMPOUNDMENT #5

Species*	Area	% Cover
Sp. cynosuroides	5,892	9%
Sp. alterniflora	17,539	28%
Sc. robustus	46	1%
Distichlis	162	1%
Ruppia-Eleocharis	38,977	62%
TOTAL	62,616	

TIDAL IMPOUNDMENT (UNIT 6)

Species	Area	% Cover
Sp. cynosuroides	36,238	48%
Sp. alterniflora	34,220	45%
Sc. robustus	5,823	7%
TOTAL	76,281	

AVERAGE % COVER FOR ALL IMPOUNDMENTS

Ruppia-Eleocharis - 53%
Sp. alterniflora - 19%
Sc. robustus - 11%
Sc. cynosuroides - 12%
Distichlis - 2%
Typha - 2%
Sc. validus - 1%

TIDAL MARSH #2

Species	Area	% Cover
Sp. alterniflora	32,574	57.5%
Mudflat and tide creek	24,062	42.5%
TOTAL	56,636	

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* *Sp.* = *Spartina*, *Sc.* = *Scripus*

impoundment (unit 6) but less than 60% in tidal marsh 2 (Fig. 7.1 and Table 7.1).

Our primary objectives for the 1983 growing season were to estimate the NAPP of major communities and make comparisons between impoundments and tidal marsh. Production measurements for each community are given in Table 7.2. An ANOVA of the seven impoundment communities showed that all communities were not equally productive ($P<.001$). Values ranged from a high of 3196.8 ± 774.3 (S.E.) grams dry weight (gdwt) m^{-2} yr^{-1} for impoundment *Spartina cynosuroides* to a low of 361.5 ± 121.4 gdwt m^{-2} yr^{-1} for impoundment *Scirpus robustus*. Estimates of *S. alterniflora* NAPP for both impoundment and tidal communities were similar to those reported for other southeastern marshes (Keefe, 1972; Turner, 1976; Hopkinson et al., 1978, Schubauer and Hopkinson, 1984). Values for *S. cynosuroides* and *Distichlis spicata* were higher than those reported in some southern areas (Keefe, 1972; Turner, 1976) but comparable to Louisiana *Distichlis* (Hopkinson et al., 1978) and to Georgia *S. cynosuroides* (Schubauer and Hopkinson, 1984). It should be noted again that our *Distichlis* and *Ruppia-Eleocharis* estimates did not include mortality and that there was an assumption that grazing was inconsequential, which may have been untrue for the *Ruppia-Eleocharis* community.

Average NAPP in gdwt per square meter per year for individual impoundments and the tidal impoundment (unit 6) also are given in Table 7.2. Impoundments with the largest percentage of cover of the most productive species had the highest average values. Average NAPP per square meter was a function of community composition and percentage of cover as well as species productivity.

Comparisons of macrophyte productivity in gdwt per square meter per month between impoundments and tidal marsh were made for all communities common to both areas. Figs. 7.2 and 7.3a show the monthly production values for the three communities found in both the impoundment and tidal-marsh systems. Total production of *Spartina alterniflora* was not significantly different between tidal marsh and impoundments, and there were only slight differences in monthly patterns of productivity between the two areas (Fig. 7.2a). Spring growth began earlier in tidal *S. alterniflora* than in the impoundments, a trend which was repeated in 1984

Table 7.2

Macrophyte NAPP (g/m^2/interval) for impoundment and tidal marsh communities by season and for the 1983 growing season.

IMPOUNDMENTS

Communities*	Spring	Summer	Fall	Winter	Annual	±	S.E.
Sp. cynosuroides	1336.2	1096.2	678.0	86.4	3196.8	±	774.3
Sp. alterniflora	476.0	1156.3	668.6	39.4	2340.3	±	481.8
Sc. robustus	184.4	147.6	27.9	1.6	361.5	±	121.4
D. spicata	717.2	1915.0	445.1	0.13	3077.4	±	968.9
Ruppia-Eleocharis	146.8	724.0	0.0	0.0	870.8	±	379.8
T. angustifolia	617.7	109.1	56.1	2.3	785.2	±	308.1
Sc. validus	1054.3	237.3	90.5	0.26	1382.3	±	444.3

TIDAL MARSH

Communities	Spring	Summer	Fall	Winter	Annual	±	S.E.
Sp. cynosuroides	1244.2	715.8	293.9	48.1	2302.0	±	858.1
Sp. alterniflora	340.9	1065.1	519.6	40.8	2024.8	±	539.5
Sc. robustus	417.3	382.8	336.1	25.7	1161.9	±	366.9

NAPP (g/m^2/year) for an average m^2 in each impoundment and the tidal marsh:

Impoundment		Tidal Marsh
#1	1,467.2	1968.0 ± 607.8
#2	1.087.0	
#3	1,541.7	
#4	1,052.9	
#5	1,506.6	
Mean for all ± S.E.:	1,331.0 ± 442.4	

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* *Sp.* = *Spartina*, *Sc.* = *Scripus*

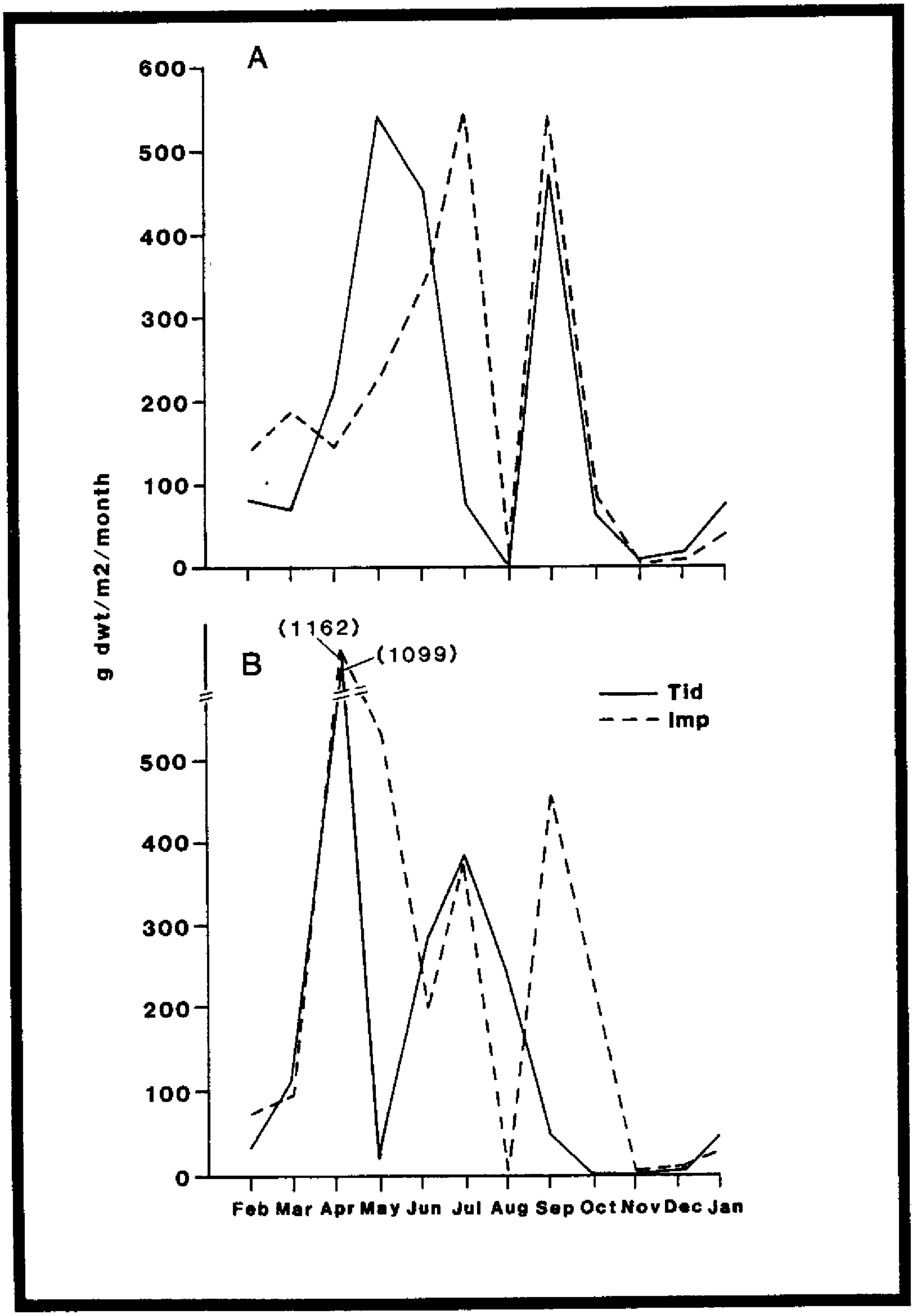

Figure 7.2 1983 comparisons of productivity between impoundments and tidal marsh. A = *Spartina alterniflora*, B = *Spartina cynosuroides*.

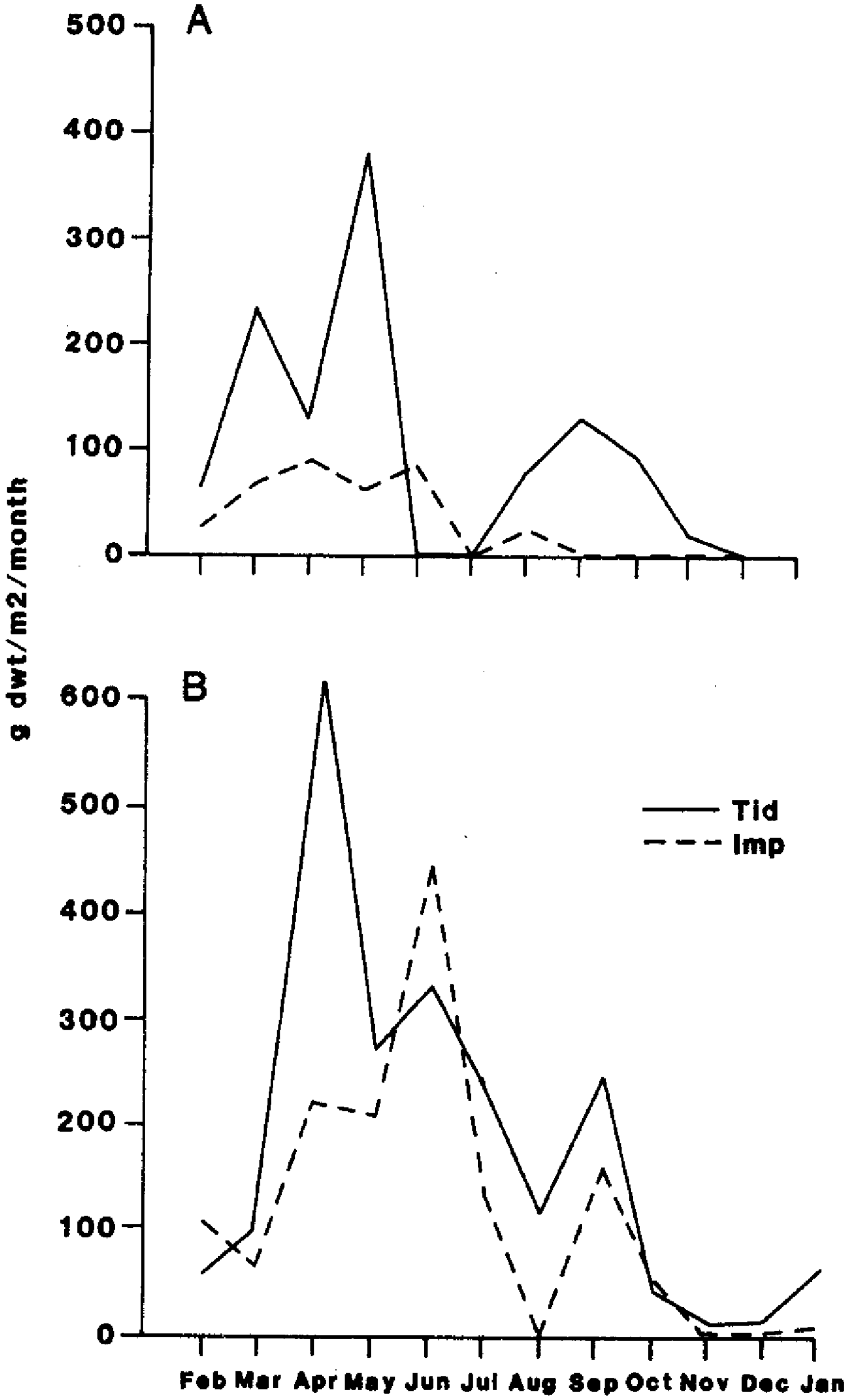

Figure 7.3 1983 comparisons of productivity between tidal marsh and impoundments. A = Scirpus robustus. B = average macrophyte production.

(see Fig. 7.5b). Similarly, no significant difference in NAPP between tidal marsh and impoundments was found for S. cynosuroides (Fig. 7.2b). The greatest period of growth for both impoundment and tidal S. cynosuroides was in early spring. Impoundment S. cynosuroides, however, showed an early autumn peak that did not occur in the tidal marsh. Scirpus robustus was the only macrophyte community to show a significant difference in productivity between impoundments and tidal marsh. Impoundment S. robustus had a mean NAPP of 30.1 gdwt m^{-2} $month^{-1}$, whereas tidal NAPP was 102.4 gdwt m^{-2} $month^{-1}$ (Fig. 7.3a). A late spring freeze in 1983 during impoundment drawdown damaged the impoundment S. robustus community, and it performed poorly the rest of the season. Tidal S. robustus also was damaged, but not as badly. The drawdown procedure used in the impoundments appeared to have exposed the impoundment S. robustus to freezing conditions while the tidal S. robustus was protected by periodic water cover. This interpretation is supported by the similarity between NAPP of impoundment S. robustus in 1984, when there was no freeze damage, and that of tidal S. robustus in 1983 (111.6 gdwt m^{-2} $month^{-1}$ and 102.4 gdwt m^{-2} $month^{-1}$, respectively). In addition, NAPP for impoundment S. robustus in 1984 was significantly higher ($P = .013$) than 1983 impoundment S. robustus. The impoundment communities remaining, Ruppia-Eleocharis, Scirpus validus, Distichlis, and Typha, had no counterparts in the tidal impoundment (unit 6).

A tidal marsh to impoundment comparison of monthly average NAPP in gdwt per square meter per month for 1983 is given in Fig. 7.3b. Average impoundment NAPP per square meter per month was not significantly different from average tidal NAPP, but tidal macrophytes showed a tendency to begin their period of activity earlier in the spring than the impoundment macrophytes. An apparent slow down or cessation of productivity in late summer was evident in all the 1983 production graphs (Figs. 7.2 and 7.3). From all comparisons of individual communities and total macrophyte productivity, it appeared that impoundment macrophytes were no less productive than their counterparts in the adjacent tidal marsh.

In 1984 the number of study impoundments was reduced to three to allow more replicates per community so that productivity among individual impoundments could be compared. In addition, we continued the impoundment-tidal marsh comparisons. Table 7.3 presents production measurements for impoundment and tidal communities for the 1984 growing season. The five impoundment communities sampled were not equally productive ($P < .001$). *Spartina cynosuroides* was the most productive species, and its level of production in 1984 (3519.3 ± 670.1 gdwt m^{-2} yr^{-1}) was similar to its level in 1983 (Table 7.2). Values for *S. alterniflora*, *Ruppia-Eleocharis*, and *Typha angustifolia* also were similar to 1983 estimates (Table 7.2). *Scirpus robustus* production was significantly higher in 1984 ($P = .013$) than in 1983, probably because there was no freeze damage in 1984 (Table 7.2 and Fig. 7.4a).

Productivity among impoundments 1, 3, and 4 was compared for the *Spartina cynosuroides*, *S. alterniflora*, *Ruppia-Eleocharis*, and *Scirpus robustus* communities. Only *Ruppia-Eleocharis* showed a significant difference in productivity (gdwt m^{-2} $month^{-1}$, Fig. 7.4b, $P = .014$) among the impoundments. When productivity was expressed as an average in gdwt per square meter per month for each impoundment (Fig. 7.5a), there was no significant difference among the three impoundments. Seasonal patterns of production for the four communities compared were similar, but there were some differences in time and extent of peaks in production. In general, we found little reason to regard impoundments 1, 3, and 4 as different from one another from the standpoint of macrophyte production.

The impoundment to tidal marsh comparison, continued from 1983, showed no significant differences in production between impoundment and tidal *Spartina alterniflora* (Fig. 7.5b) or in average NAPP between all impoundment and tidal macrophytes (Fig. 7.6a). With the exception of the 1983 *Scirpus robustus* community, there were no significant differences in productivity between impoundment and tidal macrophyte communities of the same species over the two years of the study. As already mentioned, we have attributed the low productivity of *S. robustus* in 1983 in impoundments to freeze damage, which did not occur in the tidal marsh. This may be the only event in our study that can be interpreted as an energy subsidy, in the form of warm water cover, resulting from tidal flow.

Since the *Ruppia-Eleocharis* community is the principal crop of the impoundments, we have given it some additional consideration. Peak production was reached in June, and by July-August dropped to near zero

Table 7.3

Macrophyte NAPP (g/m^2/interval) for impoundment and tidal marsh communities by season and for the 1984 growing season.

IMPOUNDMENTS

Communities*	Spring	Summer	Fall	Winter	Annual	±	S.E.
Sp. cynosuroides	1161.0	1818.3	510.6	29.4	3519.3	±	670.1
Sp. alterniflora	268.4	592.1	428.7	70.1	1359.3	±	246.9
Sc. robustus	721.0	198.4	203.4	90.0	1212.8	±	261.8
Ruppia-Eleocharis	87.8	534.4	227.2	49.3	898.7	±	187.9
T. angustifolia	424.7	230.9	8.9	7.74	672.2	±	178.6

TIDAL MARSH

Community	Spring	Summer	Fall	Winter	Annual	±	S.E.
Sp. alterniflora	721.8	844.6	359.0	74.6	2000.0	±	528.7
Mudflat	0	0	0	0	0		

NAPP (g/m^2/year) for an average m^2 in each study impoundment and a tidal marsh:

	Impoundment	Tidal Marsh
#1	1629.9 ± 416.6	1149.9 ± 303.8
#2	1658.2 ± 443.1	(2000.0 with mudflats removed)
#3	1297.6 ± 317.9	

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* Sp. = Spartina, Sc. = Scripus

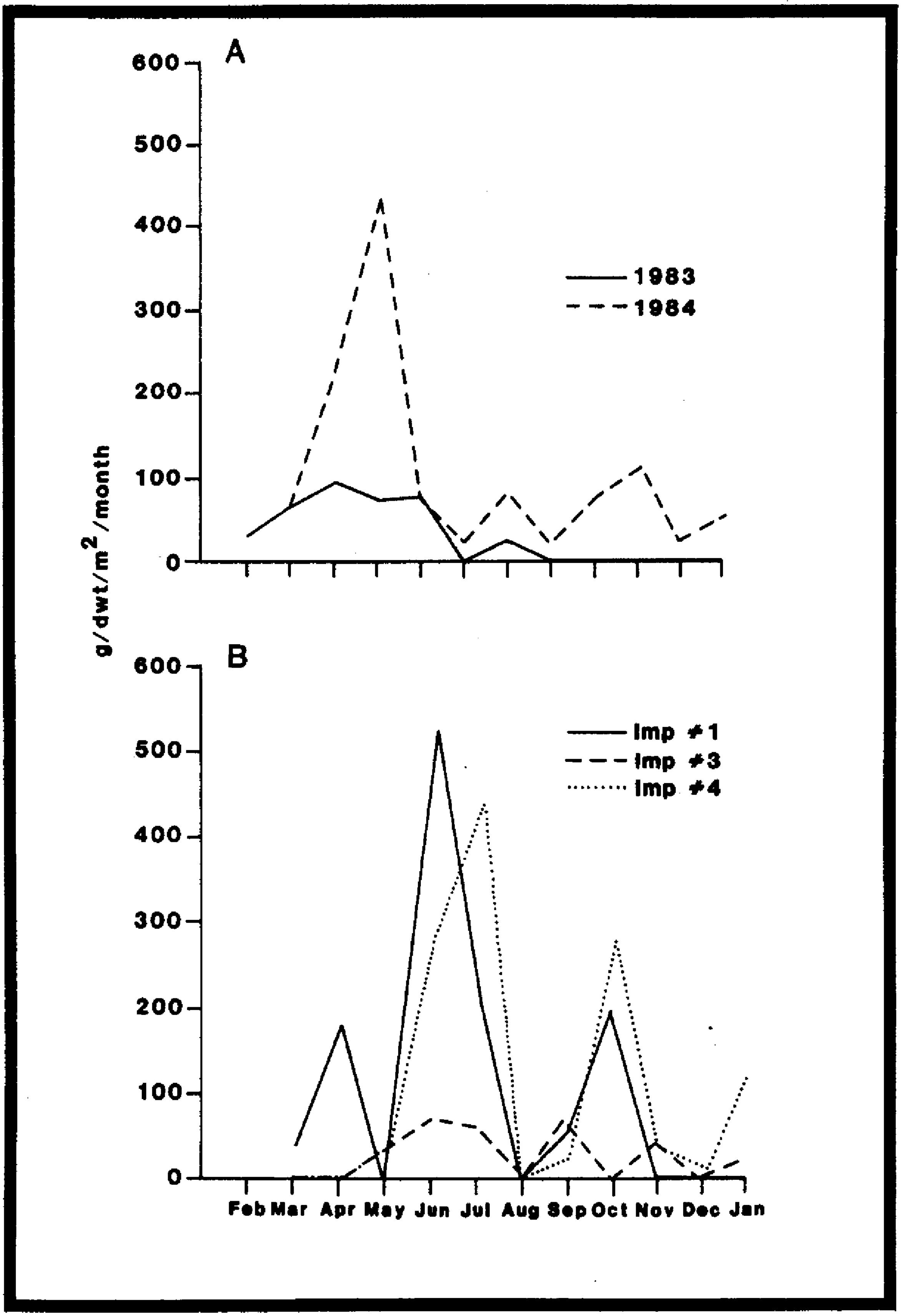

Figure 7.4 Productivity of impoundment macrophytes. A = Scirpus robustus, (1983 vs. 1984) B = 1984 Ruppia-Eleocharis community (comparison of productivity among impoundments 1, 3, and 4).

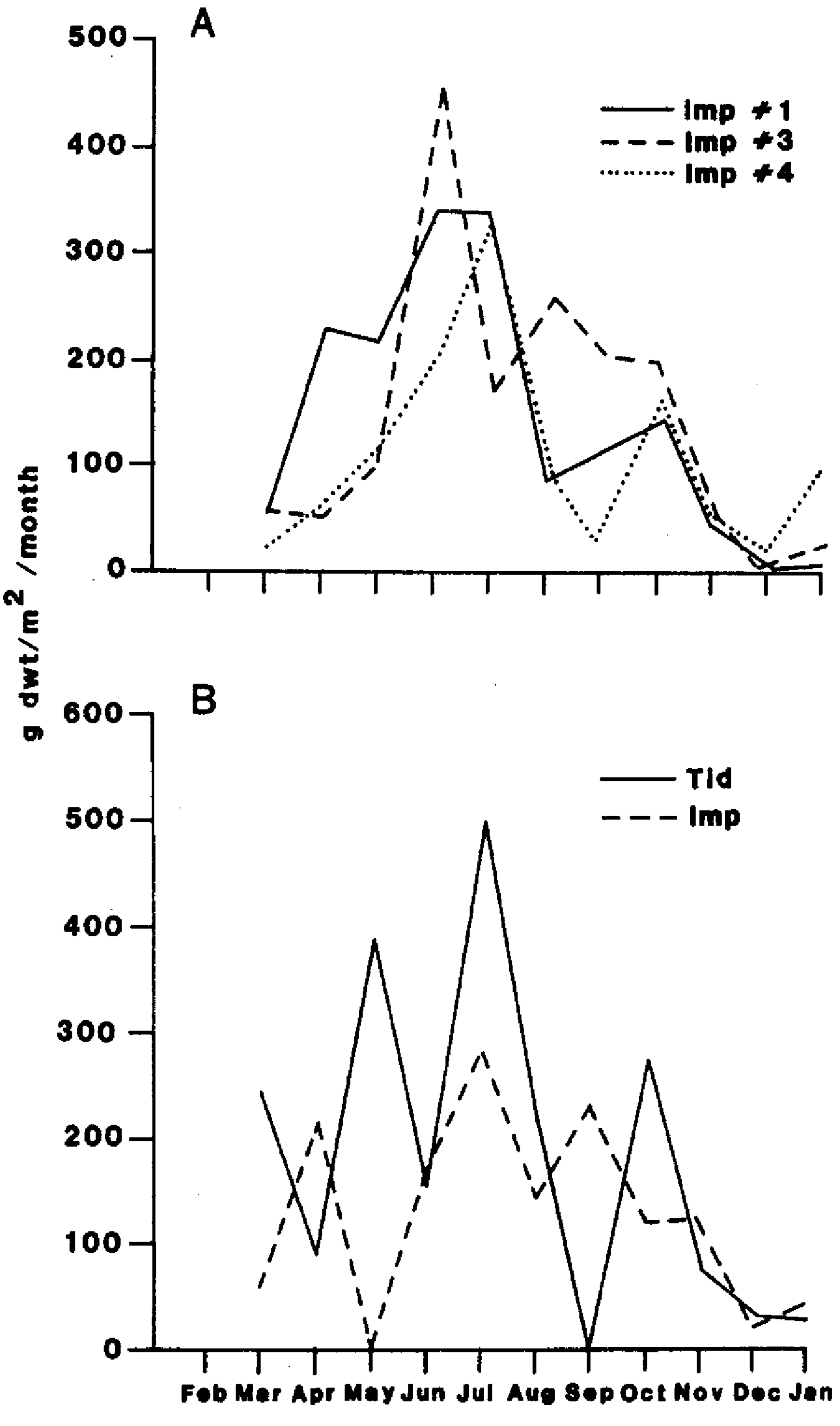

Figure 7.5 1984 macrophyte productivity. A = average production among impoundments 1, 3, and 4; B = production of *Spartina alterniflora* (tidal marsh and impoundment).

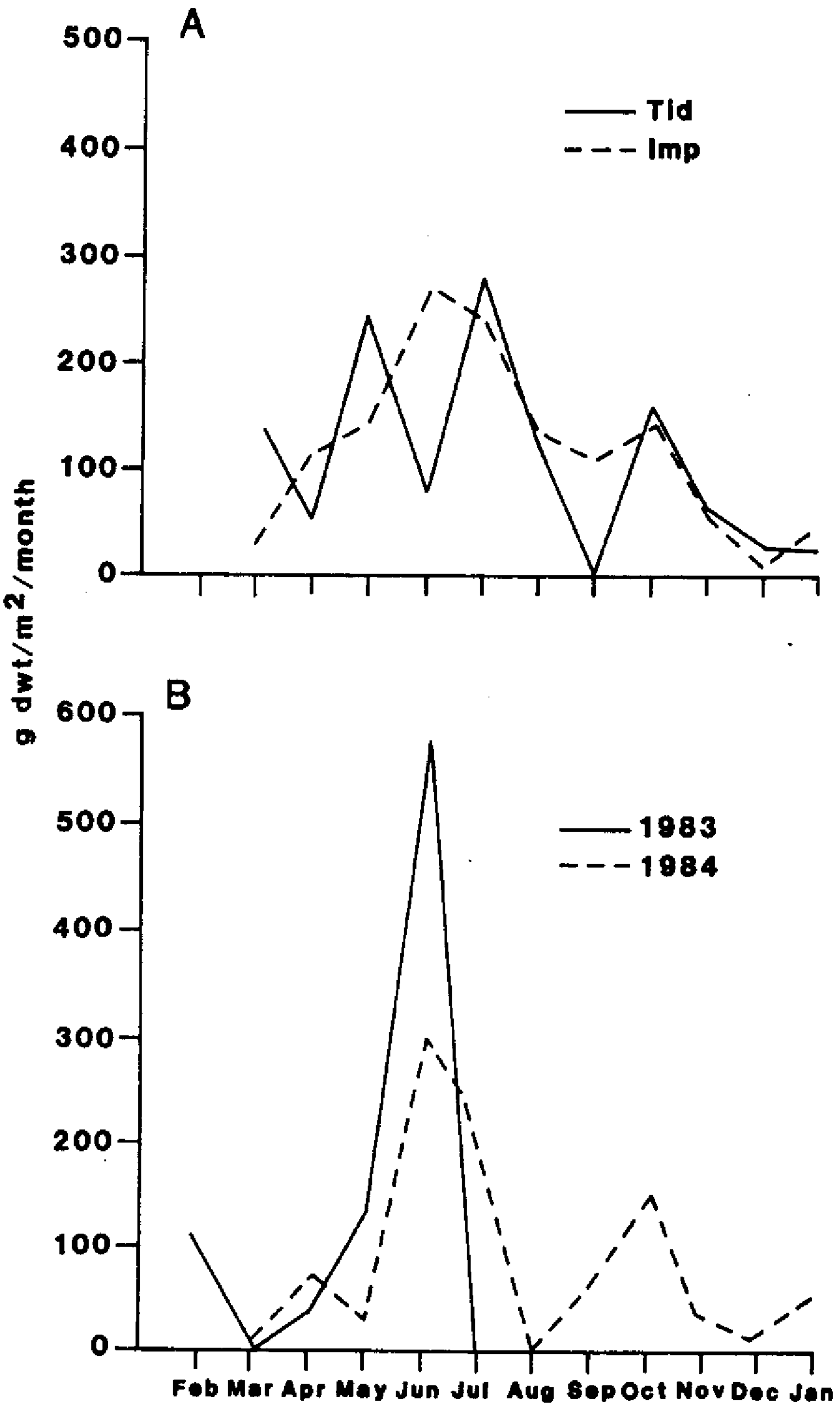

Figure 7.6 A = Comparison of average macrophyte productivity between the impoundment versus tidal marsh, 1984. B = Comparison of <u>Ruppia-Eleocharis</u> in 1983 vs. 1984.

(Fig. 7.6b). Impoundment managers always hope for a second fall peak. This did not occur in 1983. Exceptionally high temperatures during the summer may have prevented the fall peak (Joanen and Glasgow, 1985). A small autumn peak was present in 1984 (Fig. 7.6b). Fig. 7.7 shows the monthly standing crop of Ruppia-Eleocharis for 1983 and 1984. In both years it had peaked and largely disappeared before the arrival of the migratory waterfowl it was intended to feed. If 1983 and 1984 were not atypical years, this suggests that adjustments in the management program might produce more Ruppia and Eleocharis for the seasons when migratory waterfowl are present. The Ruppia-Eleocharis community was among the least productive of the impoundment communities according to our method of measurement. We want to point out again that for Ruppia-Eleocharis estimate of mortality was included in the production values obtained. Also, there was no account made of the grazing removal of NAPP by waterfowl and other herbivores. If these factors were included, the NAPP of this community might be significantly higher.

SUMMARY AND CONCLUSIONS

Table 7.4 presents a summary of various productivity comparisons we have made. The assumption of no difference in NAPP between impoundment and tidal communities of the same kind (hypothesis 1, Table 7.4) was upheld in all ANOVAs except the Scirpus robustus comparison for 1983. This difference appeared to have been due to selective freeze damage to the impoundment population that did not occur in the tidal population or to the 1984 impoundment population. That there was no difference between impoundment and tidal marsh when their productivity was expressed as an average per square meter (hypothesis 2, Table 7.4), also was upheld for both years of the study. We found, therefore, no evidence that impoundment macrophytes were less productive than tidal macrophytes and no evidence of a general energy subsidy due to tidal flow that affects macrophyte primary productivity.

We tested hypothesis 3 (Table 7.4), that there was no difference in communities of the same kind in different impoundments, by making comparisons among impoundments 1, 3, and 4 of communities that occurred in at least two of the three impoundments studied in 1984. Only the

Table 7.4

Summary of comparisons of NAPP by ANOVA
(NS - not significant at .05 level; * - significant at the .05 level)

I. Hypothesis 1: there was no difference in NAPP between impoundment and tidal communities of the same kind.

Comparison	Statistical significance
Impoundment to tidal	
1983 *Spartina alterniflora*	NS
1983 *S. cynosuroides*	NS
1983 *Scirpus robustus*	* (P=.03)
1984 *Spartina alterniflora*	NS

II. Hypothesis 2: there was no difference between impoundment and tidal marsh when their NAPP was expressed as an average per square meter.

Comparison	Statistical significance
Impoundment to tidal	
1983 average NAPP	NS
1984 average NAPP	NS

III. Hypothesis 3: there was no difference in NAPP among communities of the same kind in different impoundments.

Comparison	Statistical significance
Impoundment to impoundment	
1984 *Spartina alterniflora*	NS
1984 *S. cynosuroides*	NS
1984 *Scirpus robustus*	NS
1984 *Ruppia-Eleocharis*	* (P =.01)

IV. Hypothesis 4: there was no difference among impoundments when their NAPP was expressed as an average per square meter.

Comparison	Statistical significance
Impoundment to impoundment	
1984 average NAPP	NS

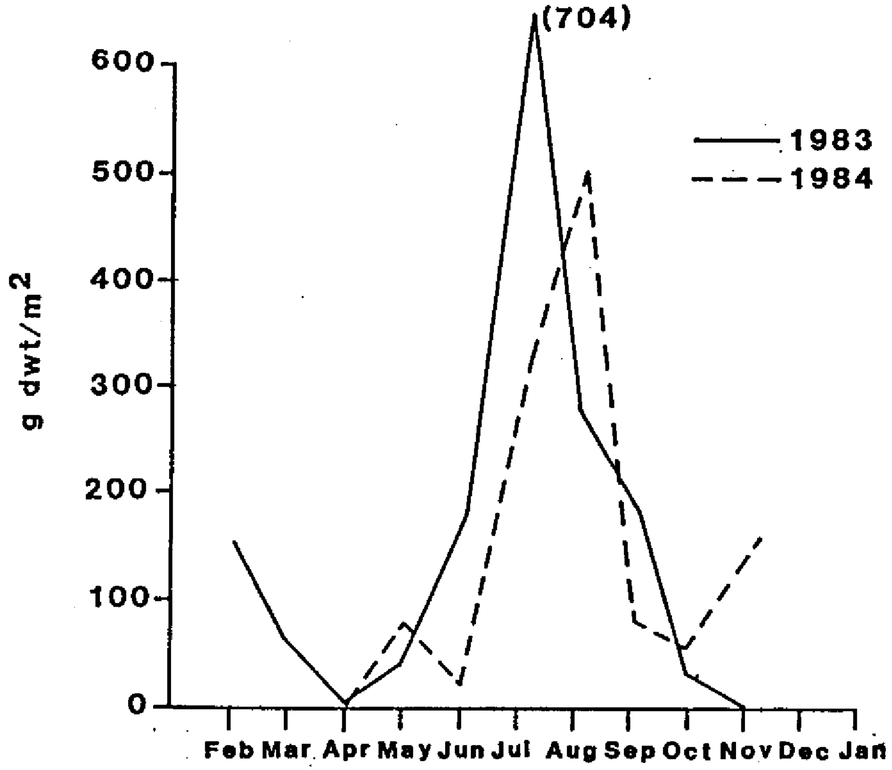

Figure 7.7 Standing crop biomass of the Ruppia-Eleocharis community in 1983 and 1984.

productivity of one community, Ruppia-Eleocharis, was significantly different. There was no obvious reason. Also, there was no difference among impoundments compared by average NAPP per square meter (hypothesis 4, Table 7.4). In general, we found that it was reasonable to consider the Cat Island impoundments as replicates from the point of view of macrophyte productivity.

Finally, we would like to note (Fig. 7.7) that changes in the management program could possibly alter the time of year when the standing crop of the Ruppia-Eleocharis community peaks so that it would be available to the migratory waterfowl it is intended to feed. An altered water-management plan might also help protect the secondary crop community, Scirpus robustus, from spring freeze damage.

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Chapter 8

Aquatic Community Metabolism and Plankton Productivity

W. D. Marshall and H. N. McKellar

INTRODUCTION

A basic change related to the impoundment of intertidal marshes is the conversion from a system dominated by emergent macrophytes to a submerged system dominated largely by aquatic communities. The related changes in total community productivity are of considerable interest in understanding the ecological functioning of impounded wetlands. Whereas the productivity of the macrophyte community was examined in terms of seasonal changes in biomass (Chapter 7), productivity in submerged aquatic habitats can be effectively addressed in terms of daily metabolism.

In this initial investigation we examined the daily and seasonal dynamics of dissolved oxygen (DO) in the impoundments as a measure of aerobic community metabolism. Diel changes in DO in the open water of the impoundments were taken as an indicator of the integrated contributions of the submerged macrophytes as well as the planktonic and benthic components. In addition, we specifically examined the seasonal changes in the planktonic contribution to total community oxygen dynamics. The major objectives of this research were, therefore, to: (1) evaluate seasonal patterns and annual sums of total aquatic community metabolism in the five experimental impoundments and to (2) quantify the relative contributions of the plankton component.

METHODS

Impoundment Morphometry

Computations for evaluating total aquatic community productivity and respiration required detailed information on depth, volume, and surface area relationships in each of the impoundments. To quantify the basic morphological features, a detailed depth profile was determined and a hypsographic curve developed for each impoundment. These data enabled the determination of mean depth, volume, and area coverage of the water at various water levels.

Along six transects across each impoundment depth measurements were recorded at 4 to 5 m intervals. We constructed hypsographic curves for each impoundment using a depth-interval frequency plot showing the depth and area relationships at various water levels (see Figs. 6.1 & 6.2) The volume, surface area, and mean depth of each impoundment was determined using the hypsographic curves and water-level readings. The volume at each water level was determined from the integrated area of the curve at each vertical water-level line. Water-level readings were standardized for each impoundment to represent the absolute depth of water over the lower edge of the shallow flats (i.e., the impoundment stage = 0 when the flats were exposed but the perimeter ditches were full). Mean depth for each water level was calculated by dividing the volume (m^3) by the surface area (m^2).

Total Aquatic Community Metabolism

Daily primary production and community respiration of the aquatic communities were determined from diel oxygen changes in impoundment water (Odum and Hoskin, 1958). The oxygen technique accounts only for aerobic pathways of community metabolism. It does not account for anaerobic respiration, which may be quite important in wetland soils (Howarth and Teal, 1980). Monthly sets of dawn and dusk readings of O_2, water temperature, and salinity were taken (YSI-58 O_2 probe; YSI-33 salinometer) at 15 stations (3 around the perimeter of each impoundment). Readings were taken within the top 10 to 15 cm of the water column. Preliminary vertical profiles in these impoundments indicated that the surface waters were well mixed down to 50 to 60 cm, with deeper stratification in the perimeter ditches. Because the mean depths of the impoundments were always < 60 cm, vertical stratification was not considered as a major factor in this study, although there were probably some times when stratification was more pronounced. Oxygen concentrations were averaged across each impoundment and used to compute net daytime productivity and nighttime respiration (McConnell, 1962; Lind, 1978). Hourly rates of nighttime respiration were extrapolated through daytime hours to estimate 24-hr respiration and gross productivity. This extrapolation may lead to underestimates of community metabolism to the extent that daytime photosynthesis stimulates respiration. Volumetric rates were multiplied by the mean depth of each impoundment to yield areal-based estimates of aquatic community metabolism. To account for some day-to-day variability, dawn-dusk O_2 changes were usually monitored for 2 consecutive days in each monthly sampling. During late June, measurements were continued for 4 consecutive days (21-24 June).

Diffusion corrections were based on a series of gas exchange experiments, using a floating plastic dome (Copeland and Duffer, 1964). Diffusion measurements were made over a range of depths (34 to 80 cm) and dates (July to February). In this limited study of diffusion in the impoundments, we found no apparent relationship in area-based diffusion rates with depth or season (Marshall, 1984), so we computed a mean diffusion constant (0.629 ± 0.053 g m^{-2} hr^{-1} at 0% saturation) which was used in diffusion corrections for all of the impoundments. One extreme value (1.084 g m^{-2} hr^{-1} at 0% saturation) was observed during unusually high winds. This value was not included in the mean.

There are several sources of potential error in our use of the free-water oxygen technique for estimating total aquatic community metabolism in these systems. First, the 15 perimeter stations used for examining O_2 changes in the water may not have fully accounted for the wide range of microhabitats in the impoundments, especially during periods of slight wind and stagnant water (late summer).

To examine the magnitude of possible error due to sampling along the perimeters of each impoundment, we conducted an intensive, multi-station metabolism study in a single impoundment (unit 3) during the late summer (27-28 July, 1984). Results suggested that using only three perimeter stations per impoundment caused little error (<5%) in the estimate of total community photosynthesis. However, the three-station estimate may have led to an underestimate of total community respiration by about 30%. Although these differences were not statistically significant, they suggested that higher rates of community oxygen comsumption may occur within the interior of the dense *Ruppia* flats and may not be fully accounted for at the perimeter stations during times of minimal water movement. However, during most meteorologic conditions (with considerable wind-driven water circulation), the abbreviated sampling scheme using 15 perimeter stations around the impoundment complex probably accounted for most of the spatial variability in the impoundments.

A second source of error derives from the growth form of *Ruppia maritima*, the dominant aquatic macrophyte in the impoundments. This rooted aquatic plant reached the water surface throughout most of the growing season. In fact, water levels in the impoundments were adjusted so that the growing tips of the *Ruppia* leaves remained at (or near) the water surface to enhance availability to waterfowl. Some O_2 exchange may have occurred directly between the *Ruppia* leaves and the atmosphere, causing an underestimate in community metabolism based on free-water O_2 changes. The magnitude of this potential underestimate was not evaluated in this study. However, because most of the *Ruppia* biomass was submerged, oxygen changes in the water probably reflected much of the *Ruppia* productivity.

Plankton Metabolism

Plankton metabolism was determined for each impoundment by the light-and-dark bottle method (Gaarder and Gran, 1927). Changes in DO concentrations in replicate light and dark bottles incubated for the daytime hours were used to calculate gross productivity and total respiration. Within 1 hr of sunrise, water was taken from each impoundment, mixed, and siphoned into duplicate light, dark, and initial bottles. The light and dark bottles were stoppered and then suspended in situ at a depth of about 10 cm, with the light bottles on top. The initial bottles were taken as quickly as possible to the field lab where the initial DO concentrations were measured, using the (YSI-58) DO meter with a stirring bottle probe. Within 1 hr of sunset the light and dark bottles were retrieved and taken to the field lab, where the DO concentrations were measured. The total incubation time varied around 12 hr for each sampling period.

Rates of plankton metabolism was calculated as:

$$P_{net}\ \text{day} = (L - D)/t$$
$$R = (I - D)/t$$
$$P_g = (P_{net}\ \text{day} + R) \times t$$

where P_{net} day is the net daytime production (g O_2 m^{-3} hr^{-1}), L is the final O_2 concentration in the light bottles (g m^{-3}), D is the final concentration in the dark bottles (g m^{-3}), t is the incubation time, R is the respiration rate (g m^{-3} hr^{-1}), I is the initial O_2 concentration (g m^{-3}), and P_g is the gross productivity for the day (g m^{-3} day^{-1}).

Total 24 hr plankton respiration (g O_2 m^{-3} day^{-1}) was estimated by extrapolating the hourly plankton respiration rate over 24 hr. The daily plankton metabolism figures for gross production and total respiration were converted from volume to area-based estimates by multiplying each figure by the mean depth of the associated impoundment. As for total community metabolism, R and P_g may be underestimated to the extent that photosynthetic production stimulates heterotrophic metabolism during the daytime.

RESULTS AND DISCUSSION

Physical Aspects

Fig. 8.1 shows the seasonal patterns of water temperature, salinity, and water level in the study impoundments. During the main study period from December 1982 through December 1984, water temperature in the impoundments ranged from a February minimum of 6°C to an August maximum 32°C. Salinities were maintained at 20 to 25 ppt throughout the growing season but dropped to less than 5 ppt during high river discharges in February and March.

Seasonal changes in water level (stage) reveal the water management scheme for the impoundments (Fig. 8.1). During the spring drawdown the

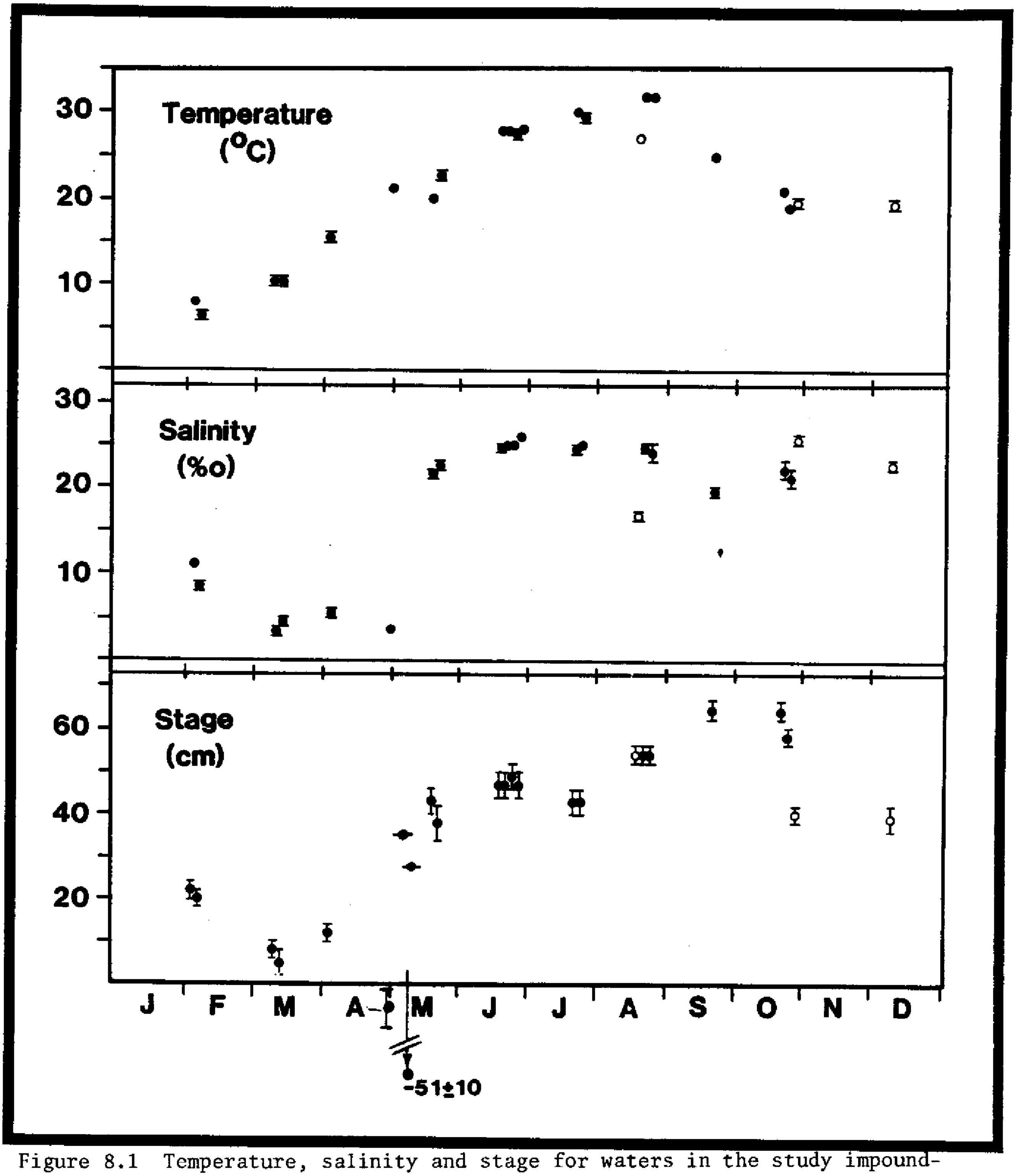

Figure 8.1 Temperature, salinity and stage for waters in the study impoundments, 1982 and 1983. Temperature and salinity data points (± SE) represent mean (n=15) daily temperature and salinity from 15 sampling stations throughout the impoundment complex. Stage data points (± SE) represent mean (n=5) stage (water level above lower edge of impoundment flats) throughout the impoundment complex. Open circles = 1982; filled circles = 1983.

impoundment stages were close to 0 cm. At these stage levels most of the shallow flats were exposed, and the water within the impoundments was in the deeper perimeter trenches. Following the drawdown period, the beds were flooded for seven days and then drained (stage = -51 cm) as a mosquito-management practice. After draining, the impoundments were immediately reflooded, after which the water level was gradually raised through the spring and summer months as the Ruppia stands gained height. Maximum stage was 60 to 70 cm during September and October. During the fall and winter, the stage was gradually lowered to make Ruppia more available to migrating waterfowl. As the waterfowl grazed, the stage was gradually lowered to the annual minimum in March (0 to 10 cm).

The basic bathymetry of these manmade basins is summarized by Table 8.1, and the hypsographic curves for each impoundment are provided in Figs. 6.1 and 6.2. Of the total area within each impoundment, 85 to 95% was characterized by a shallow, sloping flat that dropped abruptly to an outside perimeter trench. Generally, stands of emergent vegetation (Spartina and Scirpus) dominated the shallower parts of the sloping flats, and submerged stands of Ruppia dominated the deeper portions. The trenches surrounded the flats on the north, east, and south sides. The deepest point within the impoundments was within the trench at the main tidal trunk. These maximum water depths averaged approximately 60 to 140 cm deeper than the shallow flats.

Area coverage of the impoundments by impounded water varied from 100%, during the Ruppia growing season, to as low as 9% during early-spring drawdowns. Water volume in the basins varied from full pools as large as 33,900 m^3 (see Table 8.1, impoundment 1) in late summer to minimum volumes of only 5% of full pool in early spring. The mean depth of standing water over the total area of each impoundment was always relatively shallow. Mean depths within the impoundments ranged from 0.1 m in late winter to 0.5 m during summer full pool. Maximum depths within the impoundments, always found at the main tidal trunks, were as great as 2 m.

Aquatic Community Productivity and Respiration

The dawn-dusk measurements of DO exhibited large diurnal changes during all season (Fig. 8.2). The magnitude of daily change was greatest

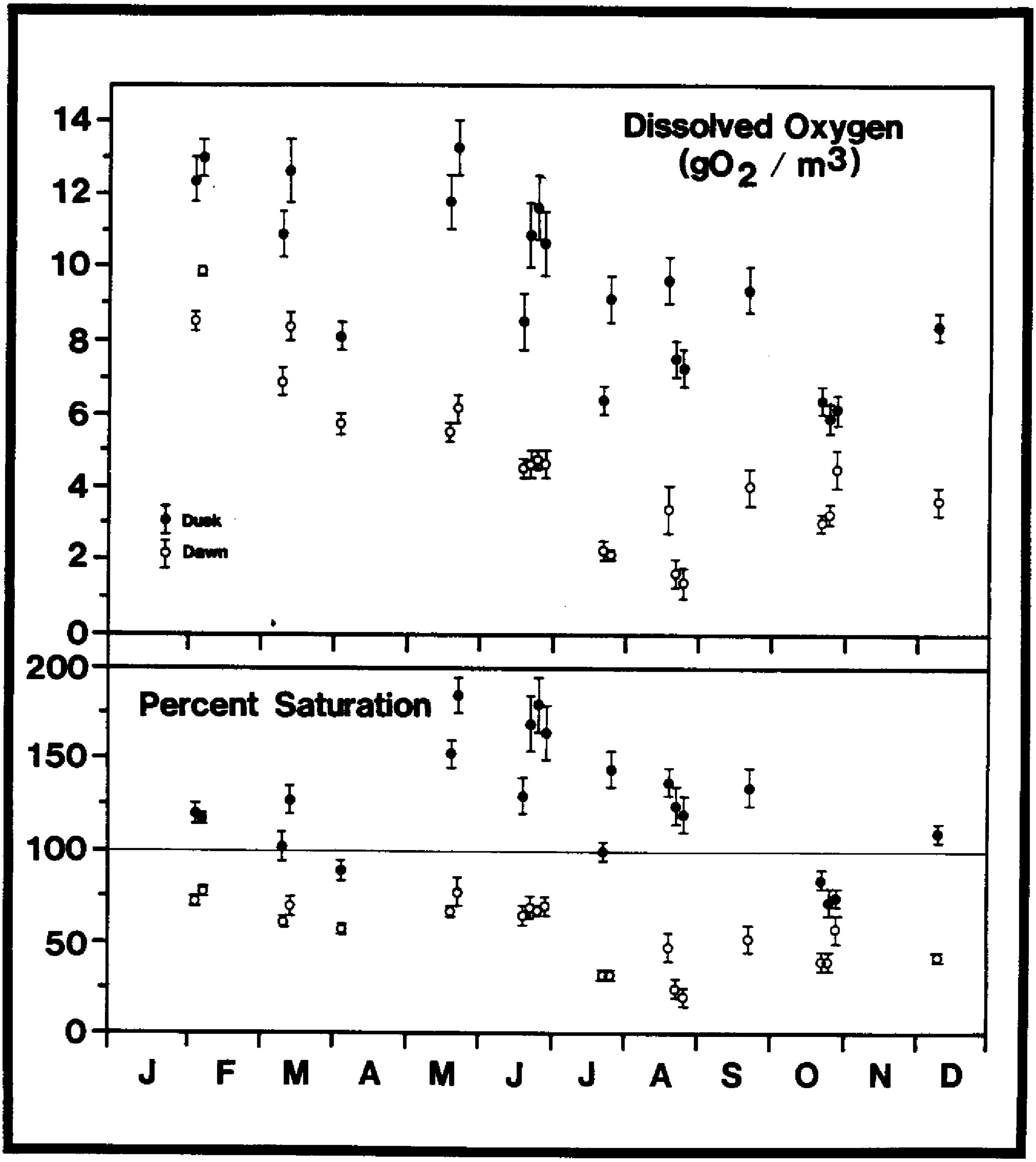

Figure 8.2 Daily (dawn and dusk) dissolved oxygen dynamics for waters in the study impoundments, 1983. Data points (± SE) represent mean (n=15) dissolved oxygen (DO) concentrations and mean (n=15) DO percent saturation from 15 sampling stations throughout the impoundment complex. Open circles = dawn values; filled circles = dusk values.

during the growing season (about 7 g O_2/m3). October and April showed the minimum daily changes in DO concentrations (about 3 g O_2/m^3).

The highest DO values recorded (18 to 19 g O_2/m^3) were observed at dusk samplings in March, May, and June. The lowest DO values recorded (0.2 to 0.5 g O_2/m^3) were observed at dawn during the months of July and August. Late summer recurrences of low morning O_2 concentrations resulted in stressful conditions for fish in some of the impoundments (see Chapter 14).

Table 8.1

Physical dimensions of the Cat Island impoundments.

	Area (ha)		Volume (m^3)		Mean Depth (m)		Full Pool
Impoundment	Max	Min	Max	Min	Max	Min	Max Depth (m)
1	7.78	0.681	33,900	3630	0.44	0.20	2.05
2	4.77	0.548	23,700	2020	0.50	0.13	1.85
3	3.53	0.441	17,900	882	0.51	0.15	1.53
4	4.10	1.89	23,000	2050	0.56	0.11	1.96
5	6.26	2.07	28,800	1330	0.46	0.06	1.27

The maximum values for dusk saturation occurred in May and June, with 184% and 181% saturation, respectively (Fig. 8.2). All mean dusk saturation levels were at 100% saturation or above, with the exceptions of April and October. At these times mean dusk DO values were low. The minimum mean value for dusk percent saturation (73%) occurred after a cloudy day in October, 1983.

Overall impoundment means showed a steady decline in dawn DO concentrations from February through August. This decline in dawn DO was inversely associated with the linear rise of mean water temperatures from February through August. The inverse relationship continued from August to December; as mean temperatures declined, the trend for dawn DO showed a gradual rise. The dawn saturation values were generally in the range of

40 to 75%, except during the months of July and August when saturation dropped to levels around 15 to 30%.

Estimates of aquatic community metabolism indicated clear seasonal trends of gross primary production, community respiration, and corresponding levels of net community production (Fig. 8.3). During late winter and early spring, gross production was typically low, with levels around 1 to 2 g O_2 m^{-2} day^{-1}. Community respiration was also relatively low, although values exceeded gross productivity in March and April, yielding periods of net system respiration. During that time most of the shallow flats were exposed by low water levels, and the aquatic habitat was limited to the perimeter ditches, an environment regarded as basically heterotrophic (P/R ratio < 1) during this time.

After the impoundments were flooded in early May, gross productivity reached maximum levels of 4 to 6 g m^{-2} day^{-1}, as Ruppia and Eleocharis became established over the shallow flats. Community respiration remained relatively low throughout May and June, producing significant periods of net community productivity (2 to 4 g m^{-2} day^{-1}) with P/R ratio > 1.0.

As water temperatures reached annual maxima of over 30°C by late summer, gross production leveled off and respiration continued to climb to August peaks of almost 10 g $m^{-2}day^{-1}$. These conditions resulted in the recurrence of net systems respiration (P/R ratio < 1.0) which persisted into the fall with the decline of gross production.

To estimate annual total community gross production and respiration within the individual impoundments, integration of the area beneath a curve of daily means was performed for each impoundment. Impoundments 2, 3, and 4 were quite similar in annual gross production, whereas 1 and 5 were considerably less productive (Table 8.2). Annual community respiration was similar among the impoundments, with impoundment 5 having the highest rate (1856 g O_2 m^{-2} yr^{-1}). Among the five impoundments, mean annual gross community productivity was 1027 g O_2 m^{-2} yr^{-1} and mean annual total respiration was 1608 g O_2 m^{-2} yr^{-1}. The P/R ratios for community metabolism (0.34 to 0.86) indicated that each of the impoundments was largely heterotrophic over an annual cycle. Impoundment 5 was the most heterotrophic, impoundment 2 the least heterotrophic.

To evaluate the significance of the differences observed between the impoundments, we used analysis of variance (SAS, General Linear Model) and

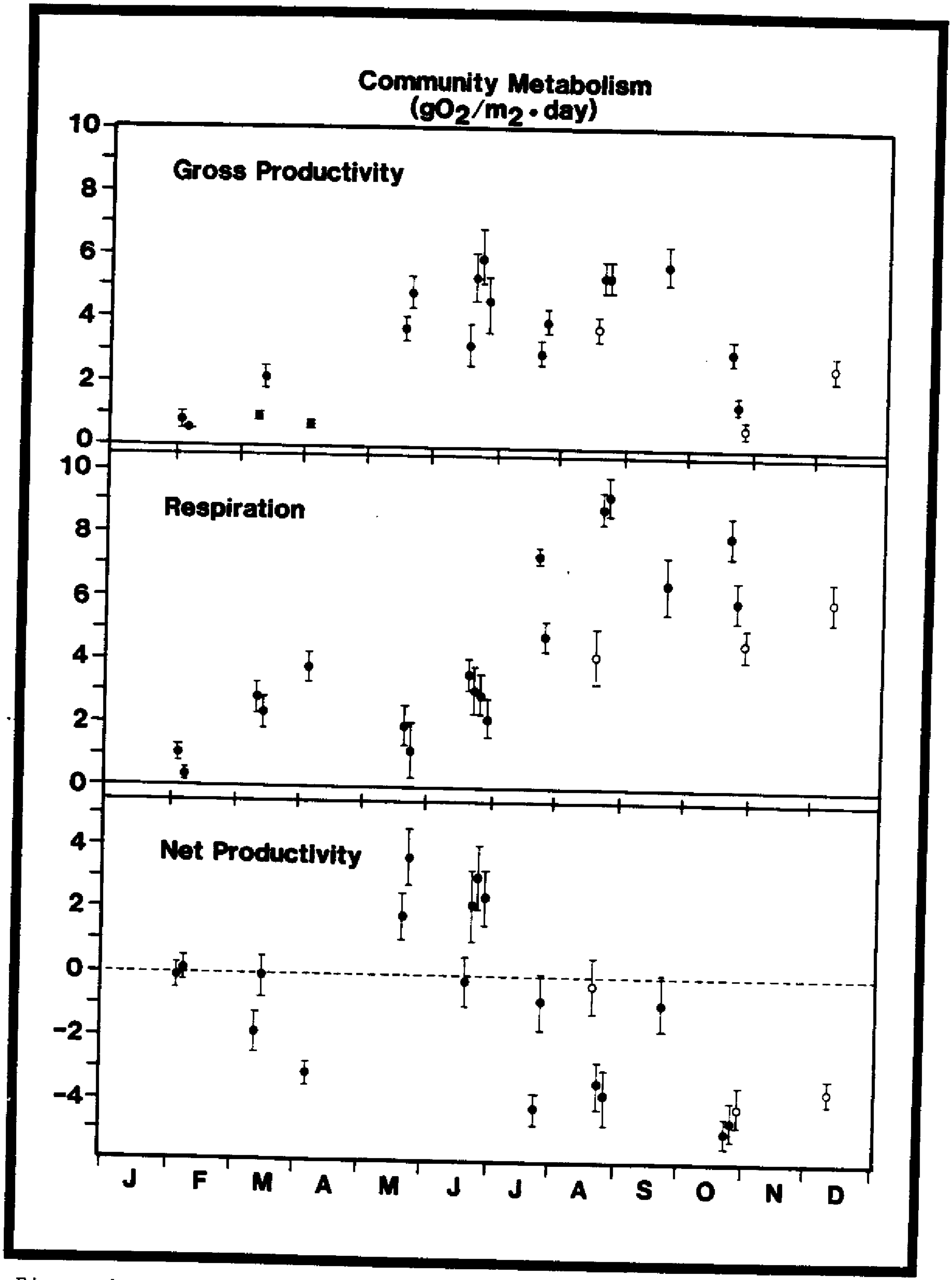

Figure 8.3 Aquatic community metabolism in the study impoundments, 1982 and 1983. Data points (± SE) represent means (n+15) from 15 sampling stations throughout the impoundment complex. Open circles = 1982; filled circles = 1983.

the Duncan test for significant differences among impoundment means for gross production (GP) and total respiration (TR). The results (Table 8.3) revealed no significant differences for GP among impoundments 1, 2, 3, and 4. Impoundment 5, however, was found to be significantly different from impoundment 2, 3, and 4. There were no significant differences found among the impoundments for TR. These tests were performed at the .05 significance level.

Table 8.2

Estimates of annual total aquatic community metabolism. Gross Productivity (GP) in g O_2/m^2; Total 24-hr respiration (TR) in g O_2/m^{-2}

Impoundment	GP/yr	GP/day	TR/yr	TR/day	P/R
1	895	2.5	1,497	4.1	0.60
2	1,151	3.2	1,339	3.7	0.86
3	1,169	3.2	1,756	4.8	0.67
4	1,292	3.5	1,592	4.4	0.81
5	626	1.7	1,856	5.2	0.34
$\bar{x}$	1,027	2.8	1,608	4.4	0.64
(SE)	(107)	(0.3)	(82)	(0.2)	

Plankton Metabolism

The annual trends for gross plankton productivity, total plankton respiration, and the subsequent net plankton productivity (Fig. 8.4) show definite seasonal patterns. Gross productivity increased from minimum values in February of < 1.0 g O_2 m^{-2} day^{-1} to maximum values in August of approximately 6 g $O_2 m^{-2}$ day^{-1}. Following the August peak, productivity dropped sharply from September to October as the growing season came to a close. Higher values for plankton respiration occurred during the growing season and peaked in September (2 g m^{-2} day^{-1}). After September, respiration gradually dropped off to minimal values near the limits of detection in the winter.

The relative ranking of impoundments for annual gross plankton production corresponded quite closely with the ranking of gross community productivity. Community and planktonic respiration did not correspond as well.

Table 8.3

Results of Duncan test for statistical differences among annual impoundment means (n = 21) for gross production (GP) in g O_2 m^{-2} day^{-1} and total respiration (TR) in g O_2 $m^{-2}day^{-1}$. Means that share same symbols are not significantly different.

Impoundment	GP		Impoundment	TR
4	3.8 *		5	5.0 *
	*			*
2	3.6 *		3	4.7 *
	*			*
3	3.5 *		2	4.0 *
	*			*
1	2.7 *	X	4	3.9 *
		X		*
5	2.0	X	1	3.7 *

To estimate annual gross plankton production and respiration within the individual impoundments, integration of the area beneath a curve of daily means was performed for each impoundment. The results of the integrations (Table 8.4) reveal a considerable range of values among the impoundments for annual total plankton metabolism. Impoundments 1 to 4 were similar for annual gross plankton production and total plankton respiration, whereas impoundment 5 was considerably less.

The overall impoundment means for annual plankton metabolism were 664 g O_2 m^{-2} yr^{-1} for gross productivity and 222 g O_2 m^{-2} yr^{-1} for total respiration. The plankton community proved to be largely autotrophic, as P/R ratios ranged from 2.6 (impoundment 1) to 3.9 (impoundment 5).

To evaluate the significance of the differences observed between the impoundments, computer-generated analysis of variance (SAS, General Linear Model) and the Duncan test for significant differences were performed on annual means for gross plankton productivity and total plankton respiration. Results of the Duncan test (Table 8.5) revealed no significant differences for gross productivity among the impoundments, although the impoundments showing the highest rates (2, 3, and 4) were the same as those showing the highest mean rates for total community metabolism (Table 8.3).

Table 8.4

Estimates of annual plankton metabolism.
Gross Productivity (GP) in g O_2/m^2;
Total 24-hr respiration (TR) in g O_2/m^2

Impoundment	GP/yr	GP/day	TR/yr	TR/day	P/R
1	675	1.8	260	0.7	2.6
2	603	1.7	213	0.6	2.8
3	791	2.2	232	0.6	3.4
4	780	2.1	285	0.8	2.7
5	469	1.3	121	0.3	3.9
$\bar{x}$	664	1.8	222	0.6	3.0
(SE)	(54)	(0.1)	(25)	(0.1)	

Figure 8.5 shows seasonal trends in the apparent percentage of planktonic contribution to total community productivity. Direct comparisons of the two aspects of aquatic community metabolism (total and planktonic) should be viewed with some caution because of the differences in conversions to area-based values and accountability for spatial variablity for the two techniques (Marshall, 1984). However, the relative differences suggest some considerable seasonal shifts in planktonic and benthic domination of aquatic community productivity. During the winter and early spring, plankton productivity was generally less than 30% of

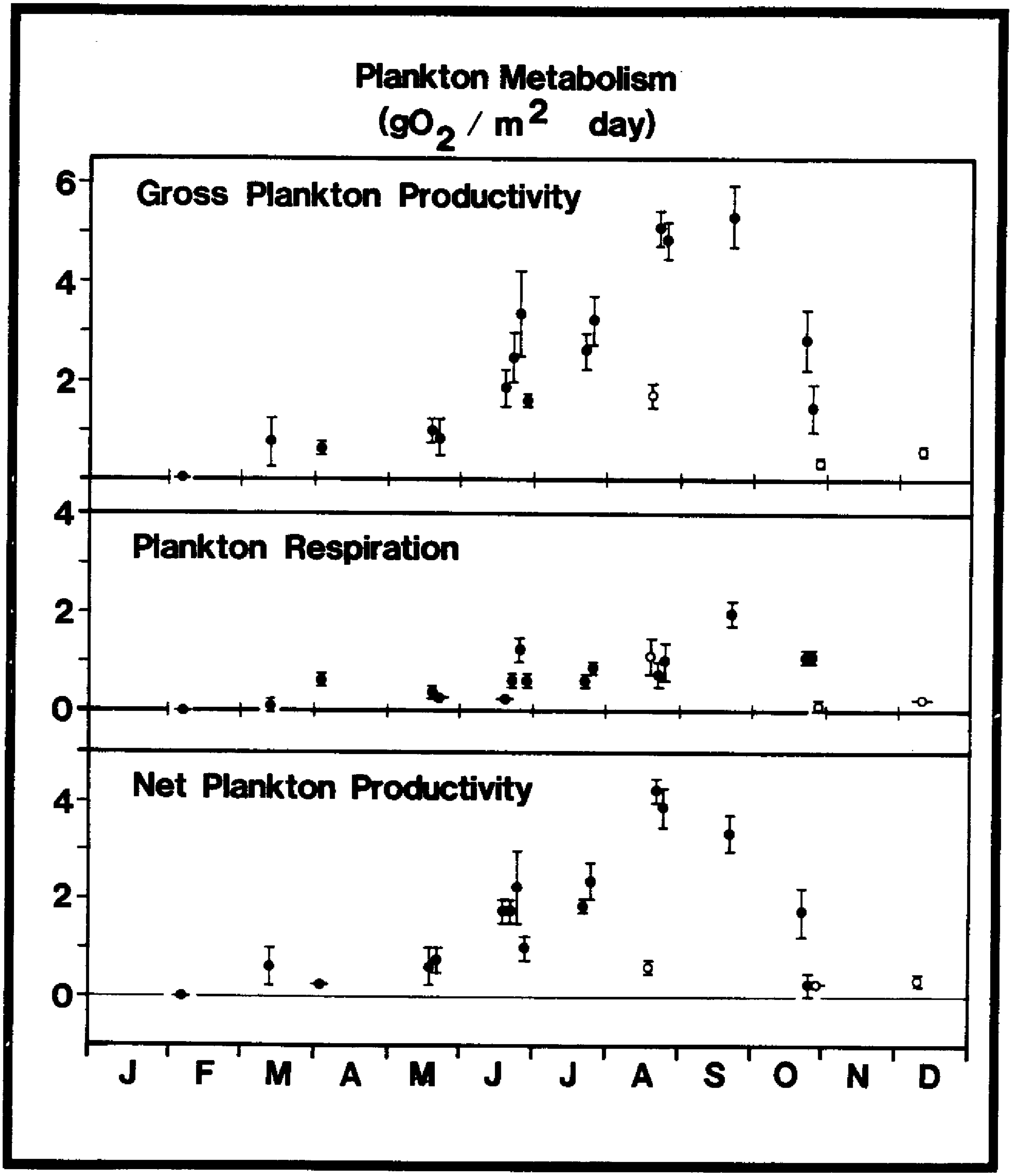

Figure 8.4 Plankton metabolism in the study impoundments, 1982 and 1983. Data points (± SE) represent means (n=5) from 5 sampling stations, one station at each impoundment. Open circles = 1982; filled circles = 1983.

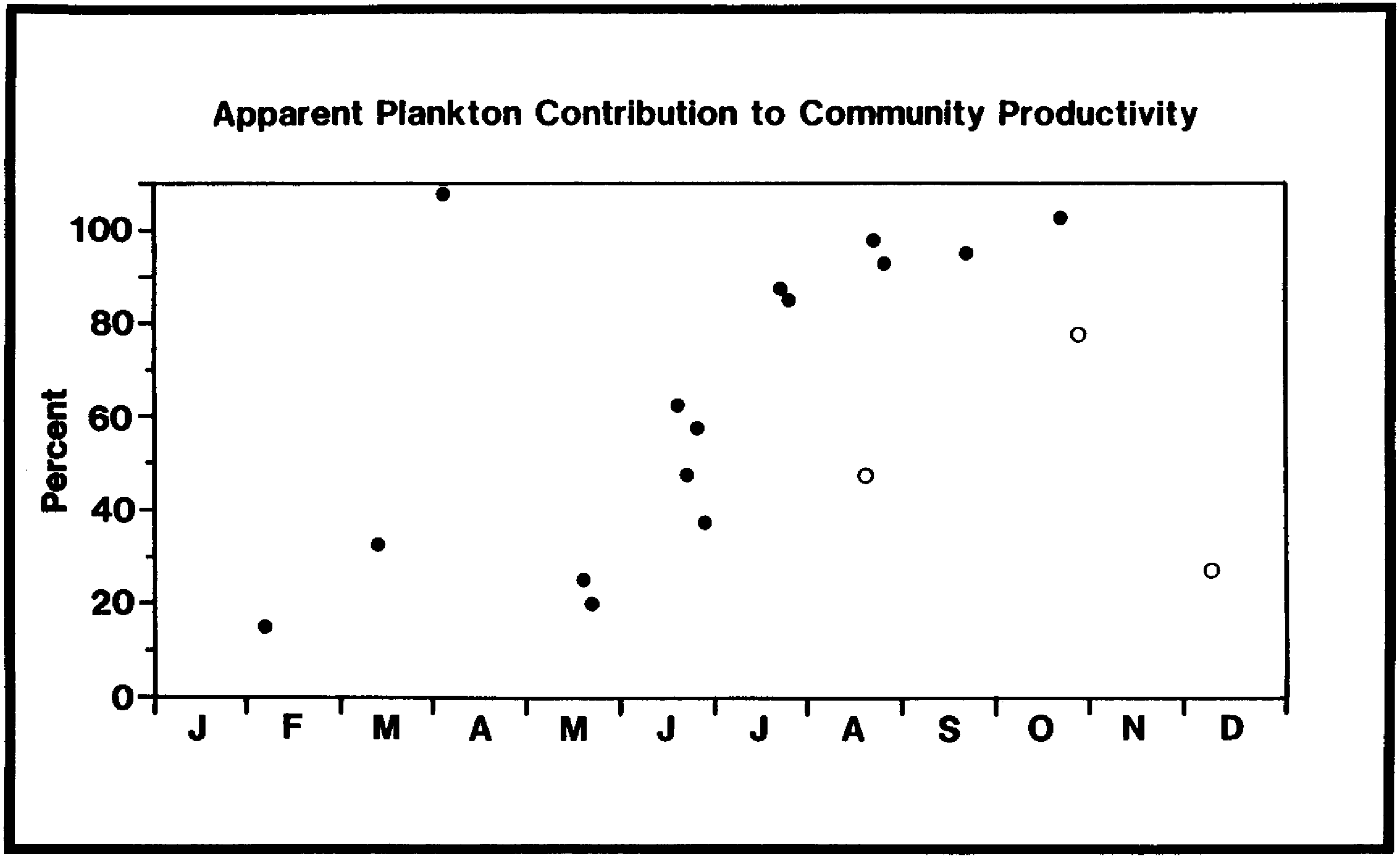

Figure 8.5 Apparent plankton contribution to total aquatic community productivity, 1982 and 1983. Data points represent the percent of daily mean community productivity contributed by daily mean plankton productivity. Open circles = 1982; filled circles = 1983.

total community production, indicating benthic domination. However, from July through late summer and fall, plankton dominated total aquatic productivity, contributing 80 to 90% to the total observed O_2 changes in impoundment waters.

Table 8.5

Results of Duncan test for statistical differences among annual impoundment means (n = 19) for gross plankton production (GPP) in g O_2 m^{-2} day^{-1} and total plankton respiration (TPR) in g O_2 m^{-2} day^{-1}. Means that share same symbols are not significantly different.

Impoundment	GPP		Impoundment	TPR		
4	2.7	*	4	1.0		X
		*				X
3	2.4	*	3	0.71	*	X
		*			*	X
2	2.1	*	1	0.71	*	X
		*			*	X
1	1.9	*	2	0.64	*	X
		*			*	
5	1.7	*	5	0.45	*	

CONCLUSIONS

Estuaries are recognized as among the most productive ecosystems in the world (Odum, 1971). As a result, they have come under the protection of major Federal law [Section 404, Clean Water Act] to preserve them from indiscriminate dredging, filling, and development. Currently, a controversy in South Carolina regarding impoundment development on marshlands hinges on policy decisions made around this law. The controversy basically involves a conflict between those who support reimpoundment of old ricefields for the potential economic benefits of aquaculture and waterfowl production versus those who seek to preserve natural marshlands for their important role in general coastal ecology (high primary productivity, nutrient cycling, organic carbon export, nursery grounds for commercially important fishes; as referenced in Chapter 2).

This study examined the rates and seasonal patterns of community production and respiration in the aquatic portions of five study impoundments (Fig. 8.3). The annual sums of community metabolism were estimated by integrating seasonal trends for each impoundment over the 12 months of 1983. Annual gross production and community respiration (averaged over all five impoundments) were 1027 ± 107 and 1608 ± 82 g O_2/m^2, respectively. The resulting P/R ratio of 0.64 indicates the importance of heterotrophic processes in the aquatic habitats of these impoundments. Although there was substantial autotrophic production of submerged macrophytes (See Chapter 7) and phytoplankton (Figs. 8.4 and 8.5), there was probably considerable input of organic matter from the emergent macrophyte community within the impoundments. Therefore, it is not surprising for the impoundments to exhibit annual P/R ratios of less than unity in the aquatic habitats because of considerable allochthonous organic inputs.

In comparison to other coastal systems, the impoundments were somewhat similar to small salt-marsh embayments such as those studied by Nixon and Oviatt (1973) in Bissel Cove, Rhode Island. The embayments are typically shallow (< 1 m) with bordering emergent marsh and submerged benthic macrophytes including Ruppia maritima. Seasonal rates and patterns of total aquatic community metabolism in the embayments were quite similar to those observed in the Cat Island impoundments (Fig. 8.3). The excess community respiration over gross production in the embayments was also attributed to organic inputs from the bordering marsh. These similarities suggest that the impoundments may support comparable levels of aquatic community energy flow as in some natural habitats within the salt-marsh environment such as the embayments described by Nixon and Oviatt.

Phytoplankton production in intertidal salt marshes usually represents a small fraction of total marsh system productivity. For the Duplin River marsh and estuary, the relative contribution of phytoplankton to total system productivity was estimated to be less than 10% (Pomeroy and Weigert, 1981). However, in impoundments, phytoplankton may contribute considerably more, because of the increased area of aquatic habitat. Data for the Cat Island impoundments clearly suggest a seasonal dominance of phytoplankton productivity in the fall. The enhanced phytoplankton productivity is relevant not only to total system production but may also be important in controlling patterns of nutrient exchange (see Chapter 6).

Seasonal patterns of total community metabolism correlated well with seasonal changes in submerged macrophytes and phytoplankton. Maximum rates of community metabolism in June (5 to 6 g O_2 m^{-2} day^{-1}, Fig. 8.3), occurred along with the rapid growth of the submerged Ruppia-Eleocharis community (Fig. 7.7, Chapter 7). The secondary peak of community metabolism in the fall corresponded to the time of maximum plankton productivity (Fig. 8.4). There were no apparent seasonal trends in the productivity of microbenthic algae, although the highest rates were observed in the winter when phytoplankton biomass was low (see Chapter 9).

Although the values of total community metabolism based on free-water oxygen changes provided a good indicator of seasonal trends in community components, the absolute rates of total community metabolism in the impoundments may have been somewhat higher. As mentioned previously, the submerged macrophyte component of the aquatic community in the impoundments (largely Ruppia maritima) may have exchanged considerable amounts of oxygen directly with the atmosphere, because the Ruppia leaves reached the water surface during much of the growing season. The magnitude of this phenomenon was not evaluated in this study. However, some degree of underestimation is suggested by comparing the net annual production of the Ruppia-Eleocharis community (870 ± 380 g dry wt/m^2; Table 7.3 in Chapter 7) with the estimated gross productivity of the total aquatic community derived from free-water oxygen changes (1027 ± 107 g O_2/m^2; Table 8.2). Converting each estimate to equivalent units of organic carbon [dry weight/organic carbon in macrophytes = 0.45 (Odum, 1971); Oxygen/organic carbon = 0.313 (assuming a photosynthetic quotient of 1.2 moles of O_2 per mole of C; Ryther, 1956)] yielded a net annual productivity of the submerged macrophytes of about 390 ± 170 g C/m^2 compared to a gross community productivity (which should be considerably larger) of only 320 ± 34 g/m^2. Although the variability of the submerged macrophyte estimate was high (> 44%), this discrepancy suggests a possible underestimate of metabolic rates based on free-water oxygen changes.

A major objective of this study was to compare total productivity of the entire impoundment community with representative rates of productivity in open tidal marshes. These comparisons are addressed in more detail in Chapter 10 and suggest that the impoundment management during this study supported levels of total community production in the impoundments that were similar to total production in adjacent tidal marshes. However, the contributions to that production via the various plant communities (marsh grasses, benthic macrophytes and microalgae, and phytoplankton) differed considerably between the impoundments and the tidal marshes. These differences have further consequences with respect to the quality of nutrient exchange between the impoundments and the adjacent estuarine water, an issue discussed in more detail in Chapter 6.

With respect to this specific phase of the productivity study, the observed seasonal shift from benthic toward plankton dominance of community productivity may have been of more direct relevance in the water management of the impoundments. The shift toward planktonic dominance occurred during (and may have been stimulated by) the diminished rates of tidal flushing in late summer in the impoundments (see Chapter 6). Efforts to provide more water exchange during the summer may reduce phytoplankton dominance and enhance continued benthic Ruppia production through the summer and fall because of the decreased shading and competition for limiting nutrients. This result may enhance waterfowl utilization of the impoundments while maintaining high rates of total community productivity.

The decreased flushing rates of the impoundments in late summer also contributed to deteriorating oxygen levels during this time. Therefore, efforts to provide more tidal exchange during the summer may also improve general water-quality conditions in the impoundments.

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Chapter 9

Production of the Microbenthic Algae

R. G. Zingmark

INTRODUCTION

In addition to the emergent macrophytes, the benthic microalgae (BMA) participate in benthic primary production. They provide a unique, nutritious food source for the benthic micro and meiofauna and for juvenile macrofauna (Lee et al., 1975; Montagna, 1984). Despite the fact that BMA have a doubling rate of approximately 24 hr and are significant processors of nutrients, they have been largely ignored by benthic ecologists. This is due in large part to the difficulty in sampling, quantifying, and manipulating the components of this community. A thorough study of impoundments must necessarily assess the biomass and productivity of the BMA. Annual rates of productivity of impounded marine and estuarine benthic microalgae from other geographical locations have been shown to be to up to two to three times greater than that of the phytoplankton overlying the same area of bottom (Pomeroy, 1959; Grøntved, 1960, 1962; Colijn and Venekamp, 1977; Colijn and de Jonge, 1984).

The major objectives of this study were: (1) to determine the spatial and temporal variations in the biomass and primary productivity of the benthic microalgae in a series of managed impoundments; (2) to determine, by comparison with similar data on the phytoplankton and aquatic macrophytes, whether the benthic microflora potentially provide a significant source of energy and materials to the consumer organisms in the impoundments and (3) to determine whether there are significant differences between the productivity of the benthic microalgae of the impoundments and the adjacent, currently unimpounded marsh, and between a nearby undisturbed natural tidal salt marsh. Funding constraints limited the sampling frequency to only a few days in each season. The results reported here must be considered preliminary and suggestive rather than complete and definitive.

METHODS

Measurements of physical variables, biomass, and productivity of the BMA were taken over four seasons in 1984 to 1985, coinciding approximately with mid-summer (July 25-28 and August 19-21), mid-fall (November 6-9), mid-winter (January 31-Feb 1), and early spring (April 3-5 and 24). Sampling sites included Paddy Field impoundments (units) 1 through 5 and Chainey Creek on Cat Island and Debidue Creek in North Inlet Estuary, an unimpounded 32 km^2 tidal salt marsh approximately 10 km distance to the north. The latter station was chosen as representative of a pristine salt marsh creek system that has never been impounded.

Physical data included temperature, salinity, and light attenuation. Subsurface temperatures were taken in early morning with a hand-held thermometer; salinity was determined with a B&L refractometer; vertical light profiles were made at 10-cm intervals using a LiCor L-185 quantum meter, equipped with a 193-SB submersible spherical quantum sensor. Attenuation (extinction) coefficients were calculated using the following formula as reported by Dring (1982):

$$\text{attenuation coefficient, } k(m^{-1}) = \frac{2.3\ (\log_e I_1 - \log_e I_2)}{d_2 - d_1}$$

where I_1 = photon influence rate at depth d_1 (any depth $<d_2$) and I_2 = photon influence rate at depth d_2 (the deepest depth measured).

Chlorophyll-a measurements were taken to represent the biomass of the phytoplankton and the benthic microalgae. For phytoplankton chlorophyl-a determinations (PCA) replicate samples of 5 to 10 ml of impoundment water were filtered through Whatman GF/F glass fiber filters to concentrate the phytoplankton. Filters were placed into scintillation vials to which was added 1 ml saturated $MgCO_3$. For benthic chlorophyll-a measurements (BCA) at least 10 cores (2.4 cm^2) were taken at random locations at each station. The top 0.5 cm of each sediment core was placed into a scintillation vial to which 1 to 2 ml saturated $MgCO_3$ was added. All samples were frozen on dry ice from 1 to 5 days, at which time 9 to 18 ml of 100% acetone was added. Samples were allowed to extract for 48 hr in the resultant 90% acetone solutions in the dark at 4°C. Chlorophyll-a and pheopigments from both sets of samples were determined fluorometrically using a Turner III-R fluorometer (Yentsch and Menzel, 1963).

Care was taken during sampling to obtain cores that were free of living vascular plants. This was especially difficult in the summer and fall, when large areas of the sediment surface were overgrown with *Ruppia maritima*. Occasionally, we discarded cores that on close examination were seen to contain free fragments of *R. maritima*. Thus, although this plant (and its abundant epiphytic flora) undoubtedly contributed significantly to benthic primary productivity and to the biomass of the ponds, we focused our attention on the biomass and productivity of the edaphic microalgal community.

Photosynthetic measurements were used to estimate the primary productivity of the benthic microalgae. The algae were sampled by taking 42-cm^2 cores from at least six random locations at each station and by placing them in pairs inside replicate 2.05 l closed, recirculating, Plexiglas incubators, constructed similarly to those described by Davis (1981). Oxygen concentrations inside the chambers were reduced to 3 to 4 ppm by purging the incubation water with N_2 gas prior to sealing the chambers. This kept the O_2 concentration from becoming saturated in the chambers, and forming bubbles affecting our results. Changes in dissolved oxygen concentration over time were monitored with temperature-compensated oxygen electrodes (Orbisphere Laboratories, Inc.) placed in the recirculating system. Three to five measurements of oxygen were made over a 40 to 60- min period with each sample. Initially, photosynthesis was measured over a range of irradiances, adjusted with neutral density filters (fiberglass window screening) so as to construct P-I curves;

however, it was found that the unfiltered samples (i.e., 100% irradiance) consistently gave maximum rates (P max), with no evidence of saturation regardless of the magnitude of the irradiance. Uptake of oxygen (primarily respiration) by the mixed-sediment community was determined similarly in the dark. Appropriate control chambers containing impoundment water but without cores were monitored so as to separate the metabolism of the plankton community in the water column from that of the benthic community. Incubations were made outdoors in ambient sunlight and inside a temperature-controlled waterbath set at the temperature measured earlier at each station. Up to two stations could be measured each day. Solar irradiance was monitored and recorded throughout the day to facilitate calculations of daily productivity.

Using the oxygen data obtained as above, it was possible to compute daily gross and daily net (24-hr) productivity of the benthic microalgae, as well as the respiration of the mixed benthic community. Hourly rates of gross productivity were calculated by adding community oxygen uptake, measured in the dark, to hourly net photosynthesis, measured in the light. Rates of oxygen change, expressed as mg O_2 m^{-2} hr^{-1} were converted to mg carbon m^{-2} hr^{-1}, assuming a photosynthetic quotient of 1.2 and a molar-to-molar conversion of O_2 to C of 12/32 or 0.3125 times the oxygen concentration (Ryther, 1956). Rates of daily gross photosynthesis (DGP) were calculated by assuming a constant hourly rate and multiplying it times the hourly length of the photoperiod. Daily net productivity (DNP) was calculated by subtracting daily community respiration (hourly respiration x 24) from the DGP.

RESULTS AND DISCUSSION

Light Attenuation and Phytoplankton Biomass

The overlying water in the impoundments and in adjacent Chainey Creek was turbid at all seasons. Attenuation coefficients in the ponds varied from 2.19 to 4.35 and in Chainey Creek from 4.13 to 6.01 . In contrast, Debidue Creek in North Inlet Estuary varied from 0.62 to 1.77. Highest coefficients in both areas occurred in summer; the lowest, mostly in the winter. Significant contributors to the turbidity were the phytoplankton, whose chlorophyll (PCA) varied from 6 mg/m^3 in Chainey Creek during the fall to 95 mg/m3 in unit 2 during the summer. In contrast, PCA in Debidue Creek water ranged from 2 to 6 mg chlorophyll-a/m^3 over the entire study. PCA was found to be more-or-less homogeneous both horizontally and vertically within each study site, and insignificant variations between replicates were noted. Except for unit 1, there was a general trend of decreasing concentrations of PCA during the study, which began in the summer (Fig. 9.1). Units 1, 2, and 3 had the highest average annual values of PCA during the year (42, 44, and 43 mg/m^3, respectively). Debidue Creek water averaged 6 mg chlorophyll-a/m^3.

Characteristics of the Sediment

The sedimentary composition of impoundment bottom layers was not uniform. Those that formed the top 8 or so cm of the cores graded from a 1 to 2-mm tan to rust, loose, floculent surface layer followed by a black, coarse, organic layer often containing dead roots and other parts of vascular plants in various stages of decay of approximately 1 to 2 cm depth. This was in turn followed by a well-packed gray or brown layer of fine silts and clays or a black, loosely organized layer of fine organic material (see Chapter 5 for a more-thorough description). The sediments of Chainey Creek and Debidue Creek appeared to be typical of those found in similar low-velocity, high-marsh creeks in *Spartina alterniflora*-dominated salt marshes along the Southeastern seaboard. These appeared to the eye as more-or-less uniform throughout the intertidal zone. They consisted of a tan surface layer of fine, organic-rich sediments, 1 to 2 mm deep, abruptly followed by a sharply demarcated black anoxic layer of fine silts and clays devoid of obvious organic particulate matter. There were no obvious differences observed in the composition of the sediments from any sample site during the various seasons.

Benthic Microalgal Biomass

Concentrations of benthic chlorophyll-a (BCA) between stations were similar during summer and winter but showed rather wide variations in the fall and spring (Fig. 9.2). Overall magnitudes of single BCA measurements from the top 0.5 cm of the cores ranged from 16 to 225 mg/m^2 in Chainey Creek and unit 2, respectively. Interestingly, the highest and lowest concentrations of BCA were measured during the fall sampling period. Mean

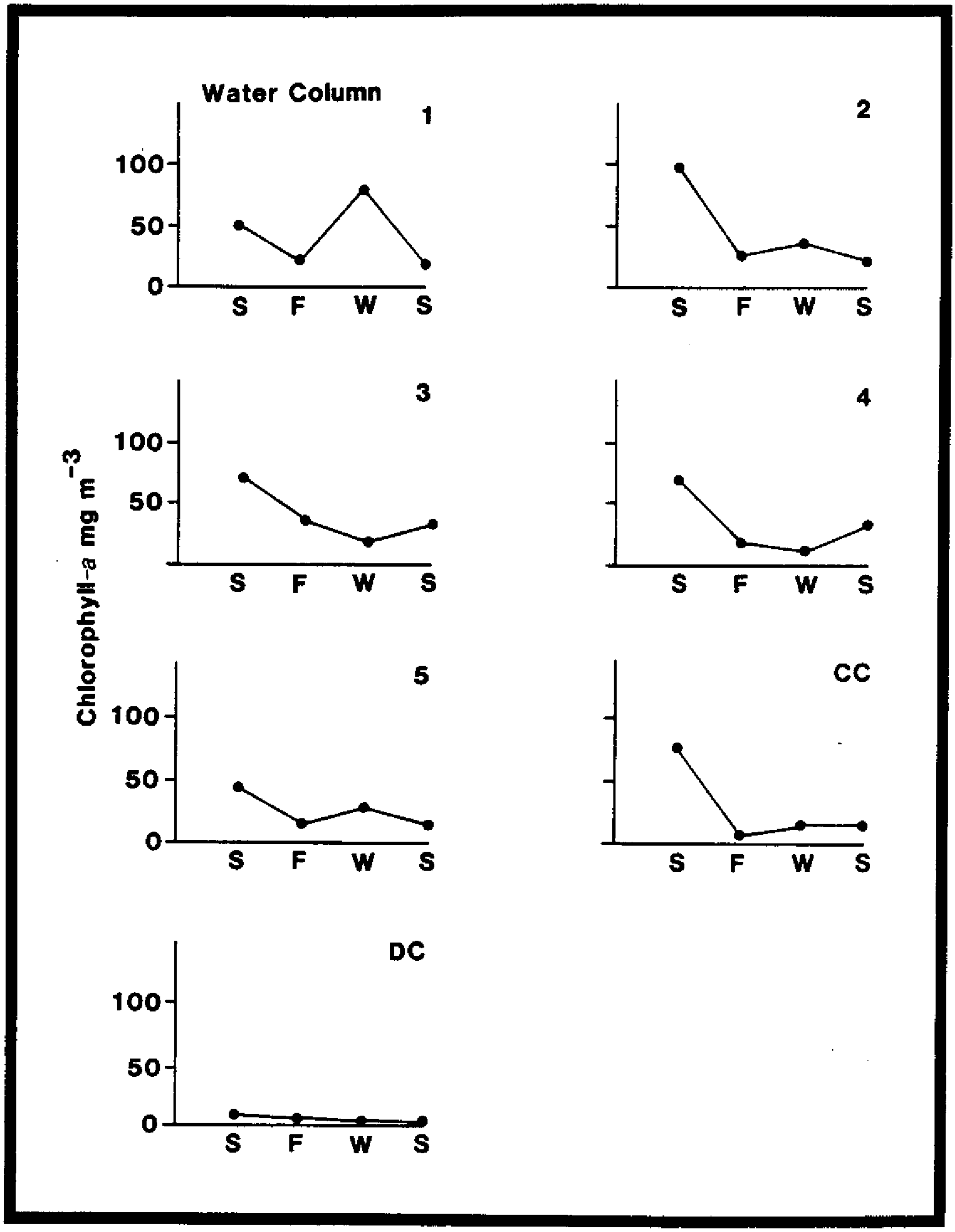

Figure 9.1 Seasonal variations in phytoplankton biomass (Chlorophyll-a) in Cat Island impoundments, Chainey Creek and Debidue Creek, North Inlet Estuary, SC.

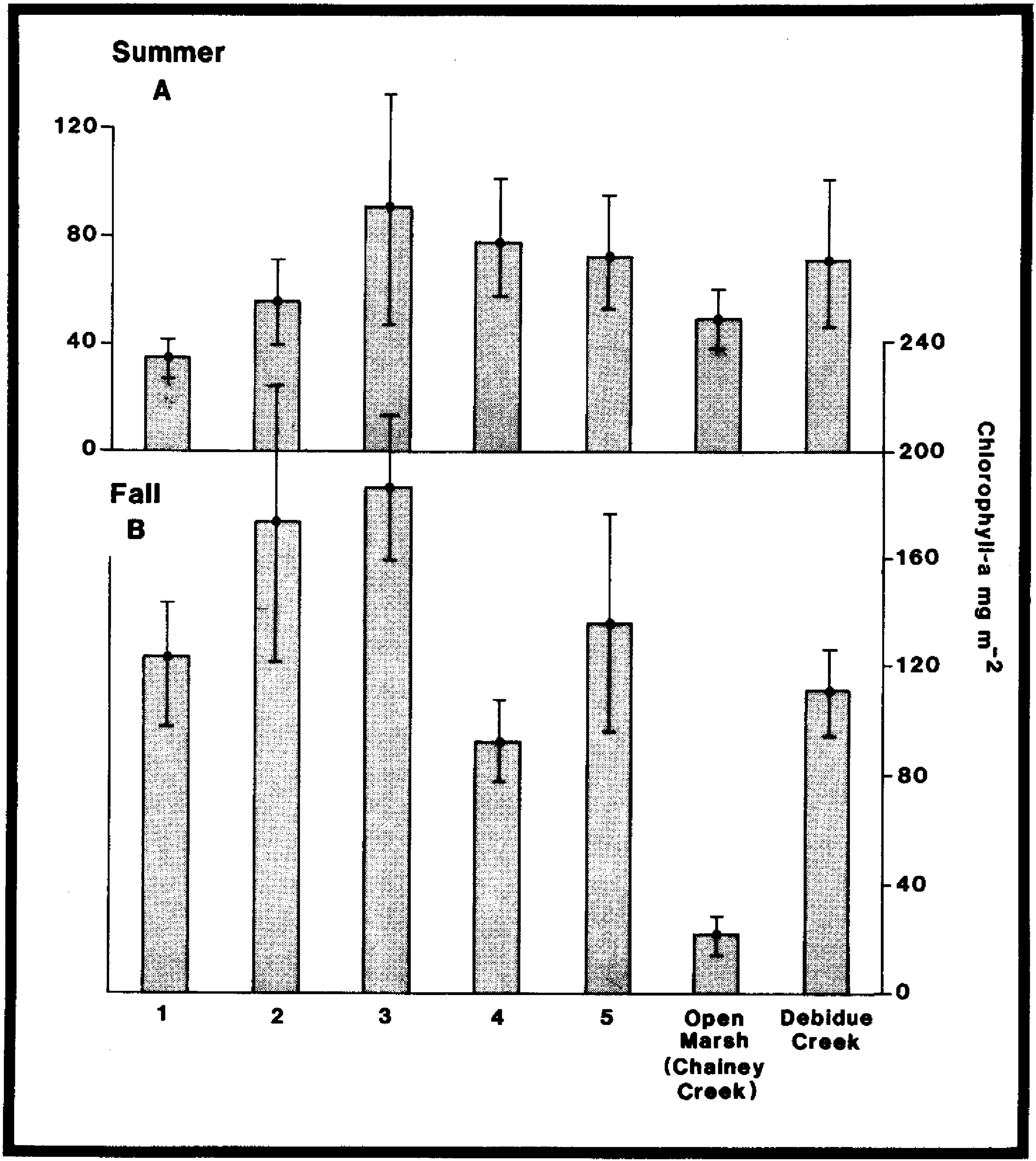

Figure 9.2a Within season comparisons of benthic microalgal biomass (Chlorophyll-a) at all sample stations. A = summer, B = fall. (Errors bars bracket the 95% confidence intervals.)

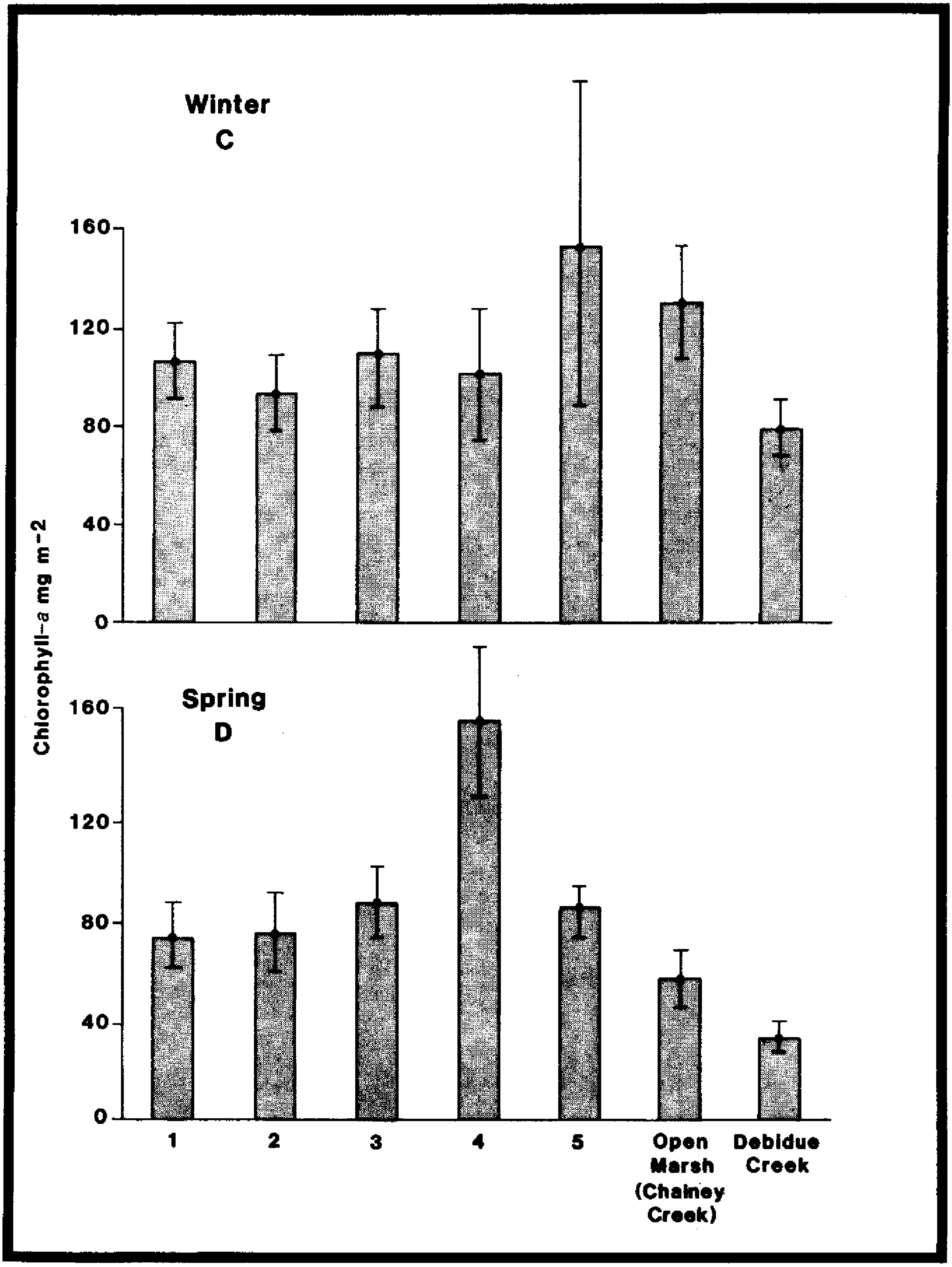

Figure 9.2b Within season comparisons of benthic microalgal biomass (Chlorophyll-a) at all sample stations. C = winter, D = spring. (Error bars bracket the 95% confidence intervals.)

concentrations of BCA varied from 22 ± 6 mg/m2 in Chainey Creek to 186 ± 28 mg/m^2 in unit 3 (Figs. 9.2 and 9.3). Highest values occurred in the spring, in unit 4 whereas those in Chainey Creek occurred in the winter (Fig. 9.3). Unit 3 had the highest average concentration of BCA during the year (118 mg/m^2), followed by unit 5 (112 mg/m^2), unit 4 (107 mg/m^2), unit 2 (100 mg/m^2), unit 1 (85 mg/m^2), Debidue Creek (77 mg/m^2) and Chainey Creek (63 mg/m^2). The values from units 2, 3, 4, and 5 were not significantly different from each other, nor were those from unit 1 and the two creek stations (ANOVA and multiple comparison test).

Concentrations of pheopigments in bottom sediments were generally similar to or higher than those of BCA in all impoundments and in Chainey Creek. Though they followed the same pattern of temporal variation as BCA, there was generally less spatial variability (Fig. 9.4). Pheopigments in Debidue Creek, however, were consistently only about one-tenth that of BCA (Figs. 9.3 and 9.4).

Benthic Microalgal Productivity

Seasonal variations in gross and net primary productivity and community respiration are summarized in Table 9.1. Daily gross production (DGP) varied during the study from 0.046 gC m^{-2} day^{-1} in unit 1 in the fall to 2.18 gC m^{-2} day^{-1} in Chainey Creek in winter. Measurements above 1 gC m^{-2} day^{-1} in at least three stations occurred at all seasons except the spring. No consistent seasonal patterns emerged from the data, however, though the wintertime was surprisingly productive. Highest values for the year were recorded in the winter in unit 5 and Chainey Creek (Table 9.1).

Daily net primary production (DNP) was negative most of the time but ranged from -0.964 gC m^{-2} day^{-1} in Debidue Creek in the fall to 1.44 gC m^{-2} day^{-1} in unit 5 in winter. Community respiration was generally higher in the fall and winter rather than in the summer (which we had expected). It ranged from 0.055 gC m^{-2} day^{-1} in the summer in unit 1 and in the spring in unit 4 to 2.79 gC m^{-2} day^{-1} in Debidue Creek in the fall.

Quarterly gross and net productivity (QGP and QNP) were extrapolated from daily values. QGP ranged from 4.18 gC m^{-2} day^{-1} in unit 1 in

Table 9.1 Summary of primary productivity and community respiration. DGP = daily gross productivity, DNP = daily net productivity, QGP = quarterly gross productivity, QNP = quarterly net productivity, DR = daily respiration. Measures of productivity are in g C m^{-2}.

Station	DGP	DR	DNP	QGP	GNP	DGP	DR	DNP	QGP	QNP
	SUMMER 1984					WINTER 1984				
Pond 1	Note 1	0.552	--	--	--	1.490	1.230	0.260	136.0	23.8
Pond 2	1.14	0.496	0.640	103.0	58.2	0.352	0.790	-0.438	32.0	-39.8
Pond 3	Note 1	0.202	--	--	--	0.214	0.698	-0.484	19.5	-44.0
Pond 4	1.21	1.380	-0.167	110.0	-15.2	Note 1	0.386	--	--	--
Pond 5	--	--	--	--	--	1.860	0.413	1.440	169.0	131.0
Chainey Cr.	Note 1	0.184	0.00	--	--	2.180	0.771	1.410	198.0	128.0
Debidue Cr.	1.05	0.0	1.050	95.6	95.6	Note 2	--	--	--	--
	FALL 1984					SPRING 1985				
Pond 1	0.046	0.716	-0.672	4.18	-61.0	0.175	0.220	-0.045	15.9	-4.17
Pond 2	Note 3		--	--	--	-0.129	0.606	-0.477	11.7	-43.50
POND 3	1.24	1.880	-0.638	113.0	-58.1	0.615	0.698	-0.083	56.0	-7.52
Pond 4	1.49	0.955	0.534	135.0	48.5	0.478	0.055	0.423	43.5	38.40
Pond 5	0.514	0.992	-0.478	46.8	-43.5	0.872	0.569	0.303	79.4	27.60
Chainey Cr.	1.00	1.410	-0.413	91.1	-37.6	0.230	0.514	-0.286	20.9	-25.90
Debidue Cr.	1.83	2.790	-0.964	166.0	-87.7	Note 4	--	--	--	--

Notes:
1. Net hourly production was more negative than hourly respiration.
2. Oxygen increased in dark chambers.
3. Respiration of control chambers without cores was greater than that in chambers with cores.
4. Oxygen increased in dark chamber.

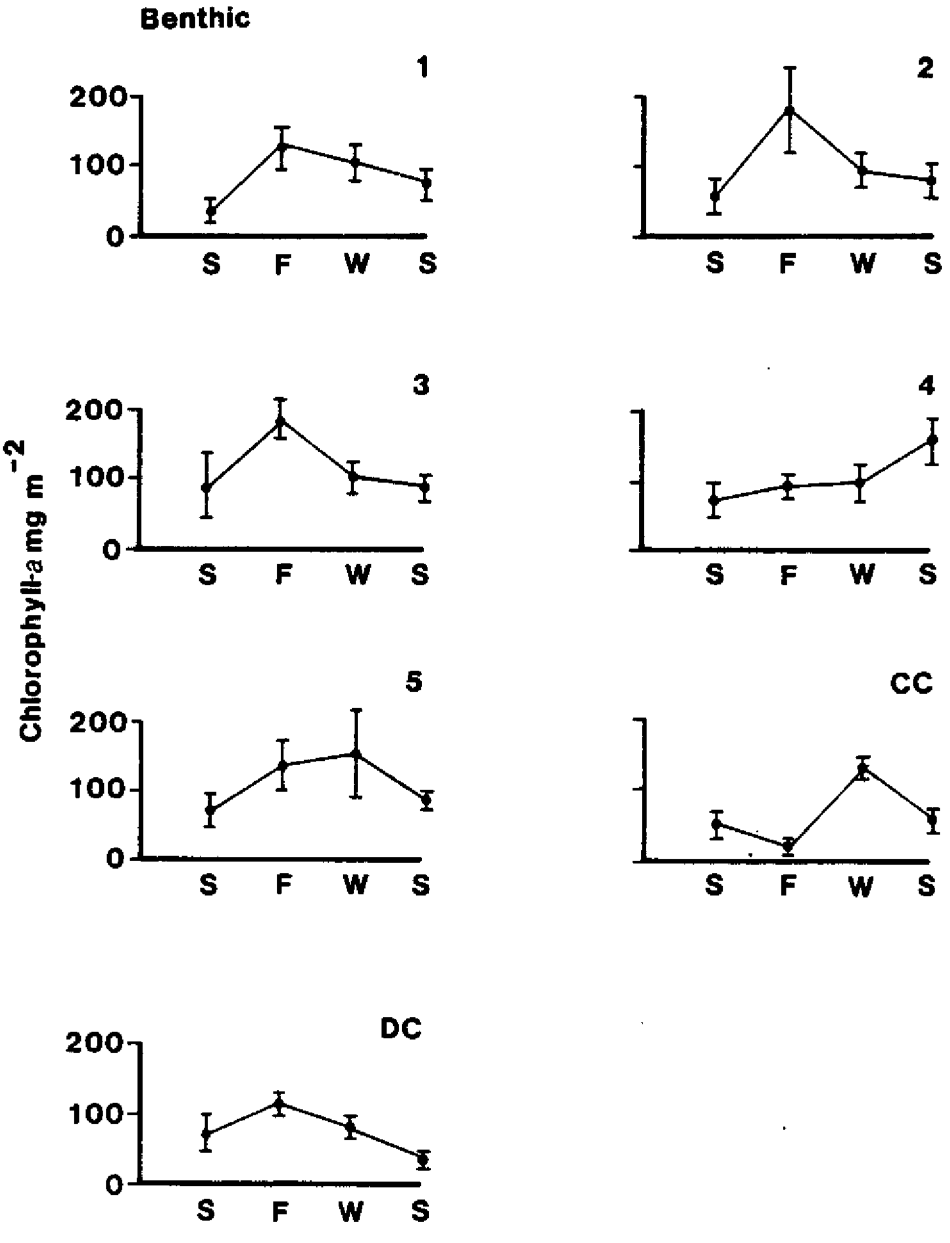

Figure 9.3 Seasonal variations in benthic microalgal biomass (Chlorophyll-a) at each station. (Error bars bracket the 95% confidence intervals.)

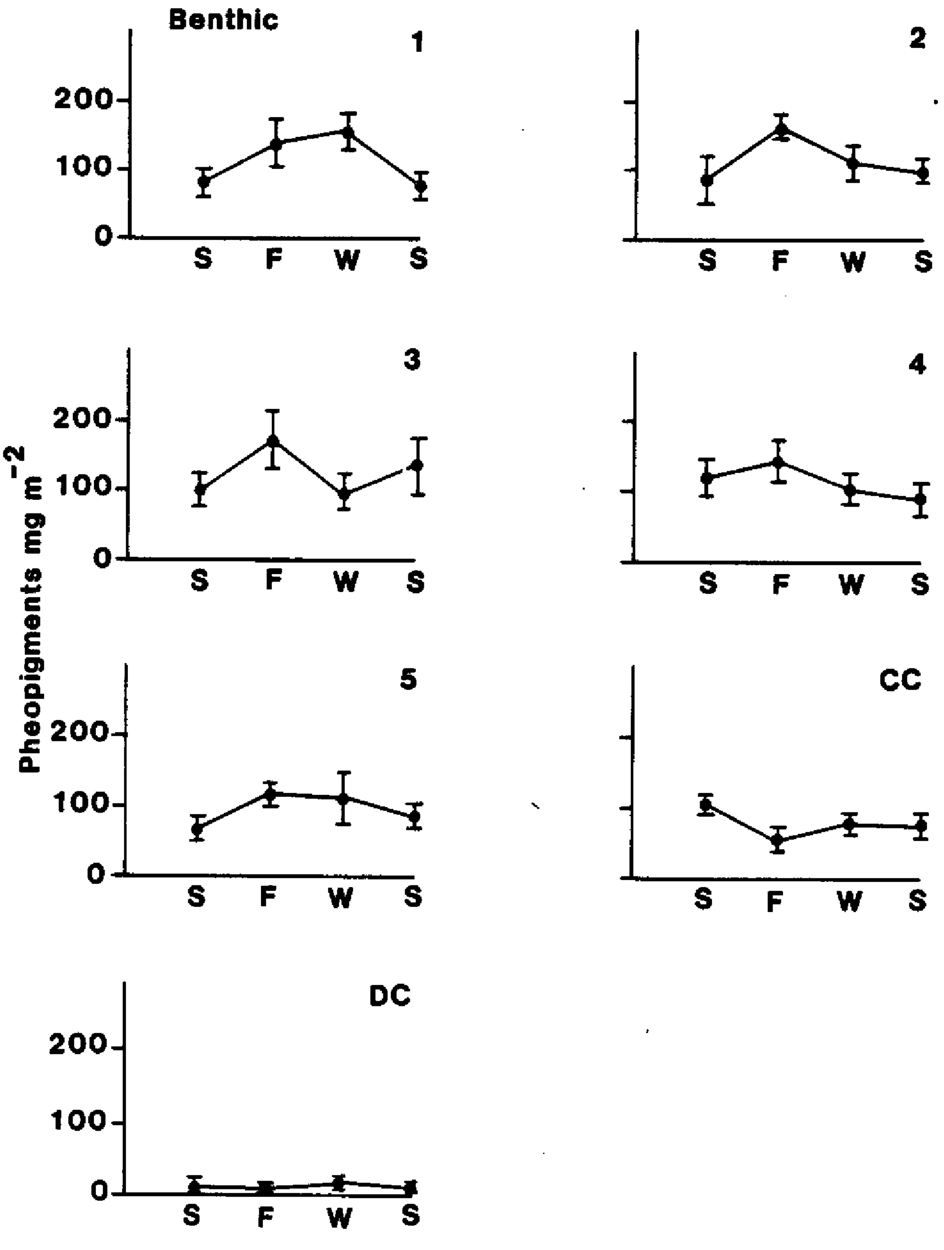

Figure 9.4 Seasonal variations in benthic microalgal pheopigments at all sample stations. (Error bars bracket the 95% confidence intervals.)

fall to 136 gC m-2 day-1 also in unit 1 but in the winter. QNP ranged from -87.7 gC m^{-2} day^{-1} in Debidue Creek in the fall to 95.6 gC m^{-2} day^{-1} also in Debidue Creek but in the summer.

Irregularities in the data as noted in Table 9.1 were generally associated with water or air leaking into the recirculating incubators. On some occasions during or after incubating we found that the presence of oxygen bubbles in the chambers or the intrusion of low-salinity cooling water into the recirculating system significantly affected the results. On such occasions, we discarded the data.

Although Riznyk et al. (1978) reported data on the productivity of BMA in a large, impounded marsh in southern California, our preliminary research represents the only reported data on the biomass and productivity of the BMA of small coastal impoundments in the Atlantic. Other studies have focused on salt marshes, shallow bays, river estuaries, and open coastal marine habitats. The values of biomass of the BMA, here reported as benthic chlorophyll-a (BCA), fall generally within the ranges reported on a square-meter basis by others (see recent reviews and comparisons by Colijn and de Jonge, 1984; Varela and Penas, 1985). The spatial variability (i.e., patchiness) of the BCA was found to be wide on occasions (Figs. 9.2 and 9.3). This appears to be typical of other benthic areas, where two to ten fold differences in BCA concentrations are not uncommon (Van den Hoek et al., 1979; Colijn and de Jonge, 1984). Impoundments 2, 3, 4, and 5 had the highest average values of BCA during the study. The only obvious differences seen between these impoundments and unit 1 that might explain why unit 1 supported a lower benthic microalgal biomass is that the depth of the overlying water in unit 1 was consistently about 10 cm deeper than the other ponds. This increased depth in turbid water would absorb significant irradiance. This factor alone, by reducing the amount of light energy reaching the bottom, could account for reduced growth of microalgae and thus reduced BCA.

Pheopigments form as the result of the breakdown of chlorophyll-a due to poor growing conditions, cell death, and/or active grazing. Concentrations of pheopigments in the impoundments and in Chainey Creek were significantly higher than those found in Debidue Creek. This is probably due to the increased dilution of the water in Debidue Creek caused by frequent tidal flushing and export. Chainey Creek is also influenced by the tides, but perhaps the movement of water is more of a back-and-forth sloshing or seiche effect than of a net flux of water out of the creek. Another possibility might be that pheopigments are exported from the impoundments into Chainey Creek but not into larger tidal creeks downstream.

Primary productivity of the BMA in the impoundments seems to be largely controlled by light. In experiments using neutral-density filters, maximum photosynthesis (P max) was always measured at irradiance levels above 1000 uEi m^{-2} sec $^{-1}$. Such irradiances seldom reach the bottom of the ponds (only in winter), because the turbidity of the overlying water during other times of the year acts as an extreme attenuating filter. Phytoplankton cells thus receive more light than their benthic counterparts and produce more biomass. At all stations it was shown that trends of PCA and BCA were more-or-less inversely proportional. Thus when PCA is high, BCA is low, and vice versa. Debidue Creek samples consistently had lower PCA concentrations than that in other stations (Fig. 9.1 to 9.3).

Neither DGP nor DNP was strongly correlated with BCA (r^2 =.18 and .11, respectively). This is contrary to what is generally true with estuarine phytoplankton (Zingmark and Satcher, in preparation) but is in agreement with what is commonly reported for the BMA (e.g. Davis and McIntire, 1983), although see also Shaffer and Onuf (1983).

CONCLUSIONS

An objective of this study was to determine whether the BMA contributed significantly to the productivity of the impoundments. Based on the hourly and daily estimates reports above, it is reasonable to assume that the BMA in the impoundments produced as much or more than in other geographical locations. As the BMA are known to contribute up to three times the productivity of phytoplankton in some coastal ecosystems (Marshall et al., 1971), they should be significant producers in the Cat Island impoundments. The benthic meiofauna, which abound in the impoundments (see Chapter 12), largely feed on BMA (Montagna et al., 1983; Montagna, 1984). The meiofauna, in turn, are fed on by macrofauna such as penaeid shrimp and other demersal invertebrates and vertebrates. A more-rigorous sampling effort is required before their true significance can be determined.

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Chapter 10

Summary and Comparison of Component Productivities

B. J. Kelley, H. N. McKellar, and R. G. Zingmark

A basic trade-off in the impoundment of coastal wetlands in South Carolina is that between an open intertidal habitat, where primary production is dominated by emergent vegetation, and an impounded aquatic habitat, where primary production is dominated by submerged macrophytes, benthic algae, and phytoplankton. In this chapter we have attempted to quantify this trade-off by making comparisons between the impoundment and tidal-marsh systems by pooling the contributions of their component communities to get an estimate of total system primary production.

To compare the three plant communities and ecosystems, we have converted all production estimates to grams of carbon per square meter per interval and macrophyte net productivity to gross productivity by using conversion factors available in the literature. System comparisons, then, are of estimated gross primary productivity in grams of carbon per square meter per year.

The comparison of system productivity using these calculations is shown in Table 10.1. Several points and assumptions need to be stated to explain the table. Production data used in the calculations was for the 1983 growing season for macrophyte and phytoplankton components and the 1984 growing season for impoundment microbenthic algae. Impoundment production values and community areas are pooled from all five study impoundments. The tidal marsh in the comparison is the tidal impoundment (unit 6) in Fig. 7.1. No direct measurements of BMA productivity were made in the vegetated portion of the tidal marsh. Using an estimate of

Table 10.1 Comparison System Productivity for Impoundments and Tidal Marsh

IMPOUNDMENTS		TIDAL MARSH	
MACROPHYTES			
SPECIES	COMMUNITY AREA X PG ($g\ C\ m^{-2}\ yr^{-1}$)	Species	COMMUNITY AREA X PG ($g\ C\ m^{-2}\ yr^{-1}$)
S. alterniflora	58,258,164	*S. alterniflora*	37,415,874
S. cynosuroides	50,781,743	*S. cynosuroides*	45,046,733
S. robustus	5,470,760	*S. robustus*	3,653,502
S. validus	2,095,263		
Distichlis	6,939,660		
Ruppia	86,224,012		
Typha	1,790,162		
TOTAL MACROPHYTE P_G	= 211,559,764 $g\ C\ yr^{-1}$	TOTAL MACROPHYTE P_G	= 86,116,109 $gC\ yr^{-1}$
PHYTOPLANKTON			
(Total Phytoplankton P_G = P_G $g\ C\ m^{-2}\ yr^{-1}$ x Community Area)			
P_G	= 208 $g\ C\ m^{-2}\ yr^{-1}$ x 129,434 m^2	P_G=0	
TOTAL	= 26,922,272 $g\ C\ yr^{-1}$		
BENTHIC MICROALGAE			
[TOTAL BMA P_G	= TOTAL FOR FLATS + 18% MACROPHYTE P_G (POMEROY AND WEIGERT, 1981]		
P_G FOR FLATS	= 312 $g\ C\ m^{-2}\ yr^{-1}$ X 129,434 m^2		
	= 40,383,408 $g\ C\ yr^{-1}$	P_G	= 18% X MACROPHYTE P_G
18% MACROPHYTE P_G	= 38,080,758 $g\ C\ yr^{-1}$		= 0.18 x 86,116,109 $g\ C\ yr^{-1}$
TOTAL	= 78,464,166 $g\ C\ yr^{-1}$		= 15,500,900 $gC\ yr^{-1}$
POOLED COMPONENTS			
GRAND TOTAL P_G	= 316,946,202		101,617,009
TOTAL AREA	= 244,180 m^2		78,671 m^2
AVERAGE P_G/m^2	= 1,298 $g\ C\ m^{-2}\ yr^{-1}$		1,292 $g\ m^{-2}\ yr^{-1}$

BMA productivity from Pomeroy and Weigert (1981) for vegetated areas, we added 18% of the macrophyte productivity to our macrophyte estimate to account for BMA productivity in the emergent plant-covered area of both the impoundments and tidal marsh. The impoundments had an additional BMA component added from measured values for the _Ruppia_ flat areas. A phytoplankton contribution was added only for the _Ruppia_ flat area of the impoundments, on the assumption that phytoplankton productivity was negligible beneath the emergent vegetation canopy of both impoundments and tidal marsh.

Based on these assumptions and calculations, Table 10.1 shows the two systems to be remarkably similar in their total primary productivity. The percentage distribution of primary productivity among production components is shown in Table 10.2. It appears that lower levels of macrophyte productivity in impoundments are offset by increased contributions from the BMA and phytoplankton in the impoundments. The comparison seems to suggest that when nutrient levels and physical conditions in two or more systems are similar, there will be a fixed rate of total primary production regardless of the growth form or species composition of the vegetative communities involved. The system values (Table 10.3) are similar to estimates of gross production for medium _Spartina_ marsh in North Carolina (calculated from Blum et al., 1978) and for salt marsh in New York (calculated from Houghton and Woodwell, 1980). They are lower than system values calculated for salt marsh in Georgia (Pomeroy and Wiegert, 1981).

Table 10.2

Distribution of primary productivity among components.

IMPOUNDMENT					TIDAL MARSH	
%	gC m^{-2} yr^{-1}				%	gC $m^{-2} yr^{-1}$
67%	866	-	Macrophytes	-	85%	1095
25%	110	-	Microbenthic Algae	-	15%	197
8%	321	-	Phytoplankton	-	--	--

In summary, two general conclusions based on these pooled comparisons can be made: (1) impoundment system productivity is quantitatively similar to tidal marsh system productivity at Cat Island and at some other locations along the East Coast of the United States; and (2) the contribution of the aquatic community (BMA, phytoplankton, and submerged macrophytes) to system productivity is greater in impoundments than in tidal marsh and has compensated for the lower productivity of some impoundment macrophyte species.

Table 10.3

Comparisons of annual system metabolism within the impoundments versus annual intertidal system metabolism in representative salt marshes (gC $m^{-2}yr^{-1}$).

SYSTEM	GROSS PRODUCTION	REFERENCE
Coastal impoundment, South Carolina	1,298	This study
Tidal impoundment, South Carolina	1,292	This study
Salt marsh, North Carolina	(T) 1,546 (M) 1,212 (S) 604	Calculated from Blum et al., 1978
Salt marsh, New York	1,340	Calculated from Houghton & Woodwell, 1980
Salt marsh, Georgia	(T) 2,700* (S) 1,700*	Pomeroy & Wiegert, 1981

T = Tall, M = Medium, S = Short _Spartina_

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* These values represent the sum of _Spartina_ productivity plus gross benthic algal productivity. There is some uncertainty whether the values for _Spartina_ were gross or net productivity.

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SECTION V

PLANKTONIC COMMUNITY

Chapter 11

Microzooplankton Abundance

A. K. Taniguchi

INTRODUCTION

It is now widely accepted that coastal wetlands are among the most productive natural ecosystems in the world. This acceptance may be questionable (Nixon, 1980). In part, this accepted view has been fostered by papers such as those by Teal (1962), Odum and de la Cruz (1967), Pomeroy et al. (1967), and Odum (1968) which dealt with organic detritus and nutrients (carbon, nitrogen, and phosphorus). From reports such as these developed a nursery area paradigm that intertidal wetlands and estuaries supply the organic and inorganic nutrients that support much of the primary and secondary production, making the waters in these locales nursery areas for many species of coastal marine fish (Nixon, 1980). But Nixon (1980) believed this nursery zone paradigm to be unsupported by direct measurement data. His evaluation was that there is no clear-cut correlation between year-class recruitment of commercially important fish and shellfish (as reflected by commercial landing statistics) and the extent of presumed nursery areas (salt marshes and estuaries).

Studies have attempted to describe salt marshes and marsh tidal creeks as primary nursery habitats for many species of larval, and in particular, juvenile marine fish (Weinstein, 1979). Yet, they failed to address the difficult issue of how year-class strength may be determined, particularly for fish larvae. There is a need to quantify, if possible, the relationship between a presumed nursery area and subsequent fish recruitment to the adult population in order to declare a marsh tidal creek, salt marsh, or estuary a fish nursery area. One important element to the concept of a fish nursery area is the microzooplankton density in the presumed nursery areas.

Fish populations of commercially and recreationally caught species are determined by a balance between population increases due to both recruitment and growth and losses (deaths) due to natural and fishing mortality. The population size may vary in a density-dependent or density-independent manner (see Jones and Hall, 1973; Cushing, 1974, 1975; Harris, 1975; Ware, 1980; Gulland, 1983). Density-dependent means there is a direct relationship between the adult population size (biomass or numbers) and population growth per unit size (e.g., recruitment of young per adult). Density-independent means that there is no relationship (e.g., physical factors are considered to have a density-independent influence because their effect on the population is the same regardless of population size). Biological mechanisms controlling populations are usually density-dependent. The density-dependent relationship referred to in this study is that which may exist between micro- and mesozooplankton and larval marine fish that depend on them for prey in salt-marsh areas.

This study's objective was to document and compare the microzooplankton and mesozooplankton standing crops in five managed salt-marsh impoundments and a marsh creek that was the common tidal saline water source for the impoundments and an adjacent shallow undisturbed salt marsh. Two null hypotheses of interest during this zooplankton study were: (1) There was no difference in microzooplankton standing crop between the five managed marsh impoundments and the tidal creek of an undistrubed marsh, and (2) There was no significant effect of months on zooplankton standing crop between the marsh impoundments and the tidal creek.

The first null hypothesis would indicate which of the six environments (the five managed impoundments and the undisturbed tidal marsh creek) might sustain the denser concentration of larval fish food. By comparing the measured microzooplankton concentrations of this study with the published accounts of prey concentrations required by larval fish in laboratory and field experiments, and those prey concentrations measured in coastal and oceanic environments, some comparisons or contrasts between marsh environments might be reached regarding their value to larval fish survival. The second null hypothesis might reveal if zooplankton densities in managed wetland impoundments were not greatly influenced by seasons, whereas significant seasonal differences in zooplankton densitites were expected to occur in the undisturbed, unmanaged tidal marsh creek environment. The densities of the zooplankton size fractions known to be required by first-feeding and young larval fish younger than 25 days after hatching (Houde & Taniguchi, 1979) were of particular interest to this study. If the five salt-marsh impoundments and the tidal marsh creek (open marsh) constituted a larval fish nursery area, then naturally occurring zooplankton densities might provide a clue of any food resource nursery role advantage for fish larvae and postlarvae in the managed salt-marsh impoundments or the undisturbed open marsh.

This study should be viewed as a beginning in the effort to provide baseline data for coastal wetlands microzooplankton and mesozooplankton standing crops in South Carolina. In general, metazoan microzooplankters have not been studied intensively in coastal wetland aquatic environments, particularly with respect to the importance of microzooplankton densities to marine fish larvae survival and growth. Miglarese and Sandifer (1982) noted that no detailed studies of zooplankton in estuarine impoundments of South Carolina had been accomplished up to the time of their review, and they could only speculate on the dynamics of mesozooplankton (200 µm to 2 mm, Omori and Ikeda, 1984) populations in coastal brackish ponds and the potential value of these populations to fish and crabs. Allen et al. (1982) and Allen et al. (1984) included zooplankton in their ecological characterization of Winyah Bay, South Carolina, but they utilized 153 µm-mesh plankton nets and could not quantitatively sample the microzooplankton fraction (20 to 200 µm, Omori and Ikeda, 1984).

If any extrapolations of data or conclusions are to be made regarding the nursery area role of small impoundments or open marshes to the typical larval marine fish, one must be ever mindful that until fish larvae complete their metamorphosis to juveniles, they are dependent on microzooplankton and small mesozooplankton. Nauplier to adult stages of copepods are the typical food of marine fish larvae (Hunter, 1981). Hunter (1980, 1981) has reviewed much of the marine larval fish and fish early life history studies of the past two decades concerning the importance of larval fish mouth size, prey size, nutritive value of different prey sizes, and larval fish-to-prey density relationships. These studies sought data on both fish early life history and stock recruitment to confirm another paradigm attributed to Hjort (1914). Hjort stated the critical period hypothesis that attributed fish year-class recruitment failures of commercially harvested species to starvation at the time of complete yolk-sac absorption. Conclusive data to support any type of critical period as a determinant of year-class strength has not yet been obtained after decades of research (Hunter, 1982).

METHODS

Zooplankton sampling gear was selected after sampling trials and consideration of reported zooplankton behavior. Water bottles, high-volume pumps, and unproven zooplankton net-sleds to be hauled by electric- or gas-powered winches were considered and rejected as sampling gear because of problems of practicality or problems due to: excessive zooplankton avoidance; excessive clogging of gear; irregular and very soft mud bottoms of managed impoundments; emergent aquatic vegetation on the impoundment beds (beds were never deeper than about 50 cm and were seasonally exposed to the atmosphere during water drawdown periods); resuspension of sediment, organic debris, and detritus when the very shallow pond bed water column was disturbed; and the interference to other impoundment researchers caused by disruptive zooplankton sampling techniques.

Micro- and mesozooplankton were collected monthly by outboard-boat and surface-towed plankton nets from the borrow ditches along the inside perimeter of all five impoundments (units 1 - 5) and the main channel of the tidal marsh creek (Chainey Creek). Zooplankton sampling was confined to transects within the impoundment perimeter borrow ditches because of the shallow water depths (<50 cm) during the months when the five impoundments were drained for waterfowl management. A towing transect was established in all impoundments along the Chainey Creek levee (see Chapter

4). Still, several sites were too shallow to be sampled during the months of March, April, and December.

The plankton nets were 30 cm in diameter in two mesh sizes; 53 µm mesh and 153 µm mesh. These nets were conical-cylindrical, designed with a length-to-net opening ratio of 7:1 to maximize net surface area and constructed entirely of the same mesh size for the cylindrical and conical sections. The configuration and length-to-opening ratios were identical to plankton nets used by Allen et al. (1982) and Allen et al. (1984) in their studies of Winyah Bay, South Carolina. (Dr. Stephen Stancyk, Belle W. Baruch Institute, Columbia, South Carolina, has filed construction specifications of the 7:1 ratio plankton nets with Ernest E. Case, Andover, New Jersey). A General Oceanics, Inc. Model 2030 flowmeter was affixed slightly off-center at the net opening. Timed surface net tows were of 1.5 to 2 min duration, with the net opening within 5 to 10 cm of the water surface. Replicate zooplankton tows were made along the transects with the 53-µm-mesh and 153-µm-mesh nets for an analysis of between-tow variability. Plankton net tows in extremely shallow water obviously agitate the water column and disturb bottom sediments and organic debris. Some evaluation of between-tow variability was desired. Logically, to minimize sediment and detritus in samples, the 53-µm-mesh net was always towed first.

Surface and bottom water temperatures and salinities were recorded from Impoundments 1-5 and Chainey Creek prior to the 53-µm-mesh plankton net tow. Zooplankton collections were generally scheduled for the full moon phase. This was about the same lunar phase when Dr. McKellar (refer to Chapters 6 and 8) collected dissolved nutrient and phytoplankton data and it was desirable to collect zooplankton data in the same approximate time frame. Because this lunar phase produces the highest tides of the lunar month, these higher tides allowed entry to the project site via the Intracoastal Waterway, Santee Bay, the open marsh, and Chainey Creek, and it facilitated the portage of a large john boat, outboard engine, and equipment over the levees separating all impoundments and Chainey Creek. The higher tides provided about 50-cm water depths in each impoundment perimeter borrow ditch parallel to the Chainey Creek levee (see Fig. 4.2).

Zooplankton samples were immediately fixed in 20% formalin as they were collected in the field. Rose Bengal stain was added to the samples in the laboratory. This stain was readily taken up by zooplankton. It facilitated the visual separation of organisms from fine sediment, detritus, and organic debris and the identification of zooplankton species. Samples were split if a preliminary count revealed very high zooplankton concentrations. Zooplankton in 1-ml aliquot subsamples were sorted by taxa and counted with a Wild Model M5 binocular dissection scope equipped with an ocular micrometer. Zooplankton in additional 1-ml aliquots were sorted until about 400 were counted in each tow sample. Copepoda were identified to species when possible because they are the primary prey for first-feeding marine fish larvae until the larvae begin to metamorphose into juveniles.

The zooplankton data were archived in the Belle W. Baruch Institute for Marine Biology and Coastal Research's full-screen managed computer library at the Baruch Institute Marine Laboratory in Georgetown, South Carolina.

A SAS General Linear Models (GLM) procedure was used to analyze the 15 months of data collected from the five impoundments and creek.

RESULTS AND DISCUSSION

Appendix Table 14.1 lists the surface and bottom water temperatures and salinities recorded from the five managed impoundments and Chainey Creek at the time the zooplankton samples were collected. An analysis of variance (ANOVA) showed no significant difference ($P = .05$) between the surface and bottom water temperatures and salinities for the impoundments and the creek; the data are pooled in Figs. 11.1 and 11.2 to show the seasonal trends. ANOVA also showed there was no significant difference in water temperature or salinity among sites.

All the taxa identified during the course of this investigation are listed in Table 11.1 and Appendix Table 11.2. Presence and densities were recorded for most taxa. Hydromedusae and ctenophores were noticed to be very abundant in some impoundments in late spring and summer as water salinity approached that of full-strength seawater. Oligochaetes, cladocerans, ostracods, and insect larvae were occasionally observed in samples during February through April, when the waters tended to be fresh (Fig. 11.2).

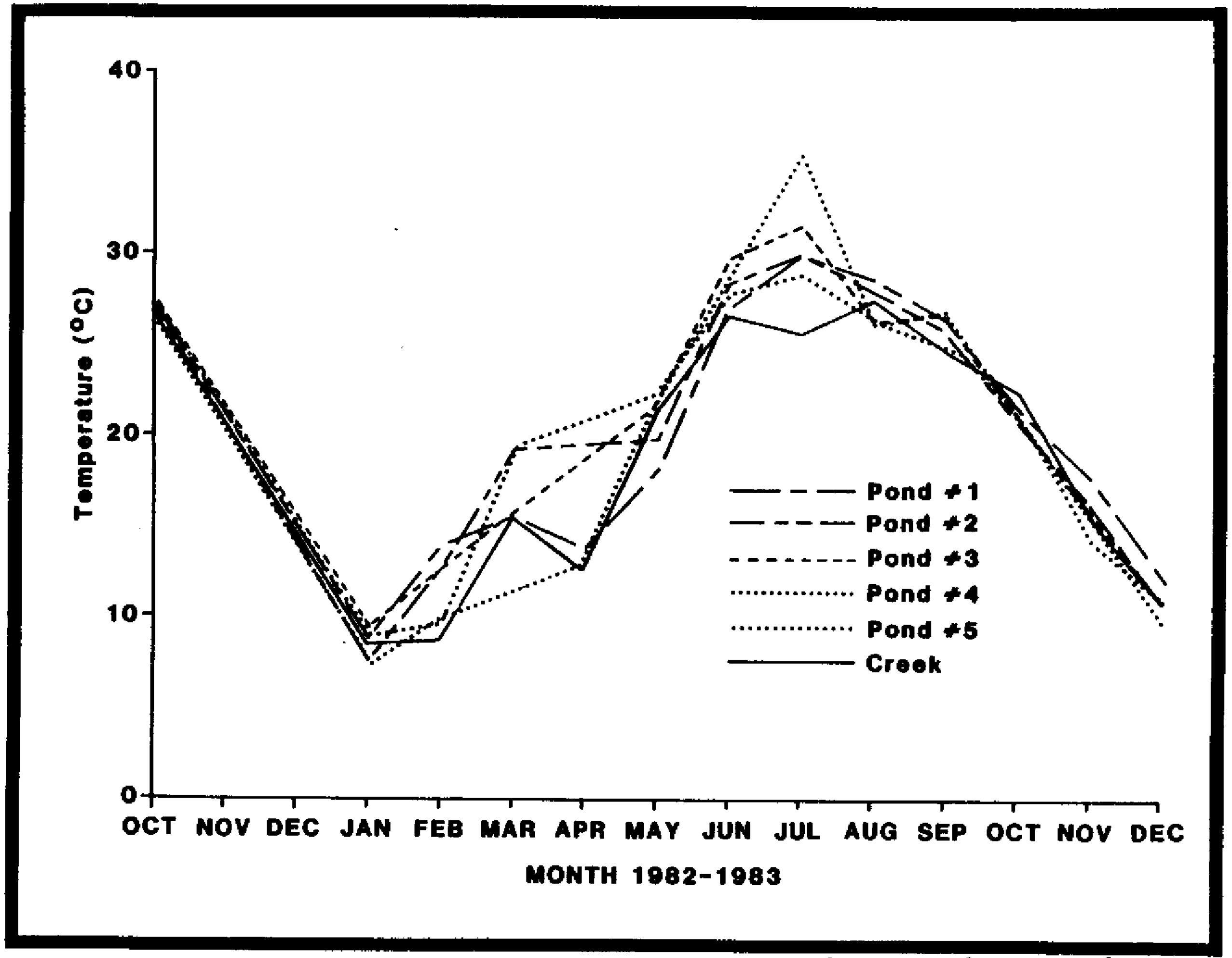

Figure 11.1 Mean water temperature for the five study impoundments and Chainey Creek. At each site, surface and bottom water temperatures were not significantly different.

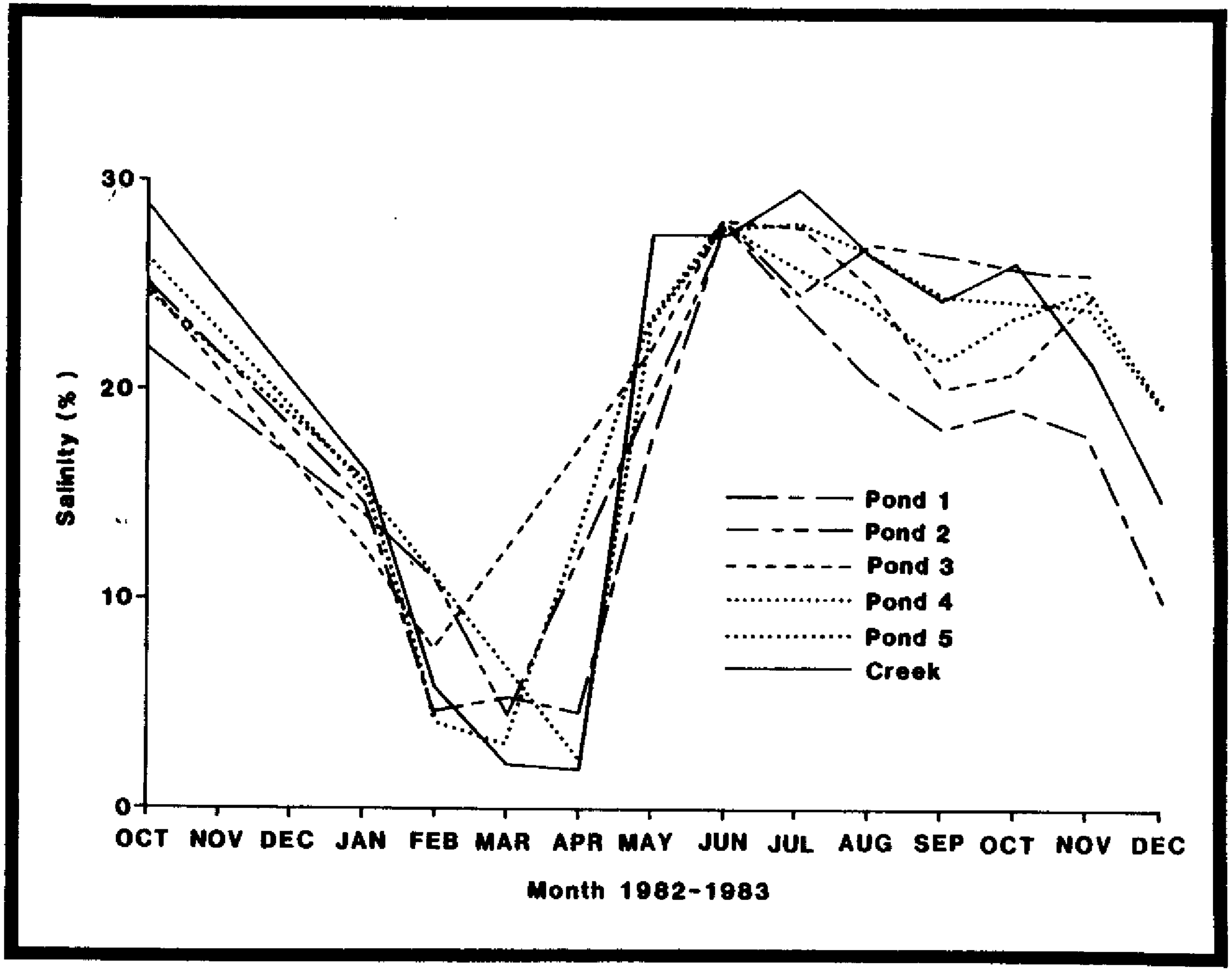

Figure 11.2 Mean water salinities for the five study impoundments and Chainey Creek. At each site, surface and bottom salinities were not significantly different.

Table 11.1

Taxa and species identified in zooplankton samples known to be consumed by marine fish larvae.

- Ciliata
  - Tintinnida
- Rotifera
- Copepoda
  - Calanoida
    - *Paracalanus* spp.
    - *Pseudodiaptomus coronatus*
    - *Eurytemora affinis*
    - *Centropages hamatus*
    - *Centropages furcatus*
    - *Labidocera aestiva*
    - *Acartia tonsa*
    - *Parvocalanus crassirostris*
    - Unidentified calanoids
    - Unidentified nauplii
- Copepoda (continued)
  - Cyclopoida
    - *Oithona colcarva*
    - *Oithona* spp.
    - *Tropocyclops* spp.
    - *Halicyclops* spp.
    - *Microcyclops* spp.
    - *Saphirella* spp.
    - *Cyclops* spp.
    - Unidentified cyclopoids
    - Unidentified nauplii
- Harpacticoida
  - *Enterpina acutifrons*
  - *Tisbe* spp.
  - Unidentified harpacticoids
  - Unidentified nauplii
- Cirripedia (Barnacle nauplii and Cyprids)

Calanoid copepods were the dominant copepod taxon. Acartia tonsa was the most important species because (1) it was most abundant under euryhaline and seawater salinity conditions, (2) it was found in all five impoundments and Chainey Creek, and (3) it numerically dominated the copepod fraction of the 53-µm-mesh and 153-µm-mesh net samples. Cyclopoid copepods were encountered mainly during the very late winter and very early spring, when fresh or very-low-salinity conditions existed in the impoundments and the creek. Harpacticoid copepods were most abundant in zooplankton samples during low-water-level or water-drawdown periods. These were periods when the towed zooplankton nets were sampling in water depths of 50 cm or less. Harpacticoid copepods are demersal or benthic in habit and, hence, are most likely to be collected during low-water-level periods when the impoundments are being managed to encourage the germination of aquatic plants to be consumed by waterfowl. On the basis of total metazoan microzooplankton counted per unit volume, analysis revealed that 98% of the variability in the microzooplankton standing crop could be explained by differences among months and sites of collection (Table 11.2).

Analysis of the annual mean total 53-um-mesh zooplankton standing crop utilizing the Student-Newman-Keuls (SNK) multiple range test revealed that across all sampling sites microzooplankton were significantly more abundant in August, and possibly September, than in any other month of the year. Furthermore, annual microzooplankton standing crops in impoundments 3, 4, and 5 tended to be alike, whereas those for impoundments 1 and 2 and the creek tended to be alike. There was no significant difference between replicate net tows (Table 11.3). Replicate tows were pooled and the mean values were plotted in Fig. 11.3. Only about 12% of the standing crop variability could be explained because of impoundment differences (Table 11.4). Thus these analyses indicated that around 86% of the variability was due to seasons (months).

Microzooplankton taxa known to be utilized as food by marine fish larvae were plotted after replicate tows were pooled (Figs. 11.4-11.8). These taxa of interest were the copepods (adults, copepodids, and nauplii), rotifers, barnacle nauplii, and the protozoan taxon Tintinnida.

ANOVA analysis and SNK multiple range testing of the microzooplankton fraction (53-um-mesh net) copepod nauplii, Acartia tonsa, rotifers,

Table 11.2 SAS GLM analysis summary for total numbers of zooplankton per unit volume collected with the 53 um-mesh net. Sampling dates were nested within sampling sites. Dependent variable = total number of zooplankton.

Source	DF	Sum of Squares	Mean Square	F-Value	PR>F	R-Square	Coeff. Var.
Model	70	95130×10^9	1359×10^9	53.21	0.0001	0.981	41.04
Error	71	1813×10^9	25×10^9				
Corrected total	141	96943×10^9					

Source	DF	Type I SS	F-Value	PR>F	DF	Type III SS	F-Value	PR>F
Pond and creek	5	11149×10^9	87.31	0.0001	5	11149×10^9	87.31	0.0001
Date nested within Pond and creek	65	83981×10^9	50.59	0.0001	65	83981×10^9	50.59	0.0001

Table 11.3

Summary of the GLM-SNK analysis of annual microzooplankton standing crops according to sampling dates, sampling sites, and net tow replicates. The letters A and B indicate standing crop means that were significantly different at the .05 level of significance.

By Months

Grouping		Mean no. per liter	n	Month
A		1,420.8	12	Aug 1983
A	B	1,064.6	12	Sep 1983
	B	593.5	12	Jul 1983
	B	458.0	6	Apr 1983
	B	301.4	12	Jun 1983
	B	233.6	8	Dec 1983
	B	226.2	12	Nov 1983
	B	202.9	8	Mar 1983
	B	155.9	12	May 1983
	B	118.5	12	Feb 1983
	B	97.0	12	Jan 1983
	B	61.5	12	Oct 1983
	B	48.4	12	Oct 1982

By sampling sites

Grouping		Mean no. per liter	n	Impoundment
A		928.5	24	5
A	B	472.7	24	4
A	B	450.0	20	3
	B	242.1	22	2
	B	210.8	26	1
	B	71.5	26	Creek

By Net Tows

Grouping	Mean no. per liter	n	Replicate tow
A	419.3	71	2
A	359.4	71	1

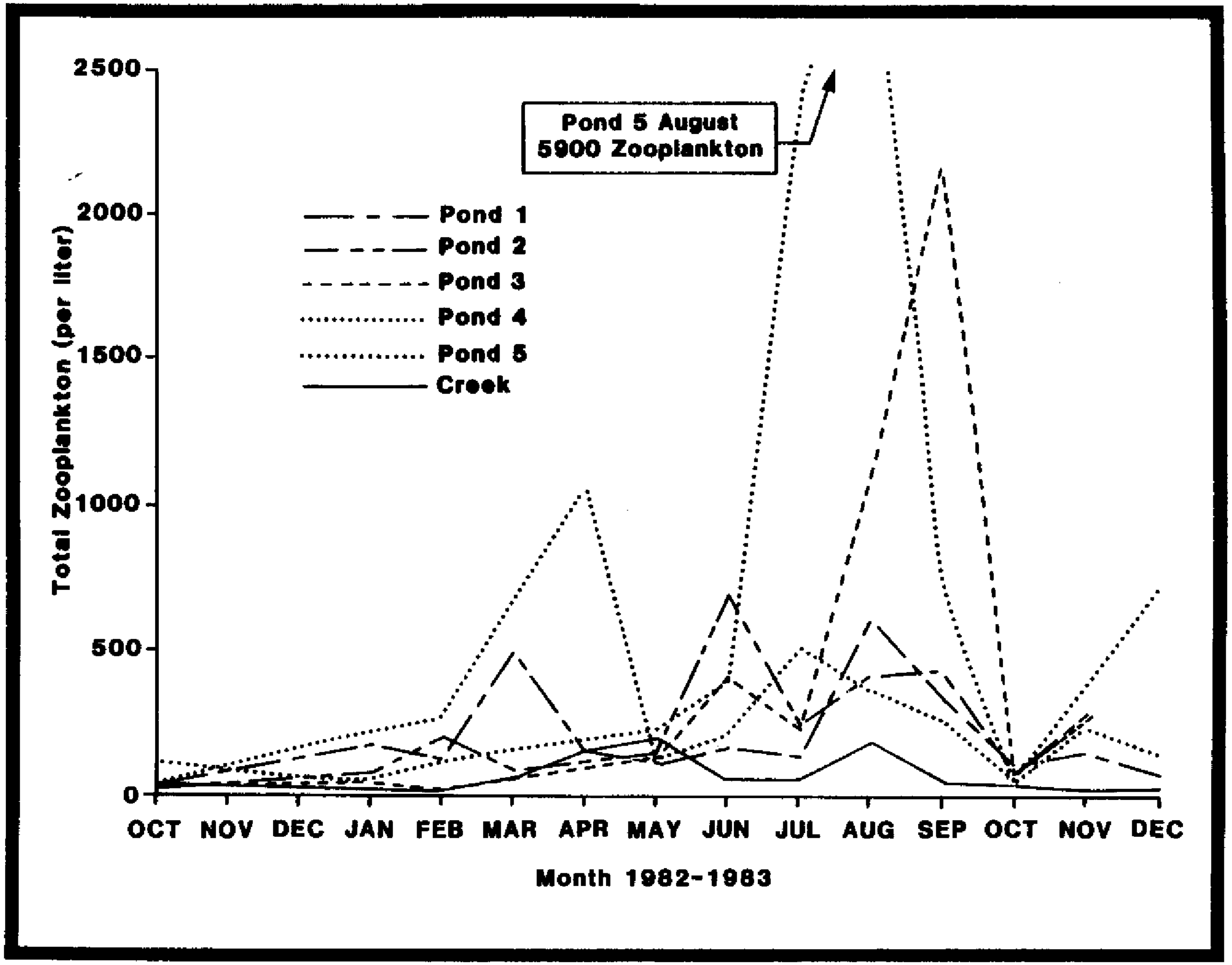

Figure 11.3 Density of all size fractions for all zooplankton taxa collected by the 53 um-mesh plankton net from the five study impoundments and Chainey Creek. Replicate tows were not significantly different: therefore, the means of pooled data are plotted.

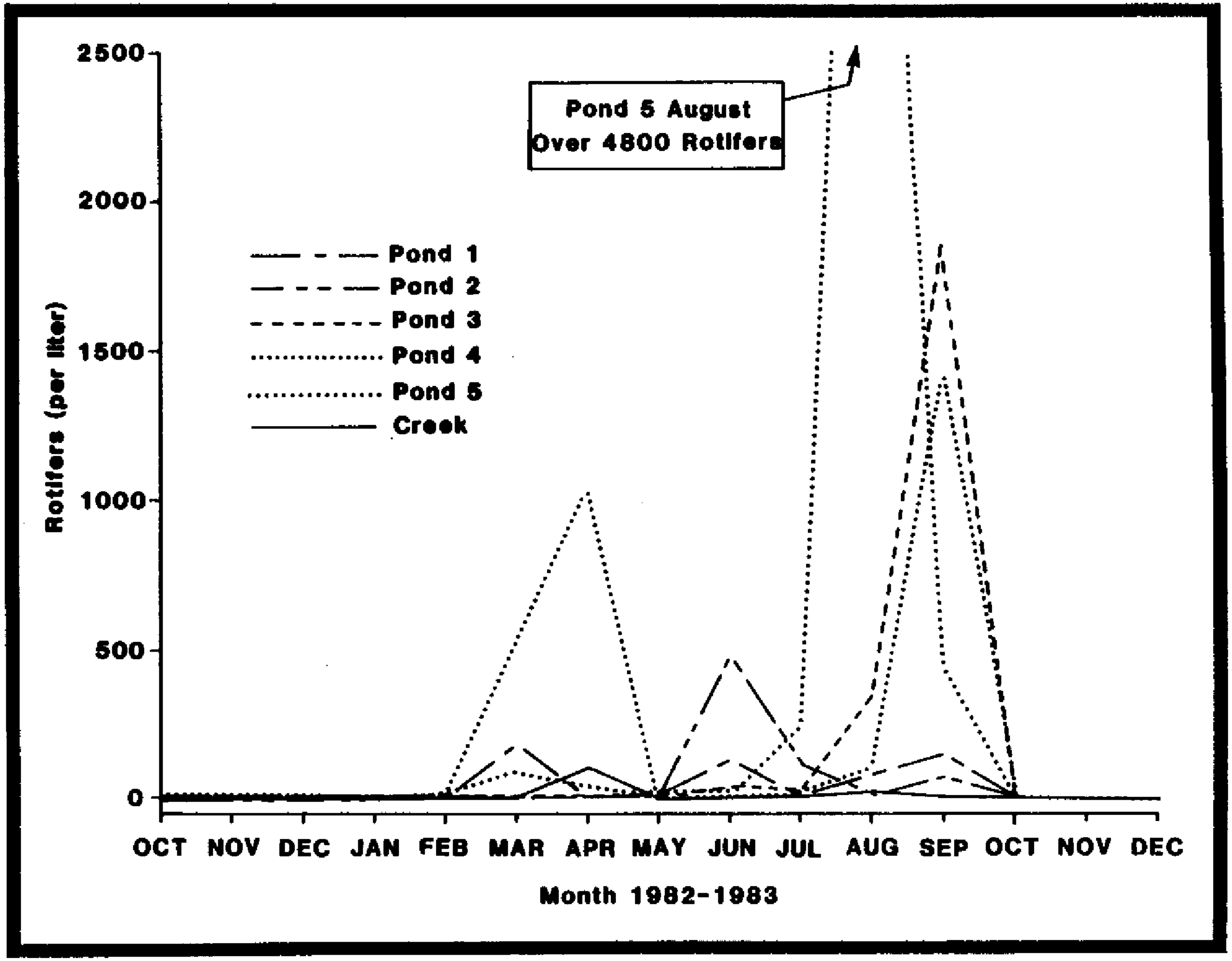

Figure 11.4 Densities of rotifers collected with the 53 um-mesh net. Plotted values are means of replicate tows.

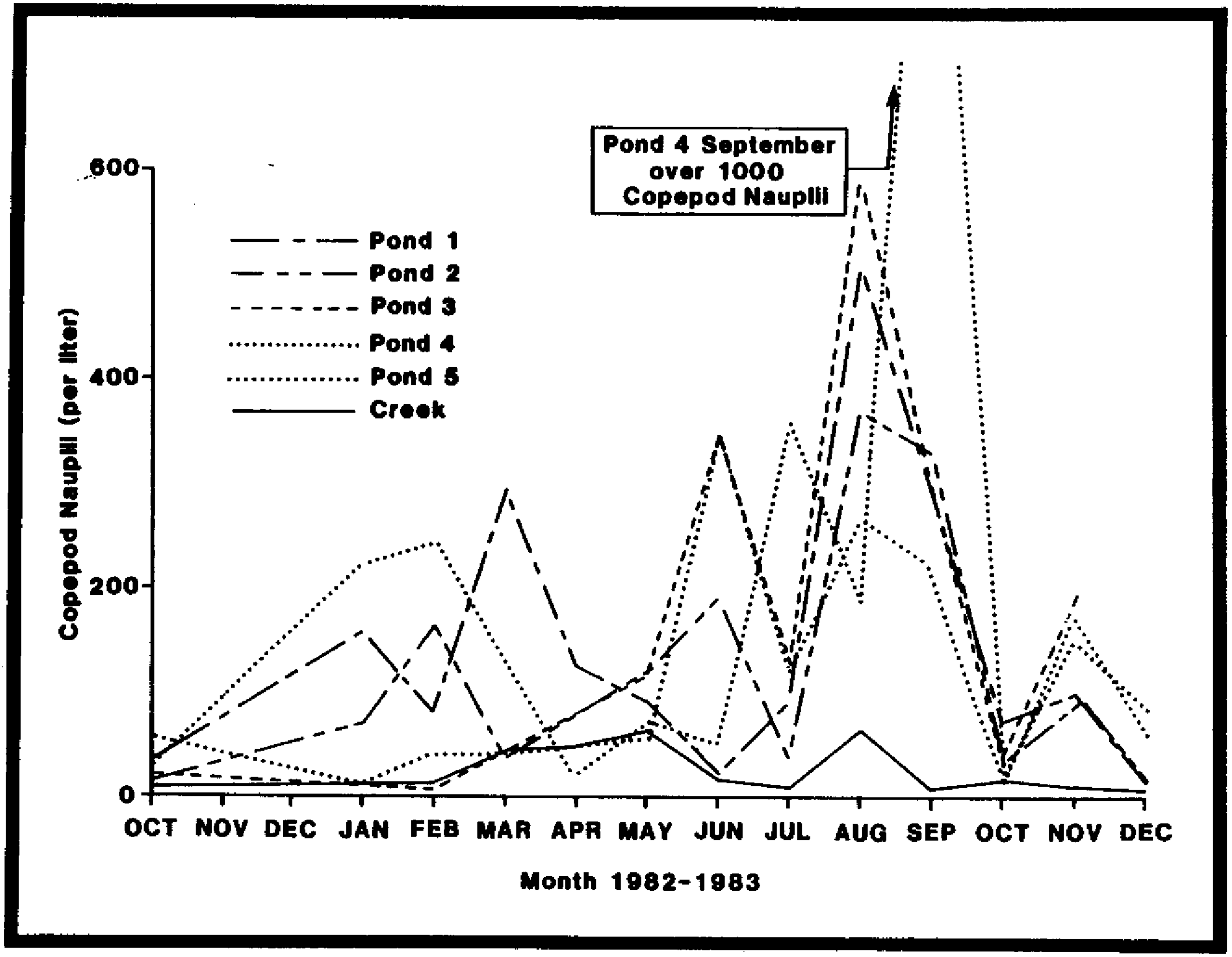

Figure 11.5 Densities of copepod nauplii collected with the 53 um-mesh net. Means of replicate tows are plotted.

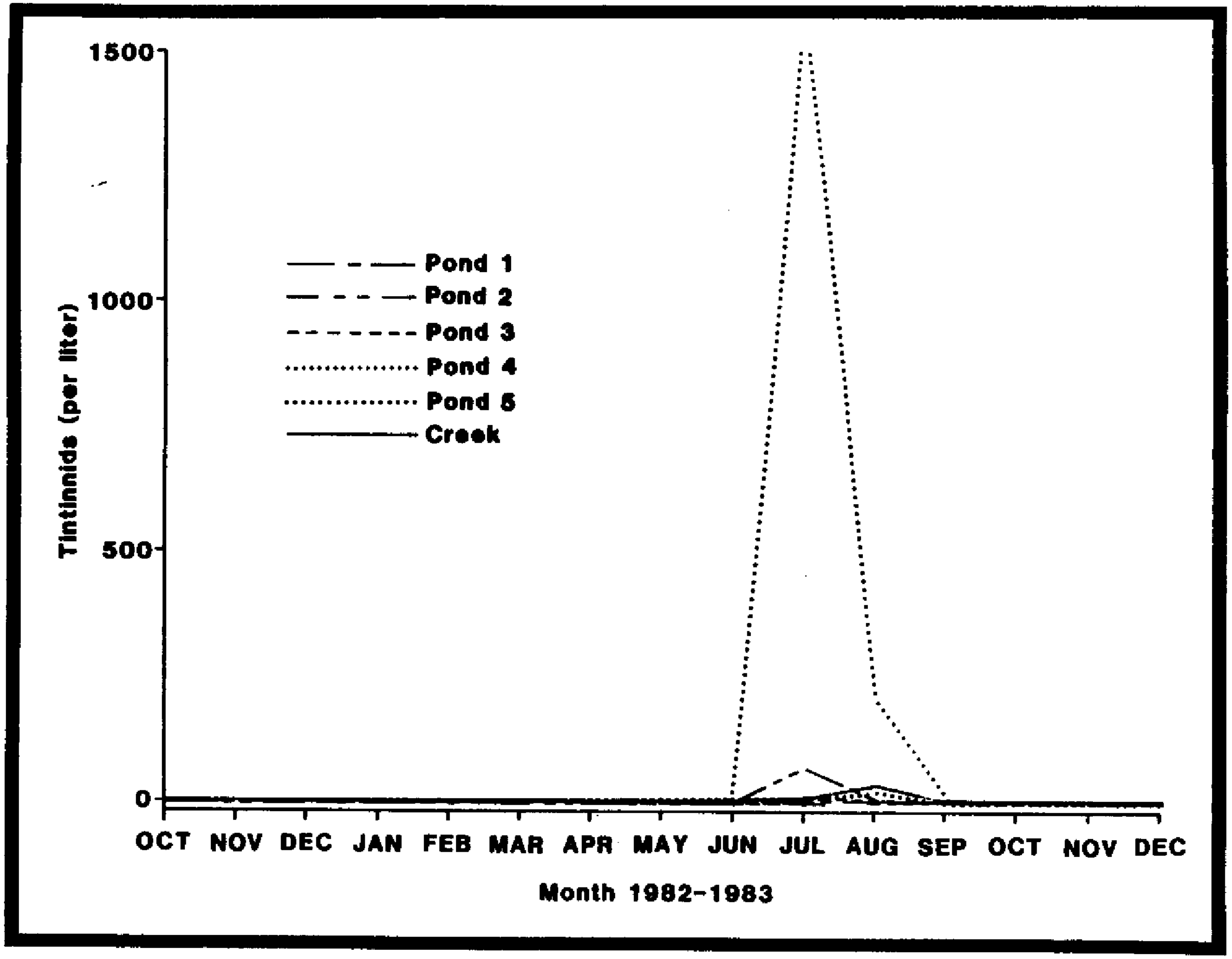

Figure 11.6 Densities of the protozoan taxon Tintinnida retained in the 53 um-mesh net. The 53 um-mesh plankton net was not expected to quantitatively sample this taxon, which can be extruded through 53 um-mesh netting during a plankton tow.

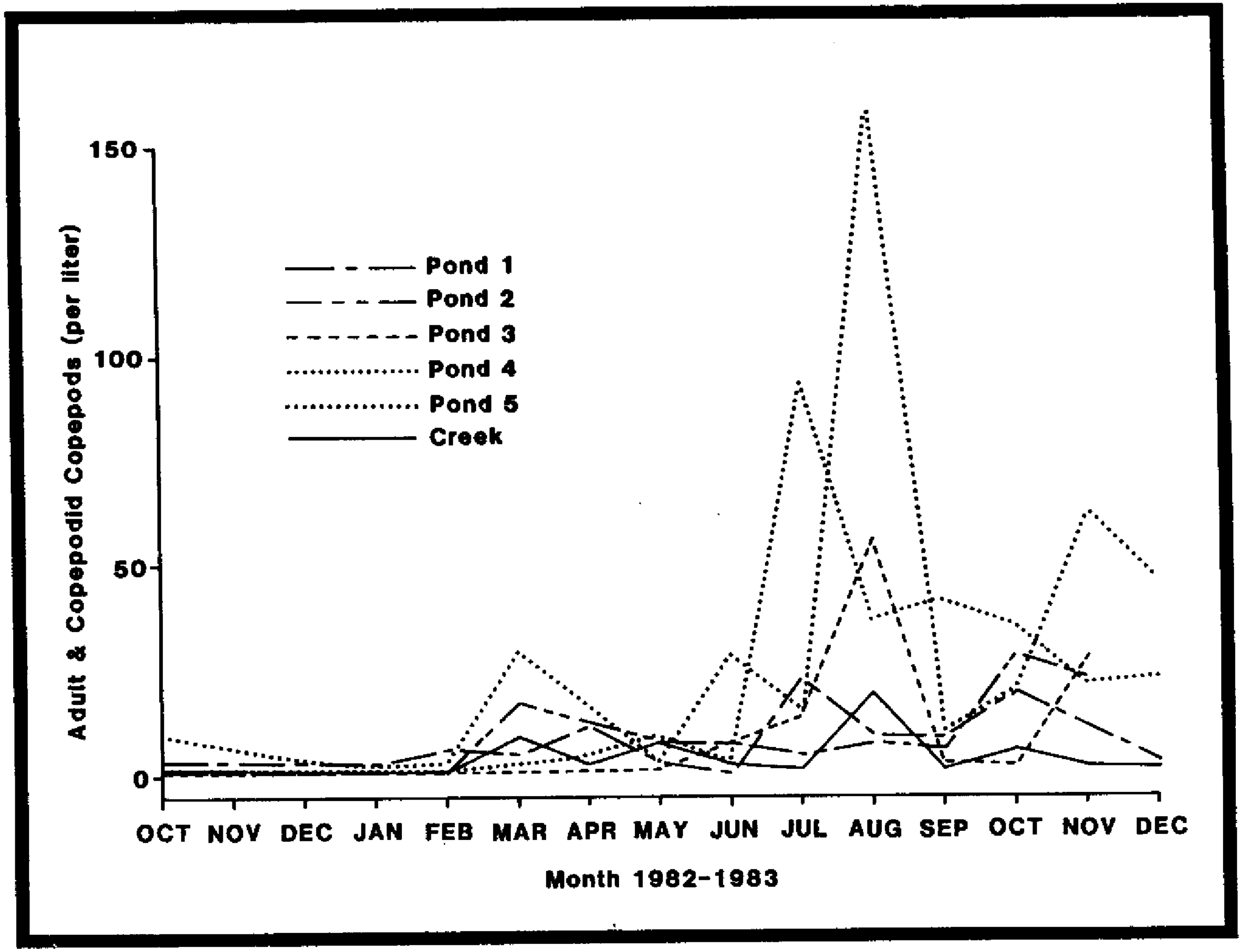

Figure 11.7 Mean standing crop of adult and copepodid stages of copepods collected with the 53 um-mesh net. The dominant species was *Acartia tonsa*. Plotted values are means of replicate tows.

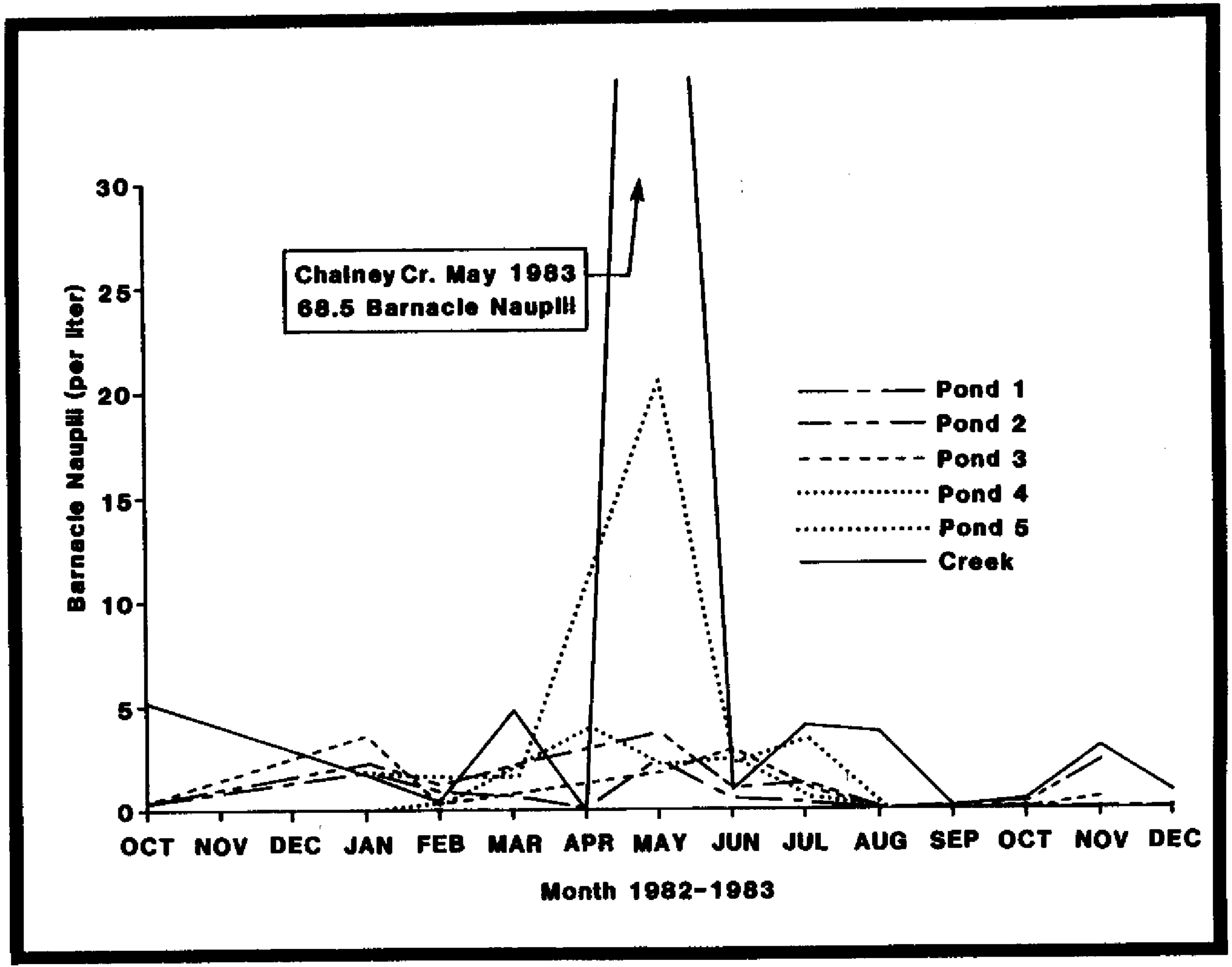

Figure 11.8 Mean densities of barnacle nauplii collected with the 53 un-mesh net. Means of replicate tows are shown.

Table 11.4 SAS GLM analysis summary examining the total numbers of 53 um-mesh net zooplankton per unit volume with respect to the impoundments and Chainey Creek. Dependent variable = total number of zooplankton.

Source	DF	Sum of Squares	Mean Square	F-Value	PR>F	R-Square	Coeff. Var.
Model	5	11149×10^9	3.53	0.005	0.005	0.115	203.97
Error	136	85794×10^9					
Corrected total	141	96943×10^9					

Source	DF	Type I SS	F-Value	PR>F	DF	Type III SS	F-Value	PR>F
Pond & Creek	5	11149×10^9	3.53	0.005	5	11149×10^9	3.53	0.005

barnacle nauplii, tintinnids, and polychaete larvae (Appendix Table 11.3) revealed that while mean monthly standing crop values did differ between some sites during some months, no easily identified trend was apparent. It also showed that for many months of the year the mean standing crops for these microzooplankton taxa were alike among the Chainey Creek and impoundment sites; however, the rank order of the sites (on the basis of mean standing crop) did change. The mean standing crop range also was revealed. Disregarding sites, the standing crop of copepod nauplii ranged from a mean of 5.6 to 1118.2 per liter, Acartia tonsa from 0.0 to 86.7 per liter, rotifers from 0.0 to 4884.7 per liter, barnacle nauplii from 0.0 to 68.5 per liter, and polychaete larvae from 0.0 to 567.3 per liter.

Similar statistical tests were conducted for the mesozooplankton fraction (153-μm-mesh net) for total copepods, Acartia tonsa, Eurytemora affinis, rotifers, barnacle cyprids, carideans, brachyurans, insects, and hydromedusae (Appendix Table 11.4). For many months of the year the mean standing crops of these mesozooplankton taxa were alike among sites, but when they did differ, the difference could be striking, as for total copepods and Acartia tonsa in August and September of 1983; and for barnacle cyprids in May and June of 1983 (Appendix Table 11.4). The mean standing crop of Acartia tonsa ranged from 0.0 to 63.0 per liter, total copepods from 0.1 to 63.5 per liter, Eurytemora affinis from 0.0 to 21.9 per liter, rotifers from 0.0 to 2.6 per liter, and barnacle cyprids from 0.0 to 5.3 per liter. The carideans, brachyurans, insects, and hydromedusae were usually present as fractional numbers of organisms per liter, although brachyurans were sampled up to 2.6 per liter and hydromedusae up to 6.8 per liter.

The ANOVA analyses revealed that significant differences in microzooplankton standing crop existed between months (P = .001) and between sites (P = .001), and both of the null hypotheses were rejected. There was a difference in microzooplankton standing crop between sites, and there was a significant effect of months (seasons) on microzooplankton standing crop. However, the rejection of the null hypotheses served only as a beginning. The evaluation of these results depended on the SNK multiple range tests.

Total microzooplankton standing crop SNK analysis revealed a significantly higher mean density of microzooplankton (1420.8 per liter) during August (Table 11.3). The analysis could not clearly categorize the mean density of 1064.6 per liter for September into an A or B grouping, but for all other months of the year the mean standing crops of zooplankton statistically were alike (ranging from 48.4 per liter in October 1982 to 593.5 per liter in July 1983; Table 11.3). A modest zooplankton bloom occurred in April, June, and July (458.0, 301.4, 593.5 per liter, respectively) which was interrupted in May (155.9 per liter). The low mean standing crop in May is attributable to the water-level management scheme followed for waterfowl management during this study. During May extensive tidal flushing of all five impoundment sites occurred as part of the waterfowl management practice, and total microzooplankton densities among sites approached that of Chainey Creek (Fig. 11.3). Similarly, the low mean standing crop of October in 1982 and 1983 (48.4 and 61.5 per liter, respectively) might be attributed to waterfowl management techniques. The impoundment water levels were lowered to permit waterfowl to graze on aquatic vegetation, and this allowed increased tidal flushing, which once again resulted in mean total microzooplankton densities approaching that of Chainey Creek (Fig. 11.3).

The significantly high mean standing crop of total microzooplankton in August was attributed to the markedly high density of rotifers (4884.7 per liter in impoundment 5 alone; see Fig. 11.4 and Appendix Table 11.3). Rotifers also exerted a strong influence on the mean densities summarized in Table 11.3 for the months of April (1036.7 rotifers per liter, impoundment 4; see Appendix Table 11.3) and September (1833.2 and 1423.4 rotifers per liter, impoundments 3 and 4, respectively; see Fig. 11.4 and Appendix Table 11.3), and were assisted in September by a copepod nauplii bloom in impoundment 4 (1118.2 per liter; see Fig. 11.5 and Appendix Table 11.3). Tintinnids (protozoan microzooplankters) strongly influenced the mean total microzooplankton ranking for the month of July (Table 11.3) by their significantly high abundance in impoundment 5 (1595.8 per liter; see Fig. 11.6 and Appendix Table 11.3).

Hunter's (1980) review summarized the salient concepts and principles of ichthyoplankton and marine fish early life history specialists regarding ichthyoplankton searching behavior for prey, prey types, prey size relations, feeding success, and the nutritive value of prey of different sizes and different taxa. If the data and results of this present zooplankton study are evaluated with respect to what is known about the food resource requirements of larval fish (see Stepien, 1976; Last, 1978a, 1978b; Houde and Taniguchi, 1979, 1981; Hunter, 1980; Taniguchi, 1982), their food intake rates (Conover, 1978), their selection for larger prey as they grow (Hunter, 1980), and the nutritive value of prey of larger sizes (Hunter, 1980, 1981), a greater food value may be assigned to the copepod taxon. Rotifers and tintinnids exhibit boom and bust cycles that are difficult to explain among sites with the data available in this study, but copepods appear to be able to provide a rather consistent larval fish food resource because of their more modest bloom cycles (in contrast to rotifers and tintinnids). Most important of all is the fact that the rotifer and tintinnid standing stocks strongly influenced the outcome of the null-hypotheses tests.

The mean standing crop of adult and copepodid-stage copepods was collected with a 53-µm-mesh net plotted in Fig. 11.7 to show the trend with time (months). The dominant copepod species was Acartia tonsa, a cosmopolitan coastal (neritic) calanoid species also found in estuarine and fully fresh waters (Brodskii, 1967).

Barnacle nauplii collected by 53-µm-mesh net were also plotted (Fig. 11.8) because they are consumed in significant numbers by fish larvae (see Stepien, 1976).

Houde and Taniguchi (1979) reviewed and summarized some reported concentrations of microzooplankton suitable as prey for marine fish larvae from coastal and estuarine areas around the world. Table 11.5 shows that copepodids and nauplii can be expected in concentrations of more than 100 per liter frequently, and occasionally greater than 2000 per liter in large estuaries. Their review and the data from this study suggest that managed marsh impoundments and the salt-marsh ecosystem may not be more productive for producing larval fish prey than coastal and estuarine areas in general.

The standing crop of mesozooplankton was lower than the standing crop of microzooplankton. Measured mean standing crops ranged from 0.1 to 63.5 per liter (Appendix Table 11.4) for the six study sites. The measurements of mesozooplankton copepod taxon densities of less than 100 organisms per liter was consistent with mesocopepod densities measured with identical 153-µm-mesh conical-cylindrical nets by Allen et al. (1982) and Allen et

Table 11.5

Reported concentrations of some microzooplankton suitable as prey for marine fish larvae from coastal and estuarine areas. Table from Houde and Taniguchi (1979).

Reference	Place	Organisms	Concentration
Burdick (1969 cited in May, 1974)	Kaneohe Bay, Hawaii	Copepod nauplii	50-100/1 common; 200/1 sometimes present
Duka (1969)	Sea of Azov	*Acartia clausi nauplii*;	62-65/1
		Other copepod nauplii and copepodids	> 30/1
		TOTAL	> 90/1
Mikhman (1969)	Gulf of Taganrog of Sea of Azov	Early stages of copepoda	39-546/1
Hargrave and Green (1970)	two eastern Canada estuaries	Copepod nauplii and copepodids	> 60/1
Reeve and Cosper (1973)	Card Sound, South Florida	Copepod stages 20-200 um in breadth;	range 23-209/1; mean for 28 collections 72/1
		Tintinnids	range 40-369/1
Heinle and Flemer (1975)	Patuxent River Estuary	*Eurytemora affinis* nauplii and copepodids	>100/1 frequently >2000/1 occasionally
Houde (unpublished data)	Biscayne Bay, South Florida	Copepod nauplii & copepodids < 100 um in breadth;	usually 50-100/1
		Tintinnids	frequently >100/1

al. (1984) from Winyah Bay, a riverine estuary about 7 km to the north via the Intracoastal Waterway from the present study sites.

The dominance of one mesocopepod species, Acartia tonsa, was clear when month-by-month comparisons of Acartia tonsa densities were made with the total copepod densities (Appendix Table 11.4). In general, Acartia tonsa standing crop did not differ among sites for most months, but in May, August, and September significant differences were detected between sites. This was especially true in August, when the mean standing crop of Acartia tonsa was significantly different between all sites (Appendix Table 11.4). Acartia tonsa densities tended to be about 30 per liter and less during much of the year and among sites. Impoundment 4 was the exception in July, when Acartia tonsa bloomed to 63 per liter.

CONCLUSIONS

This study revealed that zooplankton standing crops in managed salt-marsh impoundments tended to be higher than in the tidal creek of an undisturbed marsh. The zooplankton population dynamics appeared to be influenced greatly by unquantified individual attributes of each impoundment. The recorded zooplankton blooms from managed impoundments suggest that they are capable of producing higher densities than an undisturbed marsh ecosystem.

In South Carolina it is apparent that there is some public and agency concern against allowing the reimpounding of old rice fields that have reverted to salt marsh. One fear is that reimpoundment would deny access of marine fish larvae to an abundant food resource or exclude access to the nursery area (the breached rice fields). The microzooplankton densities measured during this study were comparable to densities that have been reported from productive open coasts and large estuaries. Results did not support the speculation that salt marshes may be sites of very high zooplankton densities required by marine fish larvae. At best, the measured zooplankton standing crops were typical of productive coastal areas. Overall the zooplankton standing crop densities of the undisturbed marsh were similar to those of an open ocean environment.

The seasonal draining of impoundments was one of the management practices to control mosquito larvae numbers and to germinate widgeon grass for waterfowl browse. These seasonal flushings of the impoundments showed zooplankton standing crops could be higher in the impoundments than in the marsh creek within a month afterwards. In general, analysis showed impoundments had higher standing crop densities than the marsh creek, although not always significantly higher. This suggests that managed impoundments in salt marshes may not exclude marine fish larvae from speculated productive zooplankton producing salt-marsh areas. The higher zooplankton densities in the impoundments appeared to be due to the impounding and management of the water mass. Further study is required, and future projects ought to attempt to quantify the zooplankton productivity and their trophodynamics within and outside of managed marsh impoundments. A necessary, but far more ambitious and extremely difficult project would be to gather evidence defining the survival and growth of fish larvae in salt marshes and correlating it with subsequent recruitment to a commercially or recreationally exploited fish stock. However, since no clear-cut, density-dependent relationship has been found anywhere between fish larvae survival and their prey abundance that could be correlated with subsequent year-class strength (Hunter, 1982), there is very little hope for one to be discovered that can support the speculative nursery area paradigm.

The null hypotheses were rejected in this study, and significant differences in microzooplankton standing crop were identified between sites and between months. Yet, closer examination and analyses of the data revealed that the statistical rejection of the null hypotheses was due to specific taxa that gained population density dominance in certain sites and during particular months. However, the interesting observation was that zooplankton densities frequently were not significantly different among sites (salt-marsh impoundments or salt-marsh creek) nor among months. The numerical standing crop domination of taxa consumed by premetamorphic larval fish may be attributed simply to a taxon (e.g., rotifers or tintinnids) out-competing other taxa after passive inoculation into the impoundments via the salt-marsh creek. The salt-marsh creek did not exhibit any extraordinary blooms, as observed in the impoundments. The zooplankton and phytoplankton exhibited their largest blooms in the fall. The interesting point of this observation is that many of the important South Carolina commercial and recreational fish species, whose larvae and postlarvae enter salt-marsh ecosystems, are mostly winter and early-spring spawners. By fall these fish are large juveniles preying on macroinvertebrates and small vertebrates.

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SECTION VI

BENTHIC COMMUNITY

GENERAL INTRODUCTION

Benthic meiofauna and macrofauna are important constituents of salt-marsh systems. Meiofauna, defined as those benthic metazoans that pass through a 0.5-mm mesh but are retained on ~63-µm mesh, are an integral part of the trophic structure of coastal ecosystems. Harpacticoid copepods are a primary food source for bottom-feeding larval and juvenile fishes such as spot, Leiostomus xanthurus (Hicks and Coull, 1983; B.C. Coull, pers. comm.). Grass shrimp, Palaemonetes pugio, have been shown to reduce meiofaunal density in a salt marsh through predation/disturbance (Bell and Coull, 1978). In addition to this direct trophic role, meiofauna may play an important role in nutrient remineralization and detrital processing, the latter making detritus available to macroconsumers (Tenore et al., 1977).

The extent to which production of the meiobenthos may be important to productivity of higher trophic levels is equivocal, however. Gerlach (1978) suggested that meiofauna are merely an additional energy source for deposit-feeding macrofauna and are not selectively fed upon because of their small size. Coull and Bell (1979) reviewed the controversy over the interactions between meiofauna and higher trophic levels and concluded that predation on meiofauna by higher trophic levels probably occurs in mud more than in sand substrates, where meiofauna serve primarily as rapid nutrient regenerators. More recent evidence suggests, however, that Coull and Bell's (1979) conclusion about the low importance of sandy substrata as feeding sites should be amended to include epibenthic and phytol copepods as important food items for fishes (Hicks and Coull, 1983).

Macrobenthos that are predominantly primary consumers in the salt-marsh ecosystem can be classified into three broad categories: grazers, detritus feeders, and suspension feeders. Generally, the feeding strategies of macrobenthos represent some combination of these categories, with the distribution of the major trophic groups dependent on the availability of specific food resources within the habitat (Perez, 1982).

Direct utilization of living vascular plants through herbivory is rare among macrobenthos (Perez, 1982). Insects, tanaids, and gastropods are among the invertebrate taxa inhabiting the salt marsh that contain true macrobenthic herbivores. Macrobenthos make greater use of vascular plant detritus. Small particles of plant litter that are created by mechanical or biological breakdown are available for consumption by marsh-deposit feeders, although it is likely that many deposit-feeding gastropods and crabs subsist on algae that is associated with larger angiosperms (Barnes and Hughes, 1982).

Most early literature on salt-marsh energetics assumed detritus was the main food source (Tenore, 1971; Teal, 1962). Recent evidence, however, suggests that algae are more important in the diet of macroconsumers than detritus (Wetzel, 1976; Haines and Montague, 1979). Littorinid, hydrobiid, and nassariid gastropods, a variety of crustaceans (Barnes and Hughes, 1982), and a number of polychaete species (Fauchald and Jumars, 1979) utilize algae through grazing. Suspension-feeding macrobenthos such as mussels utilize living phytoplankton and bacterial or fungal aggregates (Perez, 1982).

Other macrobenthic organisms such as amphipods, polychaetes, cumaceans, chironomid larvae, dolichopodid and ephydrid insects, shrimps, and crabs are apparently omnivorous, ingesting vascular plant debris as well as benthic algae and feces. Such ommivory may result from a time lag between production and consumption of detritus. The ability of many macrobenthos to utilize both food resources makes the relation between production and consumption for this group more complex than for strict herbivores.

Macroconsumers play an important role not only as direct metabolizers of energy but also as controllers of energy flow. Deposit feeders ingest the sediment and its associated detrital materials, digesting the living components, and voiding the inert nonliving components back into the salt-marsh system, where they are recolonized by bacteria, protists, and meiofauna. The role of macrobenthos as energy regulators is exemplified by grass shrimp, Palaemonetes pugio, which is a dominant inhabitant of salt-marsh systems. These shrimp mascerate detritus into a heterogeneous assortment of uneaten particles by plucking away the cellular matrix from surfaces of large detrital fragments (Welsh, 1975). Masceration of fragments provides particles that become suspended in the water column and populated by bacteria. The excretion of ammonia and phosphate by grass shrimp is responsible for heavy growth of microflora and increased protein fraction in feces and uneaten detrital fragments (Welsh, 1975).

Other benthic species such as marsh crabs and polychaetes aerate the sediments by burrowing (Field, 1983). This enhances exchanges of interstitial water with the overlying water column, resulting in replenished stocks of nutrients for bacteria (Barnes and Hughes, 1982). Fiddler crabs, *Uca* spp., are also important, in that they turn over and aerate the top layers of sediment (Edwards and Frey, 1977) allowing microorganisms to colonize. On a smaller scale, meiofauna consume bacteria, thereby releasing nutrients back into circulation and permitting continued bacterial production (Barnes and Hughes, 1982).

Chapter 12

A. Benthic Meiofauna

B. C. Coull

INTRODUCTION

The organization and structure of the meiofaunal community of salt marshes in the southeastern United States has been studied in some detail. In Georgia, Teal and Wieser (1966) examined the abundance and vertical distribution of nematodes across a salt-marsh gradient. In South Carolina, where most of the studies on meiofaunal populations of salt marshes have occurred, Coull et al. (1979) investigated the distribution of meiobenthic copepods over a gradient from creek bottom to high marsh. In a more detailed study of salt-marsh microhabitats, Bell et al. (1978) examined variations in meiofaunal assemblages around and between Spartina culms and Uca burrows. They concluded that small-scale spatial heterogeneity is a major factor determining meiofaunal distribution. Bell (1979) also found short- and long-term variation in the meiofauna of a high Spartina marsh, with little similarity of assemblages within seasons or between years. In a complementary study, Fleeger (1980) defined temporal changes in the copepod assemblages at a low-marsh site.

No studies, however, have been conducted to document the meiofaunal community within wetlands altered by man. In this preliminary study, meiofaunal abundances are compared between impounded wetlands and those in the open marsh.

METHODS

Samples of meiofauna were collected on 9 September 1982 and 22 February 1983. In the September 1982 sampling, ten cores (three from the perimeter ditch and seven from the vegetated flat) were collected from each of five experimental impoundments described in Chapter 4. During February 1983, eight cores were taken from each of the five impoundments (three from the ditch and five from the flats) as well as ten cores from nonimpounded areas near the impoundments (six from intertidal low Spartina marsh and four subtidally from nearby marsh creeks which served as control sites). All sampling was conducted by randomly collecting 1.96-cm-diameter sediment cores to a sediment depth of the redox discontinuity layer (usually <1 to 2 cm). Each sample was fixed in the field with a mixture of 10% buffered formalin and Rose Bengal stain.

In the laboratory the fauna from each core was extracted by Ludox^{TM} centrifugation (de Jonge and Bouman, 1977) and sorted to major taxon. Copepods from both sampling sets (September 1982 and February 1983) were identified to species. Nematodes from one replicate from each pond were identified to the lowest possible taxon for the February 1983 samples.

Major taxon abundances were expressed as number per 10 cm^2 of sediment surface (Hulings and Gray, 1971). Taxa such as rotifers, ostracods, and insect larvae that occurred only once were combined into a general category called "other taxa." Species were listed by percent abundance because of potential errors in converting animals from sorted samples to numbers per unit area.

Data analysis consisted of a two-level nested analysis of variance (ANOVA) comparing abundances of total meiofauna and major taxa among primary sites (impounded and nonimpounded areas) and among habitats (ditch vs. flat) within impoundments. Nested ANOVA was performed separately for each sampling date. All statistical analyses were conducted using Statistical Analysis Systems (SAS) software (SAS Institute, 1982). The significance level for all statistical tests was $\alpha = 0.05$.

RESULTS AND DISCUSSION

Nematodes and copepods were the most abundant taxa in the September 1982 samples (Table 12.1). Significant differences were observed in the numbers of total meiofauna, nematodes, copepods, polychaetes, turbellarians, and the category "other taxa" between impoundments (Table 12.2). Except for turbellarians, no significant difference was noted for mean abundance of any taxon between the perimeter ditch and vegetated flats of the impoundments (Table 12.2). No two impoundments were alike in terms of abundance of meiofauna, and the high variance associated with the abundance values (Tables 12.1 and 12.2) suggests a contagious distribution of the fauna within each impoundment. This variance was not explained by differences in abundance values between the ditch and flats. Copepods were the most frequently collected taxon, occurring in 32 of the 50 samples taken in September.

Copepods and nematodes were the most abundant taxa collected from impoundments and nonimpounded sites during February 1983 (Tables 12.3 and 12.4). Comparison of abundance of total meiofauna between impoundments (including and not including the marsh creek controls) and between ditch and flat (not including marsh creek controls) revealed no statistically significant differences (Table 12.5). Among individual taxa, however, polychaete abundances were significantly different between impoundments, and between the flat and ditch sites; copepod abundances were significantly greater on the flats than the perimeter ditch (Tables 12.3, 12.5); and abundances of other taxa were different between controls and impoundments (Table 12.5).

Although not significantly higher in total abundance of meiofauna, nonimpounded sampling sites on Cat Island appeared to harbor more species than the impoundments. This is particularly true for the subtidal sites, where 13 nematode and 11 copepod species were encountered in February (Table 12.6, 12.7). The copepod species found were typical of the habitat sampled (Coull et al., 1979). The impoundment fauna (Table 12.6) is typical of the high (short *Spartina*) North Inlet marsh (Bell, 1979, 1980; Coull et al., 1979) which has low diversity and characteristic species. Thus in terms of abundance and species composition, it appears that the

Table 12.1 Mean number of each meiofauna taxon per 10 cm2 (± SD) for each impoundment sampled on 19 September 1982. Data based on three samples from the perimeter ditch and seven from the vegetated flat of each impoundment.

	Imp. 1			Imp. 2			Imp. 3			Imp. 4			Imp. 5		
Taxon	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$
Total meiofauna	22.0	101.0	13.9 (21.7)	63	126	102.6 (107.1)	281	643	522.0 (543.0)	137.0	41.0	70.0 (69.7)	196	405	343.1 (272.9)
Nematodes	7.0	8.0	7.2 (9.7)	39	69	65.8 (94.3)	211	616	481.0 (542.0)	109.0	17.0	44.6 (62.6)	168	173	171.7 (144.7)
Copepods	13.0	2.0	5.0 (12.4)	2	5	3.8 (6.4)	8	4	5.2 (7.8)	4.0	0.6	3.9 (5.7)	26	204	151.0 (192.2)
Polychaetes	0.0	0.8	0.5 (1.2)	16	48	35.8 (30.7)	4	10	8.0 (6.9)	3.0	15.0	11.5 (10.3)	0	8	5.9 (6.8)
Turbellarians	1.2	0.0	0.4 (1.1)	7	4	4.7 (5.1)	58	12	28.0 (30.7)	2.3	0.7	7.6 (20.1)	0	11	7.6 (8.2)
Others	1.2	0.5	0.7 (1.5)	0	0	0.0	0	0	0	0.6	3.0	2.3 (3.9)	2	9	6.8 (7.2)

Table 12.2

Nested ANOVA Table for comparison of meiofauna abundance (September 1982 data) between five impoundments and the ditch and flat habitats in these impoundments [* significant at $p < 0.05$.].

	DF	SS	F Value	P > F
Total meiofauna				
Between impoundments	4	1102036	3.67	0.013*
Ditch vs. flat	5	381220	1.01	0.432
Nematodes				
Between impoundments	4	858758	3.46	0.023*
Ditch vs. flat	5	349063	1.13	0.364
Copepods				
Between impoundments	4	81412	2.81	0.039*
Ditch vs. flat	5	66957	1.85	0.128
Polychaetes				
Between impoundments	4	4683	7.37	0.002*
Ditch vs. flat	5	2504	3.15	0.181
Turbellarians				
Between impoundments	4	6246	8.84	0.0001*
Ditch vs. flat	5	5444	6.17	0.0003*
Other taxa				
Between impoundments	4	176	3.08	0.027*
Ditch vs. flat	5	98	1.37	0.256

Table 12.3 Mean number of each meiofauna taxon per 10 cm2 ($\pm$ SD) for each impoundment sampled on 22 February 1983. Data are based on three samples from the perimeter ditch and five from the vegetated flat of each impoundment.

Taxon	Imp. 1			Imp. 2			Imp. 3			Imp. 4			Imp. 5		
	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$	Ditch $\bar{x}$	Flat $\bar{x}$	$\bar{x}$
Total meiofauna	55	691	452.0 (456.0)	41.0	388	257.0 (202.0)	241	460	378.0 (183.0)	211	1,216	839.0 (1,339.0)	90	635	430.0 (497.0)
Nematodes	46	488	322.0 (329.0)	38.0	207	143.0 (97.0)	237	441	365.0 (173.0)	200	1,208	830.0 (1,340.0)	85	541	370.0 (388.0)
Copepods	3	149	94.0 (122.0)	1.0	165	103.0 (116.0)	165	12	7.9 (7.8)	4	6	5.0 (7.6)	0	87	54.0 (137)
Polychaetes	6	52	35.0 (36.0)	1.0	13	8.0 (8.6)	2	7	5.0 (4.6)	8	1	4.0 (6.1)	4	6	5.0 (3.9)
Turbellarians	0	1	0.5 (1.3)	0.0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Others	0	1	0.5 (1.3)	1.2	2	1.8 (3.8)	0	0	0.0	0	0	0.0	1	1	1.0 (2.1)

Table 12.4

Mean number of each meiofauna taxon per 10 cm^2 (± SD) for nonimpounded intertidal (Spartina marsh) and subtidal (marsh creeks) sites sampled on 22 February 1983.

Taxon	Intertidal (n = 6)	Subtidal (n = 4)
Total meiofauna	894 (427)	508 (276)
Nematodes	692 (469)	174 (80)
Copepods	189 (398)	230 (183)
Polychaetes	13 (9)	8 (6)
Turbellarians	0	0
Others	0	96 (160)

impoundment fauna is similar to what one would expect to find in high intertidal salt marshes of the South Carolina coast.

Total meiofaunal abundance was not significantly different between impoundments 3 and 5 for the two sampling periods, whereas impoundments 1, 2, and 4 showed significant ($p < 0.05$) increases in abundance in February.

The low abundance of meiofauna (Table 12.1) and copepods and the low diversity of the latter in September suggested an impoverished meiofauna assemblage in the impoundments at that time. Only samples from impoundment 3 in September (Table 12.1) approached abundance values for nonimpounded sites sampled in February. The other values for September were well below previously reported meiofauna abundances from salt marshes (Bell, 1979). February samples (Fig. 12.1; Tables 12.3 and 12.4), however, indicated increased abundance of meiofauna at impoundment sites (overall $\bar{x} = 471 \pm 219/10\ cm^2$). This value of ~500/10 cm^2 is equivalent to the mean abundance values recorded by Bell (1979) for high salt marsh. Values for nonimpounded sites (Table 12.4: subtidal 508 ± 276/10 cm^2; intertidal low marsh, 894 ± 427/10 cm^2), although higher than in the impoundments, were not significantly different from the impoundment values because of the large amount of variance associated with

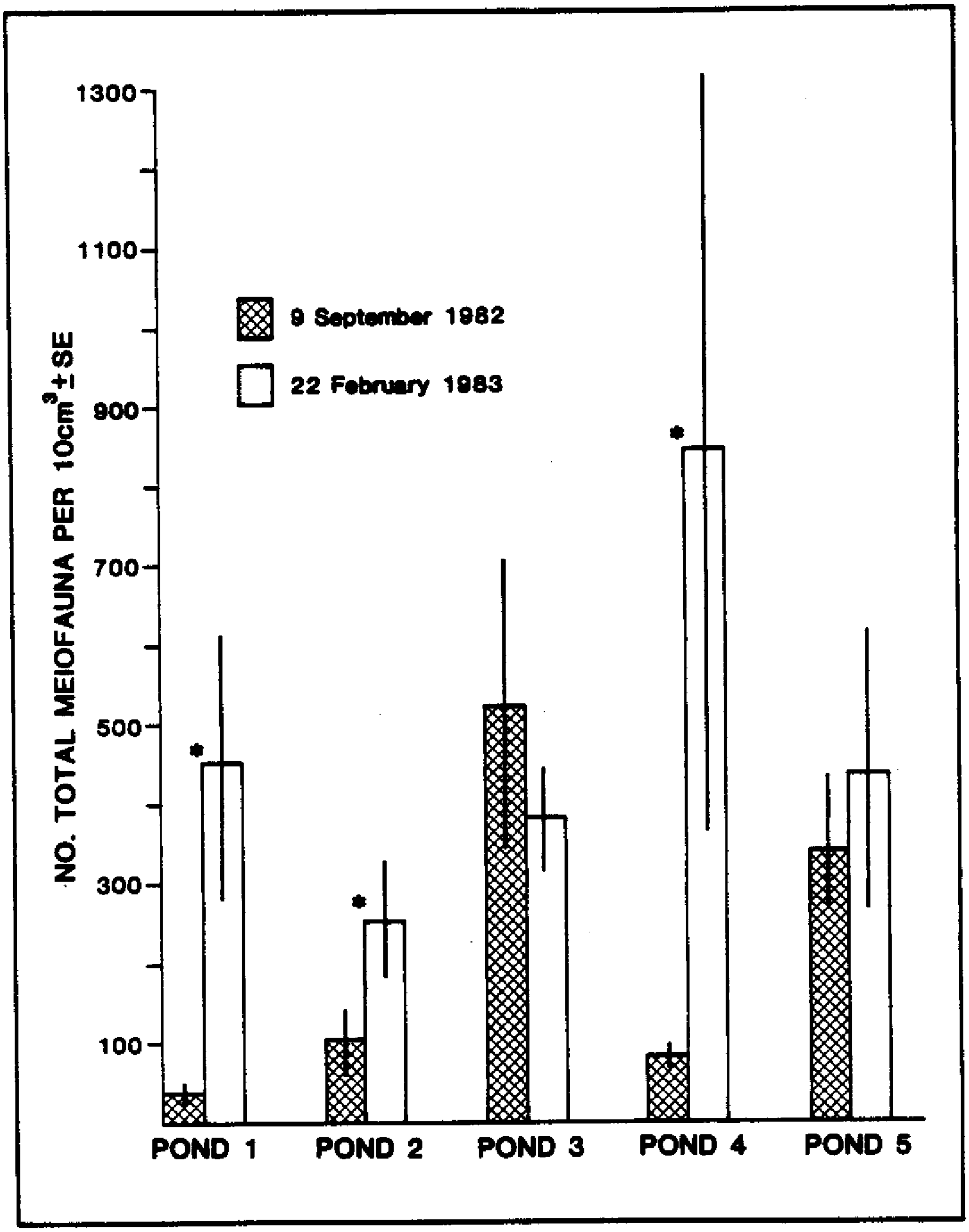

Figure 12.1 Mean abundance of total meiofauna (± SE) in the five impoundments on the two sampling dates. Those data marked with an * indicate that abundance was significantly different ($p < .05$) on the two dates.

Table 12.5

Nested ANOVA Table comparing meiofauna abundance (February 1983 data) between five impoundments (with and without nonimpounded control sites) and between ditch and flat habitats in impoundments (not including control sites). [*Significant at $p < 0.05$.]

	DF	SS	F Value	P>F
Total Meiofauna				
Between ponds (controls included)	6	2286328	1.04	0.41
Between ponds (controls not included)	4	1031506	0.61	0.66
Ditch vs. flat	5	3527721	1.66	0.17
Nematodes				
Between ponds (controls included)	6	2180618	1.06	0.40
Between ponds (controls not included)	4	1391473	0.88	0.48
Ditch vs. flat	5	2798425	1.42	0.24
Copepods				
Between ponds (controls included)	6	254247	1.44	0.22
Between ponds (controls not included)	4	40842	1.35	0.27
Ditch vs. flat	5	105237	2.79	0.03*
Polychaetes				
Between ponds (controls included)	6	3356	3.64	0.006*
Between ponds (controls not included)	4	3493	4.64	0.005*
Ditch vs. flat	5	4391	4.67	0.003*
Turbellarians				
Between ponds (controls included)	6	0.869	0.42	0.85
Between ponds (controls not included)	4	0.777	0.45	0.77
Ditch vs. flat	5	1.215	0.56	0.73
Other taxa				
Between ponds (controls included)	6	33581	2.77	0.025*
Between ponds (controls not included)	4	15.19	0.78	0.55
Ditch vs. flat	5	2.97	0.12	0.99

Table 12.6 Frequency of occurrence and percent abundance of copepods for the 22 February 1983 samples. Ten of the 40 impoundment samples had no copepods; the number of samples which had copepods of the eight collected in each impoundment is the denominator in the f column. Percent is calculated by dividing the abundance of a species by all the copepods identified at each site (n).

		Pond I		Pond II		Pond III		Pond IV		Pond V		Intertidal Control		Subtidal Control
Species	f	%(n=191)	f	%(n=156)	f	%(n=31)	f	%(n=19)	f	%(n=205)	f	%(n=133)	f	%(n=216)
Calanoida														
Pseudodioptomus sp.	2/6	2.5					1/7	5.2						
Cyclopoida														
Halicyclops coulli Herbst	5/6	16.1	2/7	1.9	1/6	3.3			3/4	3.4				
Oithona sp.									2/4	9.7				
Harpacticoida														
Amphiascus sp.													2/4	1.4
Enhydrosoma baruchi Coull													1/4	0.9
E. propinquim Brady													4/4	5.9
Halectinosoma winonae Coull			3/7	7.1									1/4	0.9
Mesochra mexicana Wilson			1/7	0.6			4/7	52.8	1/4	0.5				
Microarthridion littorale (Poppe)	1/6	1.0	5/7	42.4	6/6	38.8			1/4	33.2	2/6	2.2	4/4	5.9
Nannopus palustris (Brady)							1/7	10.5	1/4	50.8	6/6	69.2	2/4	3.6
Nitocrella aestuarina Coull & Bell							1/7	10.5						
Nitocra affinis Gurney			1/7	1.9									1/4	0.5
Paronychocamptus wilsoni Coull	6/6	80.5	5/7	41.6	5/6	54.9	3/7	21.0	2/4	2.4			4/4	8.2
Pseudobrodys pulchella Sars			3/7	4.5							3/6	3.7	4/4	71.3
Schizopera knabeni Lang											1/6	1.6		
Scottolana canadensis (Wilson)											6/6	23.3	1/4	0.5
Stenhelia (*D.*) *bifidia* Coull													1/4	0.9

Table 12.7 Percent abundance of nematode species identified from randomly selected samples collected 22 February 1983. n = total number of nematodes identified from each sample. Only one sample from each site was used to identify nematodes.

Species	Controls		Pond and Sample				
	Subtidal (n=107)	Intertidal (n=68)	1-7 (n=71)	2-4 (n=43)	3-1 (n=58)	4-7 (n=52)	5-6 (n=77)
Daptonema erectum (Wieser & Hopper)	44	2		37	21	2	75
Ptycholaimellus pandispiculatus (Hopper)	2	69	73	28		4	13
Sabatieria pulchra (Schneider)	6	2			55	21	5
Axonolaimus spinosus (Butschii)	16						
Axonolaimus demani (DeConinck & Stekhoven)			14				
Theristus sp. 1			4	16	21	6	
Chromadorida sp. 1	1					19	
Chromadorida sp. 3		9					
Chromadorita sp.	8		1			17	
Theristus sp. 2	6	12					
Sphaerolaimus gracilis deMan	8			2			

Table 12.7 Continued

Species	Controls		Pond and Sample				
	Subtidal (n=107)	Intertidal (n=68)	1-7 (n=71)	2-4 (n=43)	3-1 (n=58)	4-7 (n=52)	5-6 (n=77)
Anoplostoma viviparum (Bastian)	2	3		9		2	
Cyathelaimidae sp.	2			2		4	
Sabatieria praedatrix deMan	3	2					4
Oncholaimidae sp.			3		2		
Linhomeidae sp.					2		3
Leptolaimidae sp.	1						
Metachromadora sp.	1						
Parodontophora sp.		2					
Theristus sp. 3				2			
Theristus sp. 4		2					
Chromadorida sp.2			1				
Eurystomidae sp.			1				
Sphaerolaimus sp.				2			

the data (Table 12.5). The potential seasonal change in meiofauna abundance (Fig. 12.1) was difficult to delineate on the basis of two sampling dates, but it was consistent with the general trend reported for meiofauna at a subtidal muddy site sampled for 10 years in the North Inlet system (Fig. 12.2). The 10-year monthly means of the North Inlet data illustrate that meiofaunal abundance peaked in March and was lowest in September at the mud site. Limited temporal sampling in the impoundments, however, did not allow any conclusion that the cycle is similar. In addition, the North Inlet values were much higher, with the lowest value at the mud site (September, ~700 per 10cm^2) being the maximum abundance reached in the impoundments. Thus total abundance of meiofauna in the impoundments appears to be of the same order of magnitude as high intertidal Spartina marsh in North Inlet.

The ANOVA tables (Tables 12.2, 12.5) demonstrate the high variability within impoundments. Because of this high variance, few distinctions can be made between abundance values of meiofauna from the vegetated flats and perimeter ditches. In September, only turbellarian abundance was different between the two habitats (Table 12.2), and only copepod and polychaete abundances were significantly different between these habitats in February (Table 12.5). The differences noted in abundance of each taxon between impoundments in September (Table 12.2) was not evident in February (Table 12.6), when only abundance of copepods was different between impoundments (not including nonimpounded sites). When nonimpounded sites were included, the taxon category "others" was also different, indicating abundance differences between impoundment and other sites. The lack of differences between flat and ditch in February was surprising, because perusal of the Table 12.3 data indicates that the ditch fauna was always lower in abundance than the flat, with the exceptions of copepods in Impoundment 3 and polychaetes in Impoundment 4. The large variability undoubtedly masked any statistically significant difference in abundance between these habitats.

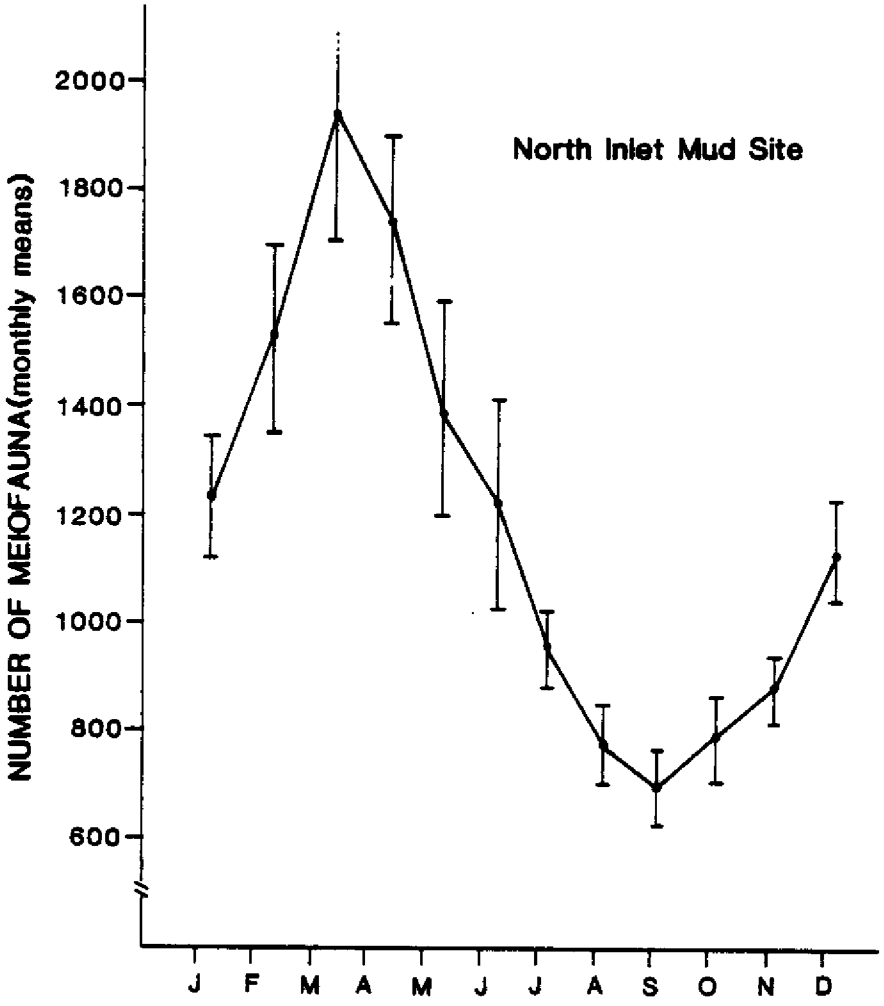

Figure 12.2 Monthly mean abundance of total meiofauna (± SE) for ten years (1972-1982) of sampling at a subtidal mud site in North Inlet, S.C.

CONCLUSIONS

The data presented herein are preliminary. Valid conclusions could not be made based on two samplings, and a complete seasonal study with more replicates would be needed to lower the inherent variability in meiofauna data. Information from this study did indicate that meiofauna occur patchily in impoundments, with abundance values approaching those shown from high intertidal *Spartina* tidal marsh. Meiofauna from the study site may have been following the seasonally variable abundance cycles known from muddy substrates in the North Inlet system, 20 km north of the impoundments.

Chapter 12

B. Benthic Macrofauna

E. L. Wenner

INTRODUCTION

Benthic macrofauna of tidal saltmarsh systems have been the subject of numerous descriptive and manipulative studies. The earliest studies included limited information on infaunal communities and were primarily concerned with energy flow in the salt-marsh systems of Georgia (Teal, 1962), Louisiana (Day et al., 1973), and Rhode Island (Nixon and Oviatt, 1973). These studies indicated that macrobenthos are important in the functioning of salt-marsh ecosystems. It has been suggested that benthic organisms influence the detritus food web (e.g., Odum et al., 1972; Odum and Heald, 1975, Tenore et al., 1982) by increasing the rates of detrital decomposition and primary production in the sediments through grazing (Hargrave, 1970; Fenchel, 1972; Fenchel and Harrison, 1976; Lopez et al., 1977). Decomposition by bacteria and fungi, however, is probably more significant in the overall decomposition process than feeding by animals (Reice and Stiven, 1983). In addition to their role as decomposers of detritus, macrobenthos are an important source of food for juvenile and adult fish (Kneib and Stiven, 1982; Chapter 14, this report) and birds (Bourne and Cottam, 1950; Heard, 1983) and thus are a means by which energy is transferred to higher trophic levels (Odum and Heald, 1972).

Although the mechanisms that influence the distribution patterns and population dynamics of macrofaunal species in salt marshes are largely unresolved, there is evidence indicating that several physical and unresolved, there is evidence indicating that several physical and biological factors are important determinants of community structure of soft-bottom benthos. Physical properties of the sediment have been recognized as important factors influencing the distribution and species composition of soft-bottom benthic infauna (McNulty et al., 1962; Bloom et al., 1972; Gray, 1974; Mayou and Howard, 1975; Saila, 1976). Temperature, salinity, dissolved oxygen, and water quality have also been reported to influence the structure of the benthos (e.g., Tenore, 1972; Boesch et al., 1976; McBee and Brehm, 1979). The importance of density and type of vegetation on macrobenthic populations has been demonstrated most effectively for seagrass beds (Santos and Simon, 1974; Stoner, 1983; Lewis, 1984), although the distribution of marsh macrobenthos is also affected by vegetation type (Cameron 1972; Subrahmanyan et al. 1976; Fell et al. 1982), density (Cammen, 1976), and patchiness (Reice and Stiven, 1983). Predation is a major biological factor that has also received a great deal more attention in soft-bottom vegetated (reviewed in Peterson, 1979) and seagrass habitats (Young and Young, 1978; Heck and Thoman, 1981) than in salt-marsh systems (Vince et al., 1976, Kneib and Stiven, 1982; Wiltse et al., 1984).

In view of the complex interaction of macrobenthos with these factors in natural marsh habitat, it is important to evaluate whether man-made manipulations of the environment alter the physical and biological properties and, ultimately, the functional role of macrobenthos in the system. Considering the large amount of information available on macrobenthos in natural salt-marsh systems, few studies have compared the structure of macrobenthos between natural and altered salt marshes. The practice of impounding estuarine wetlands for waterfowl management represents an even more striking alteration, because water circulation, hydrography, substrate, and aquatic vegetation are all affected (Copeland, 1974; Dean, 1975).

The present study provides a quantitative comparison of the macrobenthic communities of a natural *Spartina alterniflora* marsh, a marshland creek, and two impoundments. Specifically, we compared macrobenthic communities from vegetated and nonvegetated areas within the impoundments with similar types of habitat in the natural marsh and creek systems over a two-year period. Correlative study objectives were to determine the extent of seasonal changes in community structure of macrobenthos and to evaluate the effects of the water-management scheme for maximizing growth of macrophytes attractive to waterfowl on that community structure.

METHODS

Field Sampling and Laboratory Analysis

Study sites were selected that contained the dominant shallow vegetation within two impoundments (units 1 and 2) of the paddy field complex and a nearby marsh, as well as deeper nonvegetated areas of the two systems. The dominant vegetation of the lower natural marsh was *Spartina alterniflora*. In the impoundments sampled, *S. alterniflora* (tall form) and *Ruppia maritima* were dominant in impoundment 1, while *R. maritima* and *Scirpus robustus* were the dominant vegetation in impoundment 2 (see Chapter 7). In each of the two impoundments, two quadrats measuring 149 m^2 each were haphazardly selected from areas containing each of the two dominant macrophytes (Fig. 12.3). Quadrats in impoundments 1 and 2 containing *R. maritima* were designated as sites 1R and 2R, respectively. The other two quadrats in impoundment 1, designated 1Sp, were characterized by tall *S. alterniflora*, whereas the remaining two quadrats (2S) in impoundment 2 were dominated by *S. robustus*. For comparison with the shallow impounded sites, two similar-sized quadrats, designated 3M, were established in the low marsh edging Chainey Creek across from impoundments 1 and 2. The perimeter of each quadrat was skirted with rope to facilitate re-location and discourage human disturbance. In addition to the quadrats, two 18-m-long portions of the front perimeter ditch of each of the two impoundments were randomly selected and designated as sites 1D and 2D, respectively. Two comparable 18-m portions, designated site 3C, were established opposite the impoundments in Chainey Creek. For ease of relocation, these transects were marked along the edge of the perimeter ditches and creek with rope.

Sampling for macrobenthos was conducted during daylight hours at all sites during January 4-5, June 28-29, and November 1-2, 1983 and during January 26-27, April 9-10, and July 30-31, 1984. Samples were taken from the perimeter ditch and Chainey Creek sites using a Ponar grab with

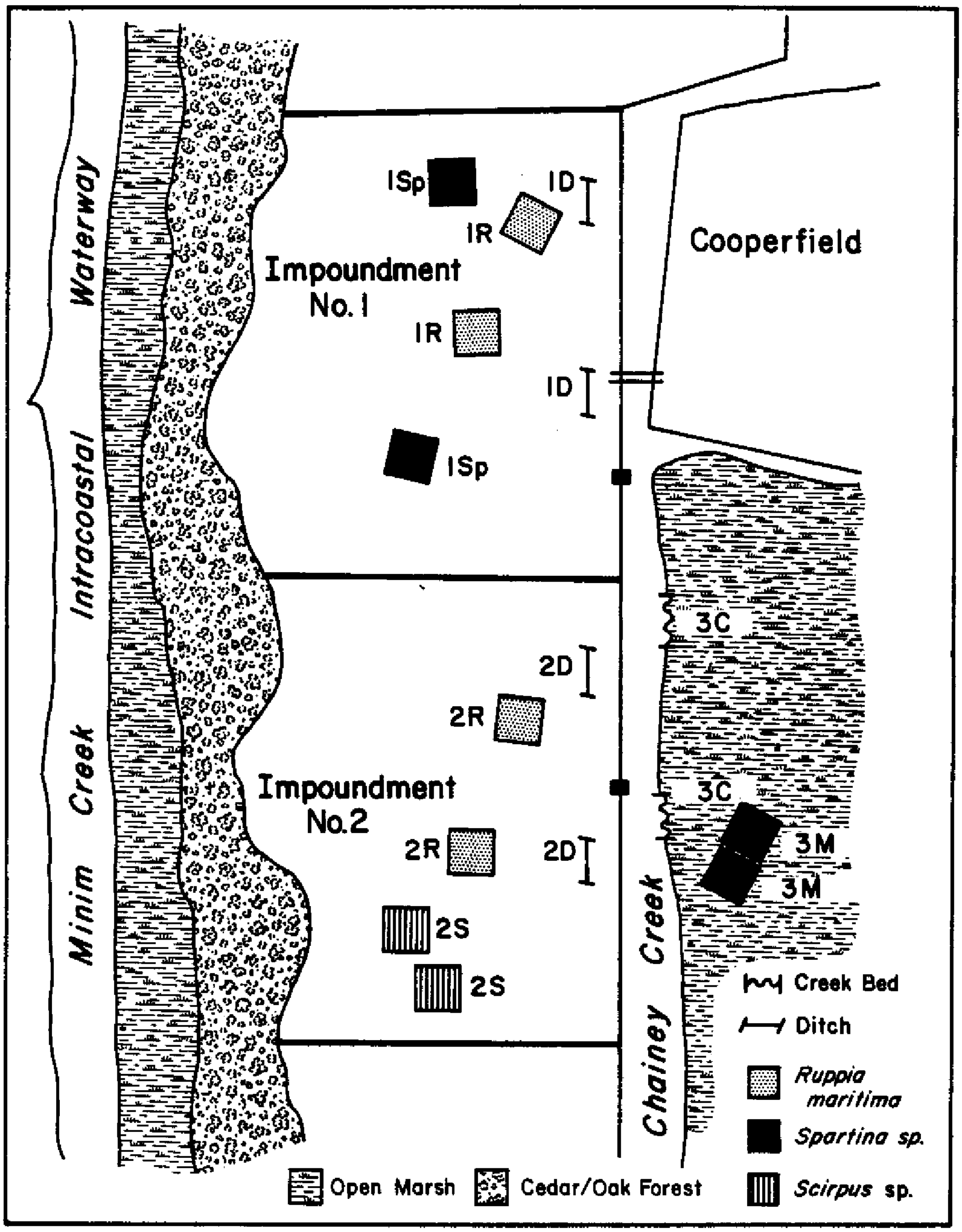

Figure 12.3 Location of replicate benthic sampling sites in vegetated and non-vegetated areas of the impoundments, Chainey Creek and the natural marsh.

0.05-m2 mouth opening. Three locations were randomly selected along each 18-m transect, and a grab sample was taken from the middle of the creek and ditch at each location. In the vegetated areas of the impoundments and marsh, three locations were randomly selected within every quadrat using a grid coordinate system. These locations were sampled to a depth of 10 cm with a hand-held corer having an 81-cm^2 mouth opening. The corer, which was constructed from galvanized iron pipe, had a sharpened cutting head and was especially developed to cut through the dense root and rhizome mat. Stoner et al. (1983) showed that corers provide the best estimate of macrofaunal density and composition in vegetated (seagrass) and nonvegetated (sand) marine habitats; however, because Chainey Creek and the perimeter ditches are deeper and not readily sampled by the corer, a grab was used, which may have underestimated the density of macrobenthos at those sites. The area sampled by the corer and grab was equilibrated by taking six cores and subsequently pooling them to form one sample with a total area of 0.05 m^2 from each of the three randomly selected locations in each quadrat. A total of 48 macrobenthic samples were taken during each sampling period.

Water level was controlled in the impoundments as described in Chapter 4. During 1984, water level in impoundment 2 remained above 20 cm, and the outside water-control gate was set to allow tidal flushing. This deviation from the 1983 water management scheme was done to determine whether changes in community structure and composition resulted from seasonality or were related to the impoundment management scheme.

Disturbance to submerged habitats was minimized by using a small, flat-bottomed boat to carry gear and personnel to the sampling sites. At dewatered impoundment sites and in the open marsh that was sampled at low tide, travel by foot was necessary to reach randomly selected locations within each quadrat. Although it was felt that this effect was minimal in view of the time elapsed between sampling periods, obviously disturbed areas were avoided during sampling. Disturbance by wildlife to sampling sites was not monitored. All sampling sites within quadrats were marked with stakes to eliminate the possibility of sampling the same site twice. New quadrats and transects were established prior to November 1983 and March 1984 to obtain samples from minimally disturbed areas of each habitat.

Hydrographic conditions noted during sampling at submerged sites included temperature, recorded by stem thermometer; salinity, measured by a Beckman 7RS-7C salinometer; and water depth. Five sediment samples were taken with a piston corer (5.1-cm diameter) in each quadrat at the conclusion of sampling in June 1983. Sediment samples were frozen and processed for determination of total and volatile solids, following methods described by Plumb (1981). Textural analysis based on wet sieving of the sand fraction and pipeting of the silt/clay fractions was used to describe particle size composition. In addition to environmental conditions noted at the time of sampling, weekly bottom temperature and salinity values were recorded in Chainey Creek from January 1983 to December 1984 as part of plankton sampling for larval fishes and penaeid shrimp (Chapter 13); and temperature, salinity, and additional dissolved oxygen values were recorded as part of the nutrient and hydrographic analysis presented in Chapter 6 and the ichythological characterization in Chapter 14. Mean monthly discharge rates in the Santee River near Russellville were supplied by the Water Resources Division of the U.S. Department of Interior.

Macrobenthic samples were washed through a 1.0-mm sieve, preserved in 10% formalin and stained with rose bengal prior to sorting. Although Lewis and Stoner (1981) showed that over 50% of the total macrofauna in seagrass beds passed through a 1.0-mm mesh, preliminary sieving with a 0.5-mm sieve proved to be extremely time consuming, because of the large amount of vegetation and clay in the impoundment samples. Therefore, abundance of some of the smaller taxa such as the sabellid polychaete Manayunkia sp. and nematodes, which are actually meiofaunal (Bell, 1979; 1982), were underestimated. Motile and solitary sessile organisms were identified to major taxon, or to species when possible, and enumerated. Colonial or encrusting organisms were identified but not counted. Adult insects such as leafhoppers, grasshoppers, wasps, and ants were not included in the data analysis, because they were not collected in large numbers and were only incidentally associated with the sediment. Insect larvae and adults included in data analysis were identified only to family. Male hydrobiid snails were identified to species, based on the shape and ornamentation of the verge (Heard, 1983), whereas females were identified only to family. The use of the corer and grab limited adequate sampling of motile or natant fauna such as decapod crustaceans; however, because this group is a conspicuous constituent of salt marshes along the southeastern United States (Teal 1962), it was included in analyses, but species densities were underestimated. A more complete study of the decapod crustaceans associated with coastal impoundments and salt-marsh systems is found in Chapter 13.

Information on the feeding habits of five common shorebirds, lesser yellowlegs, Tringa flavipes; dunlin, Caldris alpina pacifica; short billed dowitcher, Limnodromus griseus; semipalmated sandpiper, Calidus pusillus; and least sandpiper, Calidus mirutila, was obtained by analysis of esophagus and crop contents. Specimens were shot during May 1984 in an impoundment (Cooperfield) adjacent to the impoundment and open-marsh study sites sampled for macrobenthos. Immediately after collection, the specimens were injected with 10% buffered formalin, and later the esophagus and crop of specimens were removed and preserved in 10% buffered formalin. Because of advanced digestion of food items, prey were generally identified to major taxonomic group, primarily using hard parts such as polychaete mandibles, gastropod shells, insect head parts and exoskeltons, and crab claws.

Data Analysis

Measures used to compare diversity of macrobenthos among sites and sampling periods included the Shannon diversity index H' (calculated using $\log_2$) (Pielou, 1975); J', a measure of evenness and dominance (Pielou, 1969); number of species; and SR, an index of species richness (Margalef, 1958). These calculations were based on pooled data from the six samples of the two quadrats or transects in the major habitats of the impoundments and marsh. Oligochaetes, nematodes, insects, and other taxa not identified to species were excluded from diversity calculations.

Cluster analyses were used to determine patterns of similarity in the macrobenthic community at sites sampled over the two-year period. Normal and inverse analyses were performed on $\log_{10}$- transformed counts from pooled data of the six samples taken each sampling period from replicate quadrats and transects at each site, using the Bray-Curtis coefficient and a flexible sorting strategy with β of -0.25 (Clifford and Stephenson, 1975). The data were reduced prior to classification by eliminating those species that were colonial and not quantifiable, had uncertain identification, or occurred in only one core or grab sample during the study. None of the species eliminated from cluster analysis accounted for more than 0.01% of the total individuals at any particular site. Subsequent to dendrogram formation and selection of groups, nodal analysis was used to describe the degree of species and site group coincidence in terms of constancy and fidelity (Boesch, 1977).

Model I one-way analysis of variance (ANOVA) was used to test the null hypotheses that: (1) the number of species and (2) the number of individuals did not differ between sites. The latter analysis of number of individuals was performed separately for vegetated and nonvegetated sites because of the different gear used to sample each. Because sites in the impoundment, creek, and marsh systems were replicated (two quadrats or two transects per site) and replicate samples ($n = 3$) were taken from each quadrat or transect, variates considered in the ANOVA were the mean values of the three samples from each quadrat or transect. Separate ANOVAs were performed for each season, rather than in a two-way ANOVA, because season was not replicated as a "treatment" (Hurlbert, 1984). Examination of scatter plots of the mean and variance (Elliott, 1977) were used to determine dependence of the variance on the mean. If heterogeneity of variance was indicated, data were tranformed by $\log_{10}$ prior to ANOVA. Means were compared among treatment groups using the a posteriori Ryan-Einot-Gabriel-Welsch multiple F test (Ramsey, 1978). The level of significance for all statistical tests was $\alpha = 0.05$.

RESULTS AND DISCUSSION

Physical Variables

Measurements of temperature, salinity, and water depth taken concurrently with benthic sampling indicated that water depth was highly variable between impoundment sites for each sampling period (Appendix 12.1). Within the impoundments, water depth at vegetated sites was dependent on water-level manipulations aimed at encouraging production of Ruppia and other desirable waterfowl food plants. During 1983 impoundments 1 and 2 were alternatively drained and reflooded, as described in Chapter 4. In March 1984 water was drained from the beds of impoundment 1. The beds in impoundment 1 had no standing water on them except for rainwater through late May 1984. Rapid reflooding and dewatering of the flats of impoundment 1 then occurred as in 1983. Water level in impoundment 2 during 1984 was not allowed to fall below a depth of ~20 cm. This impoundment was allowed to receive natural tidal flushing. In June 1984, the water level in both impoundments was gradually increased in a manner similar to that of 1983. The perimeter ditch sites remained flooded throughout 1983 and 1984, except for two rapid flushings of the ditches in impoundment 1 after initial drawdown in late March 1984.

Water level in Chainey Creek fluctuated with tidal stage, but during all sampling periods water depths were >100 cm. The natural salt-marsh sites were intertidal and therefore subject to diurnal water-depth fluctuations.

Temperature and salinity were similar between sites during each sampling period, as well as over the two-year study duration; however, vast temporal differences in these measures occurred at sampled sites (Appendix 12.9, Fig. 12.4). Temperature maxima were noted in August, and minimum temperatures occurred in January and February 1983 and December to February 1984. Salinity in the perimeter ditches of impoundments 1 and 2 largely reflected that of Chainey Creek (Figs. 12.4 and 12.5) which is not surprising, because water-control structures were set to allow a moderate tidal exchange (see Chapter 4). Salinities generally increased in late spring and remained >15 ppt through December 1982 and 1983, after which they declined. Lowest salinities (~5 ppt) were noted in March and April of 1983 and 1984. Temporal salinity changes in Chainey Creek appeared to be strongly influenced by mean monthly discharge in the Santee River (Fig. 12.5) and rainfall (Chapter 4, Fig. 4.7). Discharge was greatest in March and April of 1983 and 1984, whereas rates were lowest from May through November 1983 and June through December 1984. The regression (Sokal and Rohlf, 1981) of salinity on $\log_{10}$-transformed values of mean river discharge was significant ($F = 121.8$, $r^2 = 0.85$). Although not measured on a monthly basis, we assumed that temperature and salinity values at the marsh site were similar to those noted during flood tide in Chainey Creek.

Dissolved oxygen in impoundments was subject to diel variation (see Chapter 4); however, when mean minimum values were considered over time,

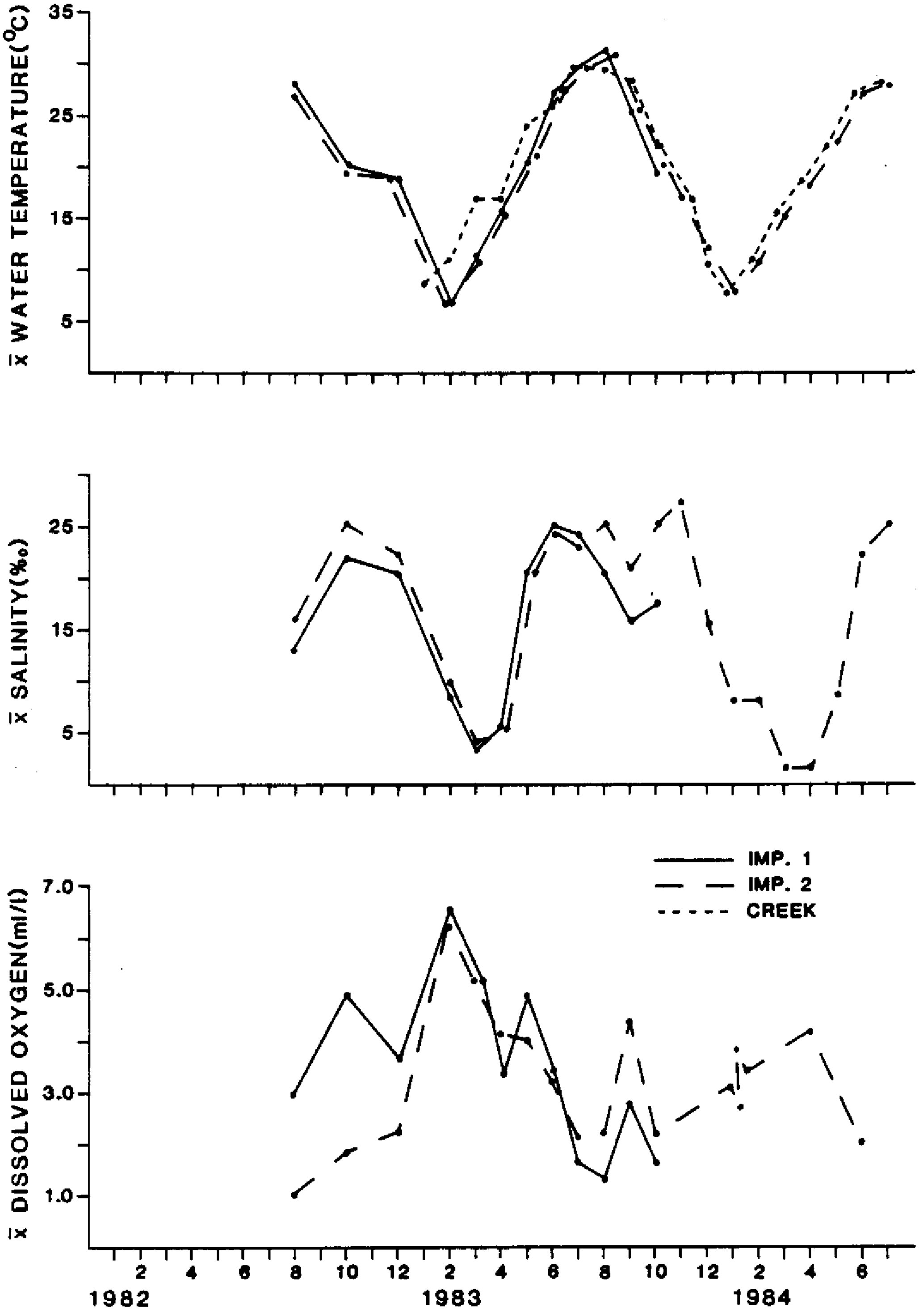

Figure 12.4 Average temperature, salinity and dissolved oxygen conditions in Chainey Creek and impoundments 1 and 2 from August 1982 to June 1984.

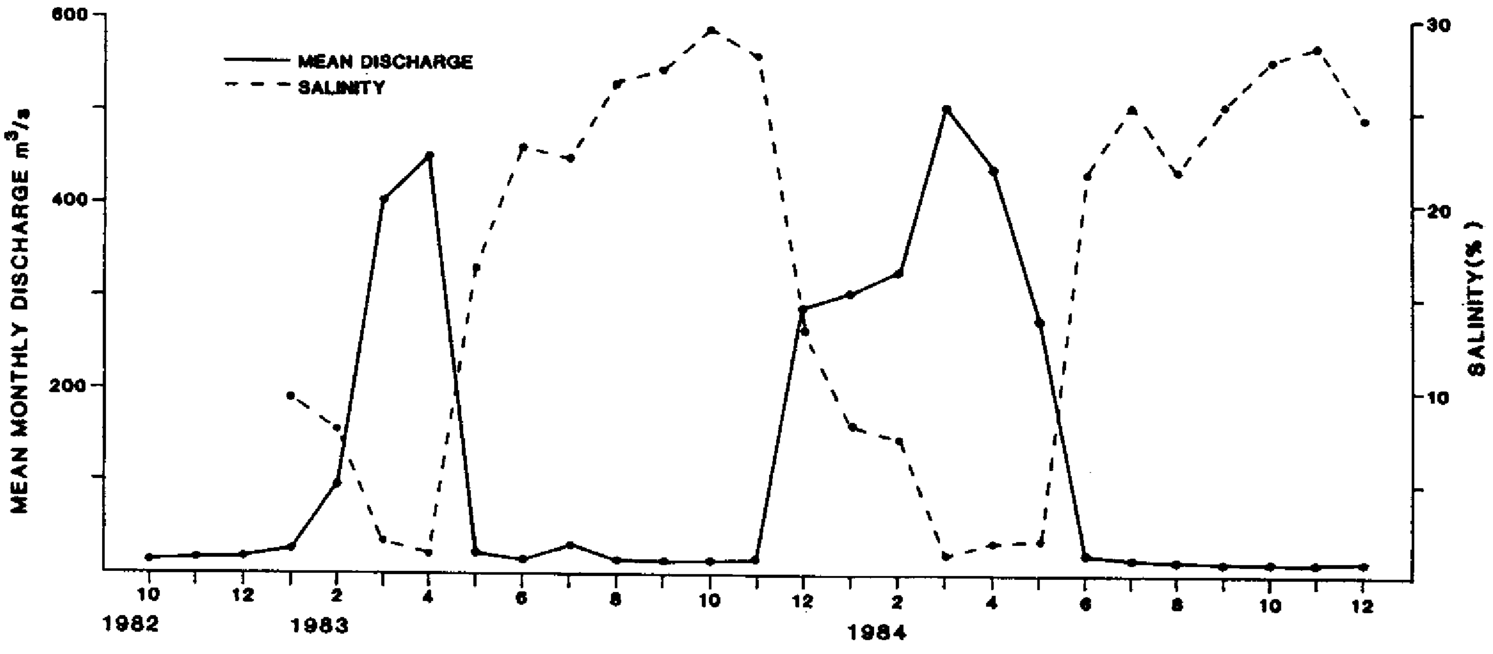

Figure 12.5 Mean monthly discharge (m^3/s) in the Santee River and bottom salinity in Chainey Creek from January 1983 to December 1984. Data sources: discharge rate - U.S. Geological Survey, Water Resources Division; salinity - larval decapod and fish studies (Chapters 13 & 14).

lowest values coincided with high temperature and, in 1983, high salinity (Fig. 12.4).

Sediments at study sites in the impoundments had similar amounts of volatile organic residue; however, values were noticeably lower in Chainey Creek (Table 12.8). Values reflected the high organic content of sediments from the vegetated areas of the impoundments and marsh and the perimeter ditches.

Size composition analyses showed two distinctly different substrates occurred in the study area: a predominantly (82.5%) coarse, sandy sediment in Chainey Creek and a clay-silt sediment at the other sites. The only other sites at which sand occurred were 1R and 1Sp in the impoundments (Table 12.8).

Species Composition

A total of 101 taxa were collected from the 288 samples during the study. Only four sessile species (*Molgula manhattensis*, *Balanus improvisus*, *Membranipora arborescens*, and *Crassostrea virginica*) were collected. These, with the exception of *M. manhattensis*, were not quantified and thus not considered further in analyses. A complete listing of all taxa collected by site is found in Appendix 12.2.

Of the 37,443 individuals collected during the study, oligochaetes were most abundant, accounting for 49% of the total number of individuals. Other numerically dominant groups included Mollusca (22%) and Polychaeta (17%). The Insecta (7%), Amphipoda (3%), and Decapoda (0.4%), which are conspicuous components of the salt-marsh community (Kneib, 1984), were either too large or too mobile to be adequately represented in core and grab collections.

Spatial differences in the number of taxa and number of individuals within the six major taxonomic groups occurred among the sampling sites (Fig. 12.6). Molluscs, polychaetes, oligochaetes, and insects were the most consistently abundant and diverse groups collected among vegetated sites sampled with the corer. Because insects were identified only to family and oligochaetes only to class, while other groups were identified to species, the number of species representing these groups is underestimated. Polychaete richness was higher in the open marsh, whereas abundance of molluscs was greater at vegetated sites in the impoundments.

Table 12.8

Particle size composition by weight and volatile solids residue of sediments collected from study sites.

	Volatile Solids Residue (%)		Particle Size Composition (%)		
Site	$\bar{x}$	s	Sand	Silt	Clay
1R	16.4	2.09	2.2	37.4	60.4
	17.6	0.89	0.0	30.1	69.9
2R	15.6	1.37	1.6	86.5	11.9
	13.5	2.36	1.8	22.4	75.8
1Sp	16.5	1.03	5.4	54.3	40.3
	16.8	2.74	0.0	43.2	56.8
2S	14.5	2.04	1.1	20.3	78.5
	17.4	2.82	--	--	--
1D	14.3	0.53	0.0	43.3	56.7
	15.5	1.48	--	--	--
2D	16.1	2.63	0.0	50.7	49.3
	17.1	1.61	0.0	80.1	19.9
3C	7.4	2.55	82.5	7.8	9.7
	10.0	3.14	--	--	--
3M	18.0	0.95	0.0	48.0	52.0
	19.0	2.87	0.0	49.5	50.5

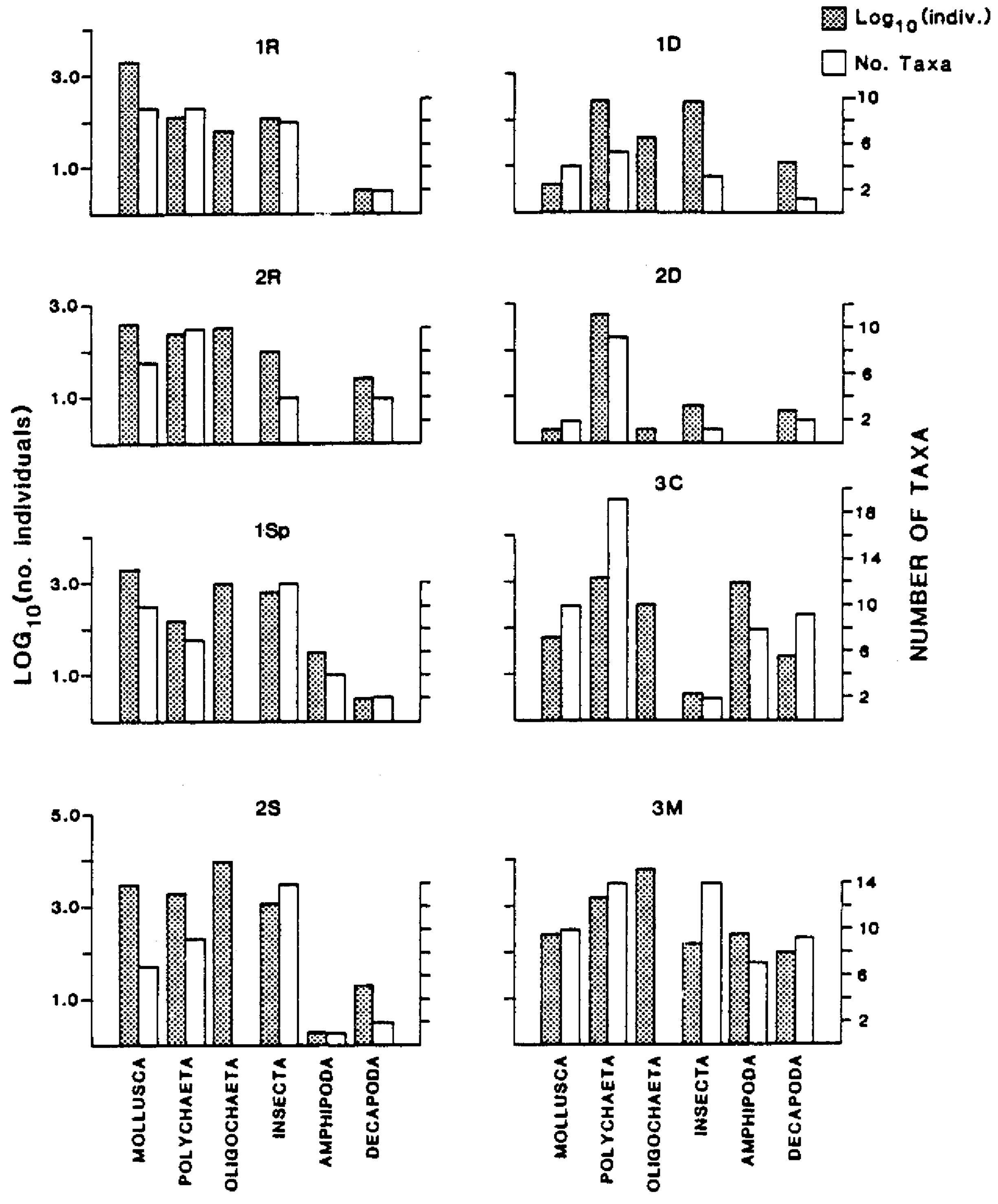

Figure 12.6 Spatial distribution of the number of taxa and $\log_{10}$ transformed number of individuals for major macrobenthic groups. A total of 36 samples were taken at each site for all sampling periods.

The diversity and abundance of amphipods and decapods was also greater at open-marsh sites. Amphipods were totally absent from impoundment sites dominated by *Ruppia maritima*.

Among sites sampled by grab, the perimeter ditches supported fewer taxa and fewer individuals from the major taxonomic groups. Only insects were more abundant in the perimeter ditches than in the creek.

Thirteen taxa each comprised over 1% and together comprised 93.2% of the total number of individuals collected at all sites. These taxa were oligochaete worms, the hydrobiid gastropods *Littoridinops monroensis*, Hydrobiidae A, and Hydrobiidae B; the polychaete worms *Streblospio benedicti*, *Capitella capitata*, *Nereis succinia*, *Hobsonia florida*, and *Stenoninereis martini*; the amphipod *Corophium lacustre*; and the insect families Chironomidae and Hydrophilidae A. These taxa are common benthic components of salt-marsh systems in the southeastern United States (Rader, 1984; Kneib and Stiven, 1982; Kneib, 1984).

Of the 13 numerically dominant taxa, all except the tubicolous spionid polychaete *Streblospio benedicti* and the tube-building amphipod *Corophium lacustre* were consistently more dense at vegetated sites than other areas (Fig. 12.7). *Corophium lacustre* was relatively restricted in its distribution to Chainey Creek (Fig. 12.7), where it was collected in association with the American oyster, *Crassostrea virginica*. Densities of *S. benedicti*, on the other hand, were highest at creek (3C) and open-marsh (3M) sites, whereas in impoundments densities were generally higher in the perimeter ditches (1D and 2D) than at vegetated sites. Spatial differences in density may have resulted from differences in food supply, organics, and sediment composition. Density of *S. benedicti* was not solely influenced by organic content of the sediment, for it was found at the open-marsh site that contained the highest percentages of organics, as well as Chainey Creek, where organics were lowest. Differences in substrate composition between vegetated sites in the impoundments and the open marsh may have also influenced the distribution and abundance of *S. benedicti*, because this worm feeds on surface deposits. Although the species was present during every sampling period, densities were lowest in the fall. A decreased abundance in our samples during that time may result from failure of the 1.0-mm sieve to retain juveniles, which dominate during the autumn months in South Carolina (Bell, 1979).

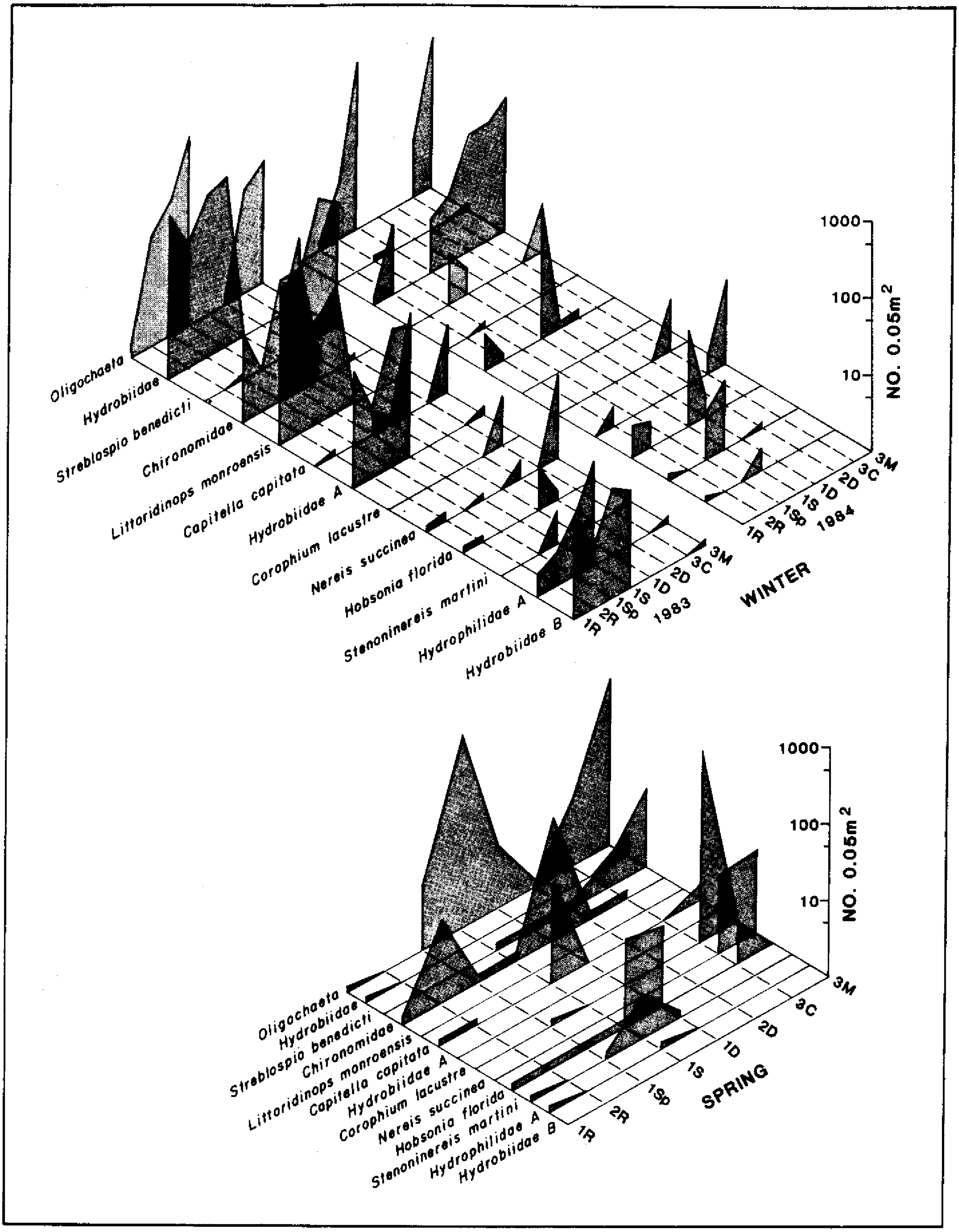

Figure 12.7 The seasonal distribution and abundance patterns of the 13 taxa that together comprised approximately 93% of the total number of individuals at all sites. Abundance is expressed as mean number per 0.05 m^2.

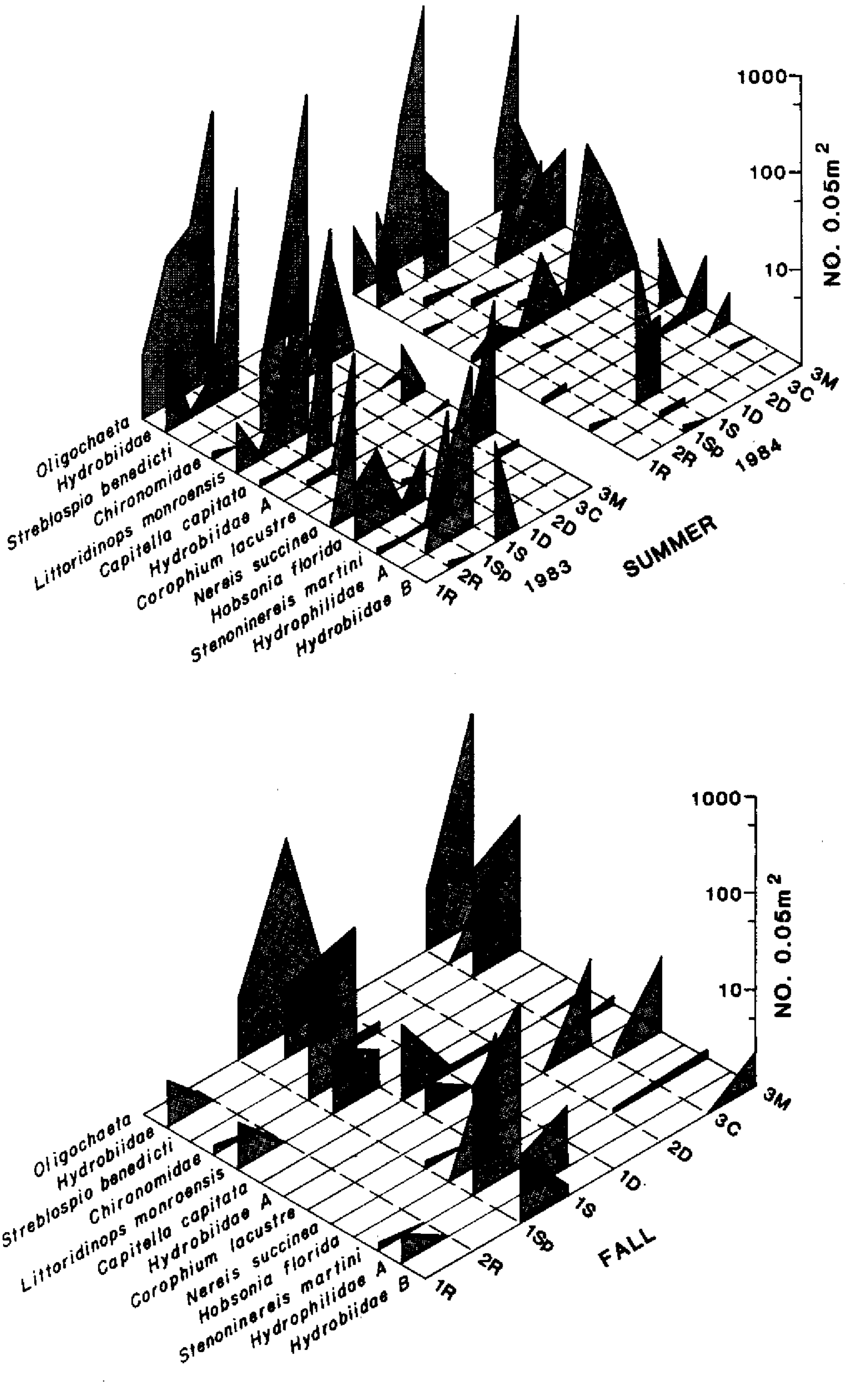

Figure 12.7 Continued.

Of the remaining numerically dominant taxa the hydrobiid snails (Hydrobiidae, Littoridinops monroensis, Hydrobiidae A, Hydrobiidae B), the insects Hydrophilidae A and Chrionomidae, and the polychaetes Capitella capitata, Hobsonia florida, and Stenoninereis martini were consistently most abundant in vegetated sites within the impoundments (Fig. 12.7). Densities of the hydrobiid snails and the chironomid insects were highest at sites 1Sp (Spartina alterniflora), 2S (Scirpus robustus), and 1R (Ruppia maritima), whereas the numerically dominant polychaetes and the hydrophilid insects had highest densities at site 2S. Furthermore, there appeared to be a marked decrease in density of these taxa at sites 1Sp and 2S from 1983 to 1984 for winter and summer collections. Physical factors that may have influenced distribution of these taxa include sediment composition, availability of organic matter and dissolved oxygen, and accumulation of hydrogen sulfide. The distribution of hydrobiid snails is reportedly influenced by resource availability (Levinton, 1979) and sediment composition, with greatest densities occurring in marsh pools and on muddy or silty substrata rich in organic matter (Heard, 1983). Hobsonia florida is also a common inhabitant of estuarine areas rich in detritus and is frequently found in Ruppia beds, but it is not restricted to fine sediments (Heard, 1983). Stenoninereis martini, on the other hand, is generally associated with silt and mud bottoms (Heard, 1983). Capitella capitata is predominantly associated with areas characterized by high levels of organic matter, changes in physical and chemical properties of the sediments, enhanced food supply, and reduced biological interactions that allow development of large populations with little competition (James and Gibson, 1980). Capitella capitata is sensitive to reduced oxygen, so that densities decrease in areas where low dissolved oxygen and high H_2S concentrations occur (Reish, 1960; 1970; Mangum and Van Winkle, 1973; James and Gibson, 1980). The high silt content and negligible flow in the perimeter ditches would likely enhance oxygen depletion and sulfide/organic matter accumulation for species sensitive to those factors, such as C. capitata.

Only two numerically dominant annelid taxa, the Oligochaeta and Nereis succinea, were consistently most abundant at vegetated sites in the impoundments, as well as in the open marsh. Oligochaeta were present during every season, with highest densities at sites 3M and 2S, whereas N.

succinea was consistently abundant in the open marsh, with highest densities occurring at impoundment sites 1R and 2R during the summer of 1983. Kneib (1984) found that oligochaetes were the most evenly distributed invertebrates in a Georgia salt marsh, being abundant in virtually all salt-marsh habitats; however, his study included sampling of benthic macrofauna only from the vegetated bank of a tidal creek landward to the furthest extent of S. alterniflora vegetation. Recognizing that interpretations must be made cautiously, because different gear types were utilized to sample vegetated and nonvegetated areas, our data nevertheless suggest that higher densities of oligochaetes occurred in vegetated areas than at other sampled sites.

Community Structure

For all species combined, macrobenthic density was highest at impoundment site 2S with 475 individuals per 0.05 m^2 (Fig. 12.8). This high density was attributed to the overwhelming abundance of oligochaetes which comprised 60% of the 17,104 individuals collected at this site (Appendix 12.2). The marsh site 3M had a density (254 individuals per 0.05 m^2) that was only slightly greater than half that observed at 2S, but the means were not significantly different (Table 12.9). Among unvegetated sites, density for all sampling periods was significantly higher in Chainey Creek than in the perimeter ditches of impoundments 1 and 2 (Fig. 12.8, Table 12.9). These patterns were consistent for each sampling period, although statistical significance of mean density between sites varied with season (Table 12.10).

Densities at each site also varied between sampling periods, with highest values observed in the winter of 1983 for all vegetated sites except 2S (Fig. 12.9). At impoundment sites 1R and 2R dominated by Ruppia maritima, densities decreased from winter through fall of 1983, when lowest values were noted. Densities in impoundment site 1Sp and open-marsh site 3M followed a pattern similar to 1R, with values markedly declining from the winter of 1983 to the winter of 1984. Impoundment site 2S, however, had highest densities in the summer of 1983, followed by a noticeable decline in the fall of 1983. At unvegetated sites, temporal changes in density were most consistent between sites 1D and 3C. Values declined at these sites from winter to summer 1983, remained low during

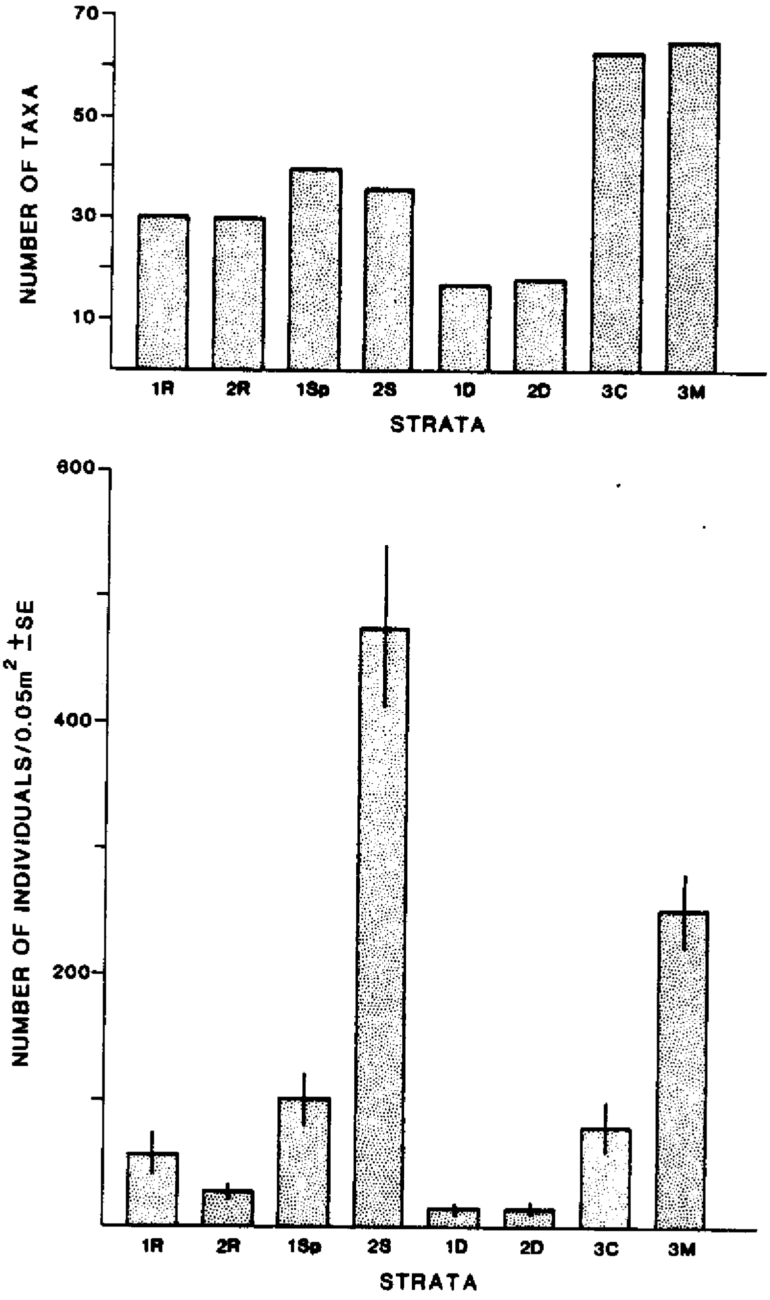

Figure 12.8 Total number of species and density of individuals at sites sampled during the two-year study. Vertical lines indicate the standard error of the mean. A total of 36 samples were taken at each site.

Table 12.9 Results of one-way analysis of variance (Model I) comparing the transformed number of macrobenthic taxa and individuals between sites for all sampling periods. ** $P < .01$; *** $P < .001$.

Source of Variation	Degrees of Freedom	Sums of Squares	F value	Results of a *posteriori* comparisons
Vegetated strata				
		Dependent Variable:	Log_{10} (no. taxa + 1)	
Between strata ($r^2 = 0.56$)	4	0.9309	7.98**	$\mu_{3M} \quad \mu_{2S} \quad \mu_{1Sp} \quad \mu_{1R} \quad \mu_{2R}$
Within Strata	25	0.7295		
Total	29	1.6604		
		Dependent Variable:	Log_{10} (no. individuals + 1)	
Between strata ($r^2 = 0.60$)	4	8.5339	9.25***	$\mu_{2S} \quad \mu_{3M} \quad \mu_{1Sp} \quad \mu_{1R} \quad \mu_{2R}$
Within strata	25	5.7679		
Total	29	14.3019		
Unvegetated strata				
		Dependent Variable:	Log_{10} (no. taxa + 1)	
Between strata ($r^2 = 0.89$)	2	0.9539	60.18***	$\underline{\mu_{3C}} > \underline{\mu_{1D} \quad \mu_{2D}}$
Within strata	15	0.1188		
Total	17	1.0728		
		Dependent Variable:	Log_{10} (no. individuals + 1)	
Between strata ($r^2 = 0.55$)	2	1.5217	9.20**	$\underline{\mu_{3C}} > \underline{\mu_{2D} \quad \mu_{1D}}$
Within strata	15	1.2404		
Total	17	2.7622		

Table 12.10 Results of one-way analysis of variance (Model I) comparing the transformed number [$\log_{10}(x + 1)$] of macrobenthic taxa and individuals between sites for each sampling period. Separate analyses were performed for data from vegetated and unvegetated sites. Means presented were retransformed to linear scale. Taxa = Log_{10} (no. taxa + 1); Indiv. = Log_{10} (no. individuals + 1); ns - not significant; * P <.05; ** P <.01; *** P < .0001.

	Vegetated Sites								Unvegetated Sites					
	r^2	Degress of Freedom	F Value						r^2	Degrees of Freedom	F Value			
Winter 1983														
				1R	2R	2S	1Sp	3M				1D	2D	3C
Taxa	0.94	5/9	20.40**	8.3	8.6	10.6	12.1	17.4	0.88	3/5	11.00**	3.7	4.11	10.2
				2R	1R	1Sp	3M	2S						
Indiv.	0.95	5/9	26.35**	104.1	285.2	368.7	553.4	645.1	0.59	3/5	2.15_{NS}	24.1	25.3	101.4
Winter 1984														
				1Sp	2R	1R	2S	3M				ID	2D	3C
Taxa	0.93	5/9	16.29**	2.1	2.5	2.8	6.3	8.3	0.81	3/5	6.2	2.6	1.6	5.5
Indiv.	0.97	5/9	40.40***	10.4	9.9	4.9	242.6	170.9	0.97	3/5	50.5**	9.6	33.2	49.5
Fall														
				1R	2S		1Sp	3M				ID	2D	3C
Taxa	0.93	4/7	16.62**	3.2	9.9		10.6	12.3	0.96	3/5	38.8**	0.9	1.2	6.8
Indiv.	0.91	4/7	13.26*	5.9	176.1		70.2	207.7	0.88	3/5	11.2*	1.5	1.5	27.1
Spring														
				1R	2R	1Sp	2S	3M				1D	1D	3C
Taxa	0.93	5/9	16.57**	1.5	2.3	2.3	5.2	7.6	0.89	3/5	13.2*	1.8	2.7	8.6
Indiv.	0.92	5/9	13.85**	1.5	8.9	8.2	284.4	154.9	0.79	3/5	5.89	1.8	58.1	85.2
Summer 1983														
				1R	2R	1Sp	3M	2S					ID	3C
Taxa	0.88	5/9	9.49*	6.7	6.9	9.2	13.8	15.1	0.99	2/3	4422.99***		0.3	9.7
Indiv.	0.99	5/9	238.64***	34.5	64.1	111.2	291.4	1026.1	0.99	2/3	426.06**		0.3	57.0
Summer 1984														
				2R	1R	1Sp	3M	2S				ID	2D	3C
Taxa	0.94	5/9	20.66**	2.6	3.7	6.5	11.8	7.6	0.96	3/5	38.1**	0.5	3.3	6.6
Indiv.	0.91	5/9	12.13**	5.6	17.8	51.6	100.2	380.1	0.98	3/5	86.6**	0.9	37.0	68.6

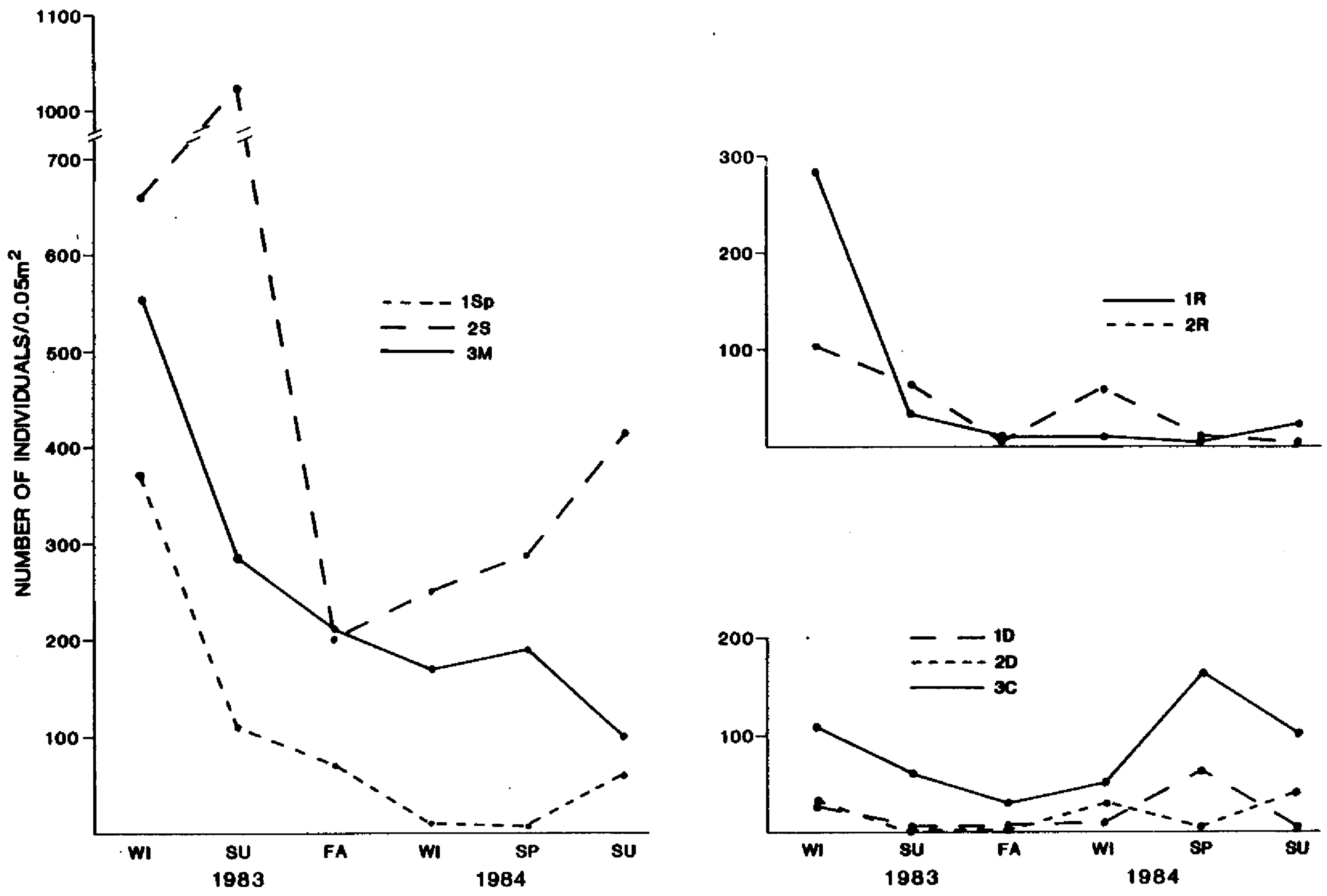

Figure 12.9 Density of benthic macroinvertebrates observed during each sampling period for each site.

fall then increased to highest observed densities in spring 1984 (Fig. 12.9).

Macrofaunal densities observed during this study showed comparable temporal trends to those from other salt marshes in the southeastern United States (Cammen, 1979; Teal, 1962; Kneib and Stiven, 1982). These investigators noted that lowest infaunal densities coincided with highest abundances of dominant natant species of the salt marsh, such as fish and shrimp, and suggested that increased predation on infauna may be an explanation for observed decreases in densities.

Results of our study were not as conclusive and suggest that other factors may be affecting densities in this system as well. In 1983, most sites clearly showed a temporal pattern of lowered density in summer and fall that coincided with increased abundances of natant predators. The exception to this pattern occurred at impoundment site 2S, where density increased in the summer of 1983, largely because of overwhelming numerical dominance by oligochaetes. Oligochaetes, however, are burrowing deposit feeders that are not as vulnerable to predation or physical environmental conditions as those taxa that inhabit or feed at the sediment surface (Kneib and Stiven, 1982). Abundances of fish predators such as Micropogonias undulatus and Leiostomus xanthurus that predominantly consume macrobenthic prey were highest in spring and early summer in both the impoundments and Chainey Creek (see Chapter 14). Other natant species such as Fundulus heteroclitus, Palaemonetes pugio, and Penaeus setiferus are recruited to salt-marsh systems and the impoundments during summer. These species are known predators on macrobenthos in marshes (Kneib and Stiven, 1982) and may have been important in reducing densities of macrobenthos at most of the study sites in the summer and fall of 1983.

In addition to predation by fishes and decapod crustaceans, birds were probably important in reducing densities of macrobenthos through predation. Shorebird predation has been shown to reduce epifaunal abundances on mud flats at low tide (Goss-Custard, 1977; Grant, 1981; Quammen, 1984; Pienkowski, 1981). Evans et al. (1979) found that shorebirds removed about 90% of the standing crops of large Hydrobia and Nereis during a single winter. Observations of shorebirds in the impoundments revealed that foraging was heavy on exposed flats following drawdown in spring. Examination of crops and intestines from five species of birds (lesser yellowlegs, *Tringa flavipes*; dunlin, *Caldris alpina pacifica*; dowitches, *Limnodromus grisius*; semipalmated sandpiper, *Calidris pusillus*; and least sandpiper, *Calidris minutilla*) revealed that polychaetes and insects were important food items (Table 12.11). Foraging ability, and hence the resultant effect on macrobenthos in impoundments, is probably maximized during periods of low water level or drawdown. Thus increased predation in spring by birds, compounded with that of natant predators, may at least partially explain the reduced densities of macrobenthos in summer.

Although decreased densities noted at most sites during the summer and fall sampling would tend to support the hypothesis that the factors mentioned above were influential, this hypothesis is confounded by the fact that temporal faunal densities in 1984 differed markedly from those in 1983. At no site, except Chainey Creek (3C), did densities in 1984 exceed those of sampling periods in 1983, suggesting that predation intensity may vary from year to year and that factors other than predation may have regulated densities at the study sites.

Physical conditions, which had wide fluctuations at sites over the two-year study, may explain some of the annual differences. Conditions during the summer of 1983 were atypical, in that there was little rainfall, salinity rose to 25 ppt, and dissolved oxygen in the impoundments was critically low(~2 mg/l). The persistence of these conditions into the fall created stressful conditions in the impoundments that may have affected the marsh fauna.

Decreased oxygen levels become critical at impoundment sites, where sediments have a high silt content and there is low sedimentary flushing of small particle sizes. This situation is likely to enhance oxygen depletion and the accumulation of sulfides and organic matter. A further complication from lowering of the water level is enhanced leaching and oxidation of the marsh soils (Wilkinson, 1970). If marsh sediments are not kept moist, sulfides are oxidized to form sulfuric acid and cat clays, which can reduce sediment pH to 2.5 or less (Neely, 1962). Wilkinson (1970) noted that soil pH was variable, ranging from 3.2 to 8.3 in an impoundment that had extensive drawndown from March to October. Densities of invertebrates such as molluscs and crustaceans that depend on alkaline conditions for shell building may be affected if low pH occurred at the

Table 12.11 Number of individual food items from stomachs of five species of shore birds taken from the open marsh (M) and a nearby large impoundment (I), with number of stomachs listed under M and I. * Indicates additional body parts or wing fragments. Counts were taken only from heads.

	Calidris pusillus		*Tringa flavipes*		*Calidris alpina pacifica*	*Limnodromus griseus*	*Calidris minutilla*
	M	*I*	*M*	*I*	*I*	*I*	*I*
Food Items	11	7	1	5	6	6	5
Hemiptera							
adults	5		47	155			*
Chironomidae							
larvae	437	319	18	51	154	641	29
Culicidae				7	1	1	
Tabanidae				8			
Hydrophilidae A							
larvae				72			1
Coleoptera							
adults	2		1	29	1*	11	4*
Hymenoptera							1
Polychaeta							
mandibles							
c.f. *Nereis*	6 prs	39 prs.	2 prs.	56 prs.		529 prs.	
Gastropoda	2		7	28	2	25	
Ostracoda	845	39	4	4		2	
Nematoda	1	2					
Foraminifera	119	349					57
Scirpus Seeds	60	72	1	7	401	216	20
Crab claws					2		
Total	1477	820	80	417	561	1425	112

sediment-water interface in the study impoundments. Studies of groundwater chemistry, however, revealed no areas of low pH that would indicate cat clay development (Chapter 5).

Since predation was probably acting to reduce macrobenthic densities in the summer and fall, the added impact of unusually harsh environmental conditions could have had a long-term depressive effect on the density of macrobenthos. The alternative management of impoundment 2, which was not drained in 1984, apparently had little effect on the macrobenthos. Interestingly, there was some evidence of recovery in 1984 at site 2S, largely because of dominance by oligochaetes. Previous studies have found that the population structure and distribution of oligochaetes is controlled by specialized food requirements (Giere, 1975) rather than sediment composition or other physical factors.

Density patterns observed at unvegetated sites were more easily explained than those at other sites. The perimeter ditches had consistently lower densities of macrobenthos than the creek. Differences in waterflow, sediment composition, and dissolved oxygen were largely responsible. The sediments in the perimeter ditches were highly reduced silt and clay, of the sulphuretum type described by Fenchel (1969). Since these ditches are deeper than the flats, they act as sinks for organic material and are highly stratified because of poor water circulation. Anoxic conditions frequently occur in highly stratified areas such as canals (Taylor and Saloman, 1968; Gilmore and Trent, 1974) and boat harbors (Reish, 1961). The severe conditions noted during the summer of 1983 undoubtedly intensified anoxic conditions in the perimeter ditches, with the result that few animals were collected at either ditch site (Fig. 12.9). In addition to poor water quality in the perimeter ditches, the particle size composition of sediments may also have been unfavorable for benthos. Perimeter ditch sediments were predominantly silt and clay, while the creek bottom had a greater percentage composition of coarser sediments. Benthic infauna have been reported to be more abundant in sediments with low to intermediate amounts of silt and clay (Gilmore and Trent, 1974).

The total number of taxa, which is less likely than number of individuals to be biased by utilization of different sampling gear (Stoner et al., 1983), was highest for the open marsh (3M) and Chainey Creek (3C) sites (Fig. 12.8). Values at these sites greatly exceeded those observed elsewhere, although no statistically significant difference in number of taxa was found between these sites and those in the impoundments dominated by Spartina alterniflora and Scirpus robustus (Table 12.12). Comparisons of mean number of taxa between vegetated sites revealed no statistically significant difference between the open marsh and impoundment sites 2S and 1Sp, whereas among unvegetated sites, Chainey Creek had statistically more taxa than did the perimeter ditches of impoundments 1 and 2 (Table 12.9). These patterns remained relatively consistent for each sampling period, with the mean number of taxa being significantly greater in the open marsh than at other sites only during winter 1983 (Table 12.10). Chainey Creek had significantly more taxa than did the perimeter ditches for all sampling periods except winter and summer 1984.

H' diversity showed spatial variations that largely reflected how even individuals were distributed among species, rather than the number of species or species richness (Appendix 12.3).

Because the seasonal changes in number of macrobenthic taxa at the study sites were similar to those observed for density, physical factors were probably important contributors to the decline in species richness noted at several sites in the summer and fall of 1983. The comparatively low diversity in the perimeter ditches is particularly indicative of stressful conditions. Altered redox conditions, with lower oxygen and increased hydrogen sulfide, may have caused depletion of fauna. Tenore (1972) noted that anoxic conditions in the Pamlico River estuary of North Carolina resulted in a depletion of macrobenthos and establishment of a "pioneer" community that was less diverse. The extremely reduced nature of the sediments suggests that the perimeter ditches are a physically regulated habitat that can be colonized by only a few opportunistic benthic species that are adapted for survival in harsh environments.

The differences observed in community structure among vegetated sites may reflect differences in habitat complexity and predation effects. Stoner (1980) found that species richness of macrobenthos in seagrass beds increased with increasing plant biomass. Furthermore, predation effects may be lessened in dense vegetated habitats because of lessened predator efficiency (Stoner, 1982). Lewis and Stoner (1983) cautioned that behaviorial preference may also be an important determinant of the number

Table 12.12 Results of one-way analysis of variance to test for significant differences in transformed ($\log_{10} + 1$) number of taxa between all study sites. *** $P < .001$.

Source	Degrees of Freedom	Sums of Squares	F Value	Results of *a posteriori* comparison[1]
Between strata ($r^2 = 0.75$)	7	2.564	17.27***	3M 2S 3C 1Sp 1R 2R 1D 2D
Within strata	40	0.8484		
Total	47	3.4122		

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[1] Ryan-Einot-Gabriel-Welsh F test

of species in seagrass beds. Field studies such as that described by Rader (1984), which correlate densities of macrobenthos with the microdistribution of plants and the area and volume of vegetation, need to be implemented before valid explanations for spatial diversity patterns of macrobenthos among different vegetation of marshes and impoundments can be obtained.

Faunal Assemblages

Normal cluster analysis of pooled replicate samples taken from each location for each sampling period indicated groupings that were related to stratum type rather than season (Fig. 12.10). The first two groups contained all the sites sampled in the open marsh and Chainey Creek. These groups were most similar in species composition to each other and there was high internal similarity of sites within each group, indicating that a characteristic and persistent suite of macrobenthos existed among sampling periods.

Groups 3, 4, and 5 consisted of all the perimeter ditch sites, as well as a few vegetated sites (1R, 2R, and 1Sp) within the impoundments. These groups were most similar to each other in species composition, but there was not much similarity within each group. The remaining vegetated impoundment sites formed group 6. Most sites within this group did not have strong similarity to each other in terms of species composition.

Inverse cluster analysis of the 66 taxa remaining after data reduction resulted in the selection of 13 groups (Table 12.13). The major branches of the inverse cluster dendrogram indicated that groups A through C were very dissimilar to the others, with their constituent species occurring frequently in a specific stratum or in several strata (Figure 12.11). Group A consisted of taxa that were consistently collected in and restricted to the open-marsh site 3M, despite their relatively low abundance compared to other species collected at all sites (2.7% of total individuals) and in the marsh (9.9% of total individuals). Of taxa comprising this group the amphipods *G. palustris* and *O. uhleri* were collected only at site 3M.

Taxa in group B were among the numerically dominant macrobenthos collected during the study. These taxa were not restricted to any particular strata, as indicated by low fidelity values, but were

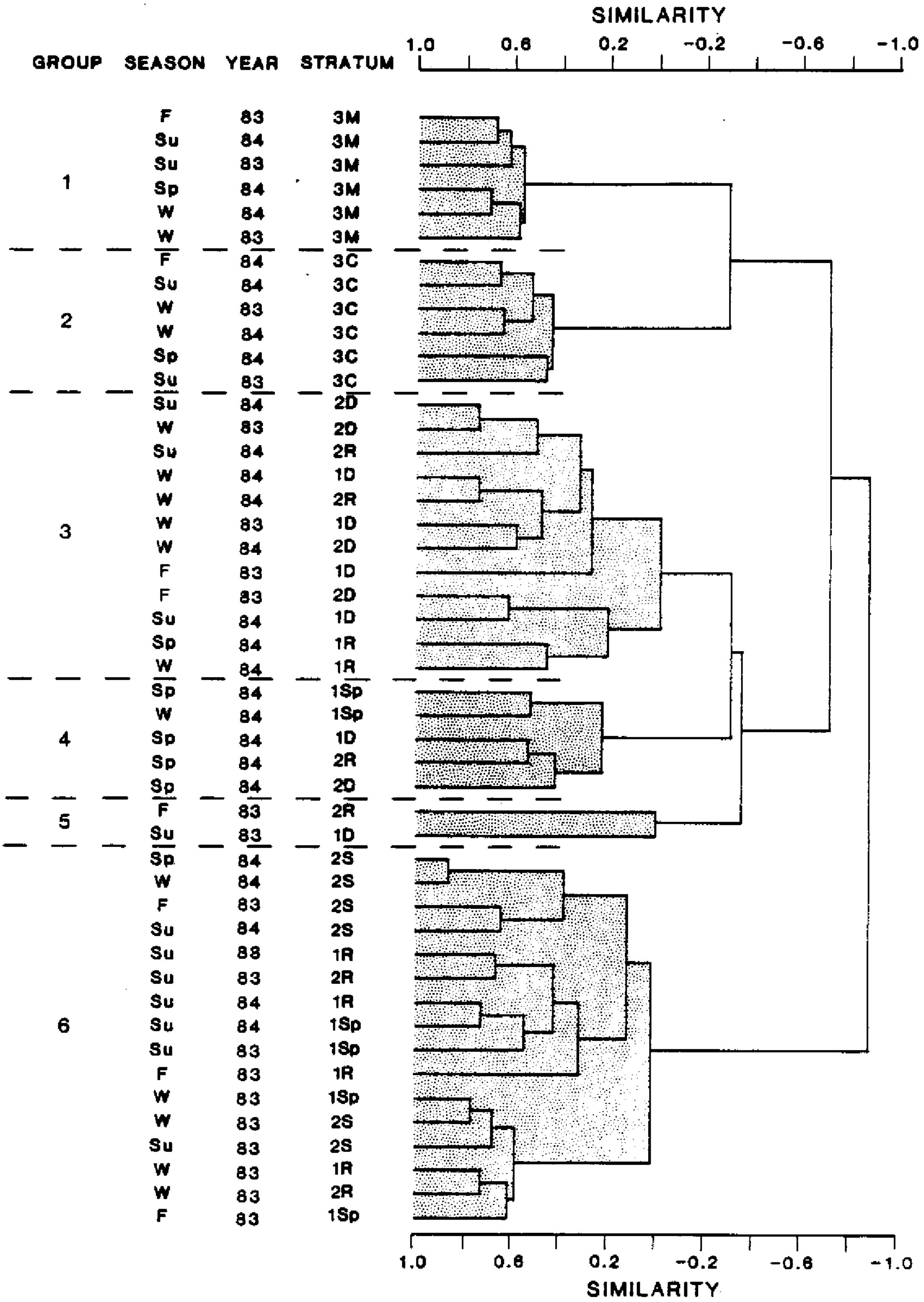

Figure 12.10 Dendrogram resulting from normal cluster analysis of benthic samples taken from strata over the two-year study period.

Table 12.13

Faunal groups resulting from inverse cluster analysis of data collected from grab and core samples over all sampling periods. (A = Amphipoda, As = Ascidiacea, B = Branchiura, D = Decapoda, I = Insecta, Is = Isopoda, M = Mollusca, P = Polychaeta, T = Tanaidacea).

Group A
- *Gammarus palustris* (A)
- *Orchestia uhleri* (A)
- *Manayunkia* sp. (P)
- *Cassinidea lunifrons* (Is)
- *Hargeria rapax* (T)
- *Uca* sp. (D)
- Ceratopogonidae (I)

Group B
- *Stenoninereis martini* (P)
- *Capitella capitata* (P)
- *Hobsonia florida* (P)
- *Streblospio benedicti* (P)
- *Nereis succinea* (P)
- Oligochaeta

Group C
- Coenagrionidae (I)
- Hydrobiidae C (M)
- Libellulidae (I)
- Tabanidae (I)
- Hydrobiidae A (M)
- Hydrobiidae B (M)
- *Littoridinops monroensis* (M)
- Chironomidae (I)
- Hydrophilidae A (I)
- Hydrobiidae D (M)

Group D
- *Macoma balthica* (M)
- *Scolecolepides viridis* (P)
- *Tellina* sp. (M)

Group E
- *Palaemonetes vulgaris* (D)
- *Rhithropanopeus harrisii* (D)
- *Melita nitida* (A)
- *Corophium lacustre*
- *Laeonereis culveri* (P)
- Nemertinea (P)
- *Polydora* sp. (P)

Group F
- *Geukensia demissa* (M)
- Muscidae (I)
- Collembola (I)

Group G
- *Callinectes sapidus* (D)
- *Edotea montosa* (I)
- *Panopeus herbstii* (D)
- *Polydora ligni* (P)
- *Uca minax* (D)
- Dolichopodidae

Table 12.13 continued

Group H

- Cuculidae (I)
- *Gammarus mucronatus* (A)

Group I

- *Palaemonetes pugio* (P)
- *Eteone heteropoda* (P)
- *Mulinia lateralis* (M)
- *Heteromastus filiformis* (P)
- *Nemertinea* A
- *Nemertinea* B
- *Molgula manhattensis* (As)

Group J

- *Glycera americana* (P)
- *Sabellaria vulgaris* (P)

Group K

- Hydrophilidae B (I)
- Tipulidae (I)
- *Gammarus tigrinus* (A)
- Haliplidae (I)

Group L

- *Uca pugnax* (D)
- Ephydridae (I)
- *Polydora* sp. A (P)
- *Melita appendiculata* (A)

Group M

- *Argulus* sp. (B)
- *Onobops jacksoni* (M)
- *Macoma* sp. (M)
- Hirudinea

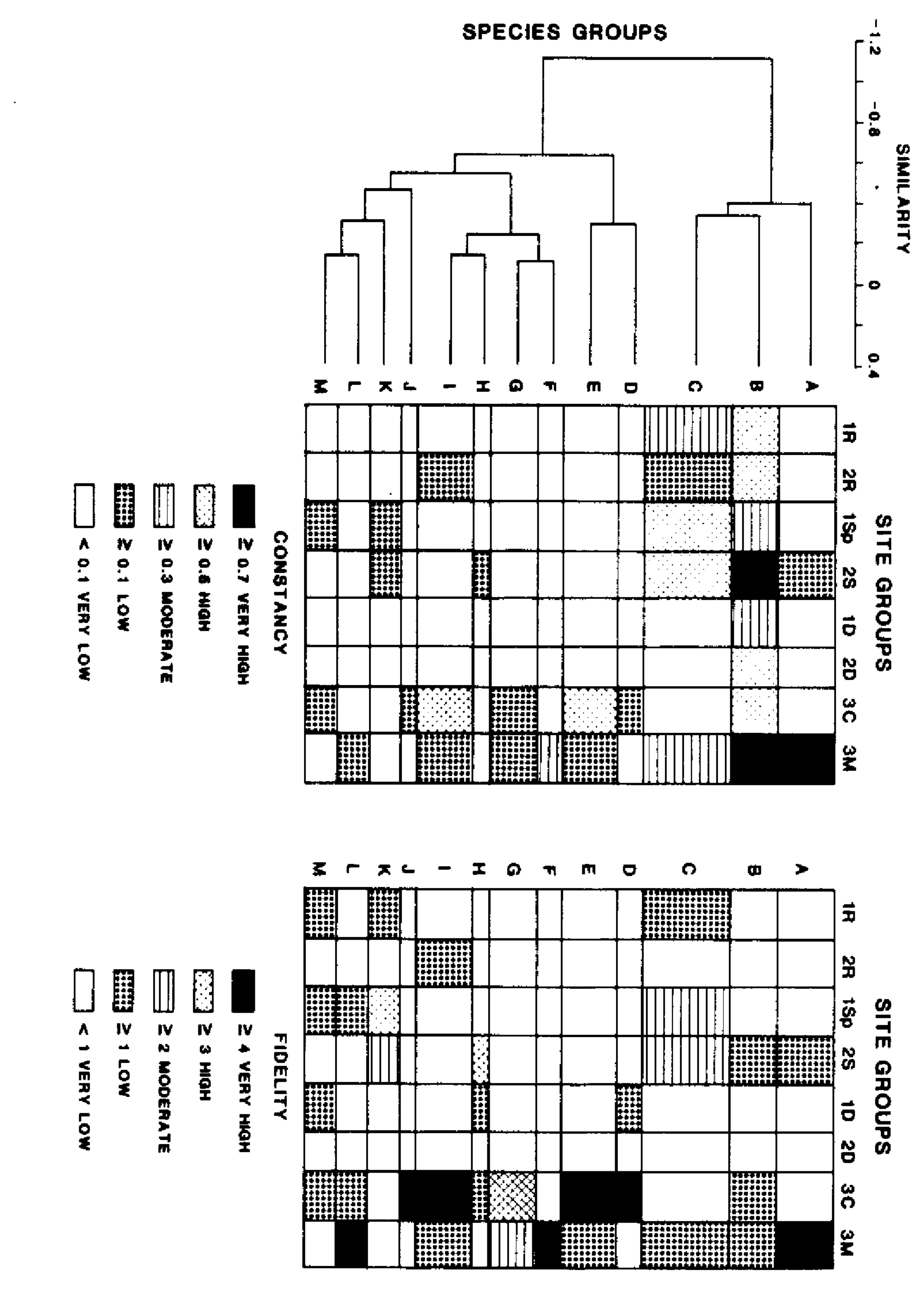

Figure 12.11 Inverse classification hierarchy and nodal diagram showing constancy and fidelity of site-species group coincidence.

consistently collected at most sites, with highest constancy at sites 2S and 3M.

Group C, which consisted totally of insects and hydrobiid snails, contained several numerically dominant taxa; however, this faunal assemblage was associated only with vegetated sites and displayed high constancy only in collections from impoundment sites 1Sp and 2S. These taxa are apparently an assemblage that occupies frequently flooded vegetated habitats. Hydrobiid snails have been reported by Heard (1983) to reach high densities in marsh pools and other wet areas of Gulf tidal marshes. The Tabanidae, as well as other insects, are influenced by tidal flooding and zonation of vegetation (Daiber, 1982), with highest densities occurring in frequently flooded habitats with dense vegetation (Dukes et al., 1974).

The remaining faunal assemblages (D-M) occurred relatively infrequently, but most were restricted in their distribution to specific sites. Groups D, E, G, I, and J consisted of taxa that displayed very high fidelity to Chainey Creek sites (3C), but with the exception of taxa in groups E and I, were not consistently collected there. Taxa in these groups, which were collected only from Chainey Creek included the molluscs *Mulinia lateralis* and *Tellina* sp.; the polychaetes *Glycera americana*, *Heteromastus filiformis*, *Sabellaria vulgaris* and *Scolecolepides viridis*; the crab *Rhithropanopeus harrisii*; and the nemertineans A and B. In addition to an apparent spatial restriction to the marsh creek, *G. americana* and *S. vulgaris* which formed Group J were collected only in the fall; *R. harrisii* was collected only in the spring; and *S. viridis* and *Macoma balthica*, which was also collected at site 1D, occurred only in the summer. Occurrence of *G. americana*, *S. viridis* , *S. vulgaris*, and *M. lateralis* coincided with high salinities in summer and fall.

Groups F and L were highly faithful to collections from the open-marsh site, but were neither very abundant in our samples nor highly constant in collections from that site. The fiddler crab *Uca pugnax* and the insect family Muscidae were collected only at site 3M.

The remaining species assemblages forming groups H, K, and M were not consistently collected at any site; however, taxa in groups H and K were highly faithful to impoundment sites 2S and 1Sp, respectively. The association of these taxa with impoundment sites is consistent with what is known of their ecology. The amphipods *G. tigrinis* and *G. mucronatus* are common subtidal inhabitants of brackish estuarine areas, where they are associated with vegetation and debris (Bousfield, 1973). Impoundment sites 1Sp and 2S provided not only a submerged habitat, but the large culms and stems of *Spartina* and *Scirpus* at these sites may have provided shelter and food for the cuculid, tipulid, and haliplid insects.

The macrobenthos collected during this study can be grouped into four broad groups based on habitat preference: (1) an open-marsh assemblage, (2) a creek assemblage, (3) a eurytopic assemblage, and (4) an impoundment assemblage. The group that was mainly restricted to the open-marsh habitat consisted of two component assemblages: (1) those species such as *G. palustris*, *O. uhleri*, *Manayunkia* sp., and *Hargeria rapax* that were consistently abundant in this habitat and (2) those that were relatively rare or not adequately sampled by the gear, such as *Geukensia demissa*, *Uca pugnax*, and *Melita appendiculata*. Closely related in faunal composition to the open-marsh assemblage was the creek fauna, which contained typical estuarine species that occur over a broad salinity gradient (e.g., *Macoma balthica*, *P. vulgaris*, and *H. filiformis*) and transient species that are present in the marsh creek only during certain seasons and salinity conditions (e.g., *G. americana*, *S. vulgaris*, and *M. lateralis*). The third major macrobenthic assemblage in the study area consisted of taxa that were numerically dominant and frequently collected at most sites. Many of the most abundant taxa (Fig. 12.7) collected in the study were included in this group (e.g., *S. martini*, *C. capitata*, *H. florida*, *S. benedicti*, *N. succinea*, and Oligochaeta). The final group of taxa were characteristic of vegetated sites within the impoundments. Insects such as the numerically dominant Coenagrionidae, Chironomidae, and Hydrophilidae A, as well as hydrobiid snails, were the major constituents of this group.

Although estuarine macrobenthic organisms are tolerant of a wide range of physical variables that enable them to live in a variety of habitats, the zonation of faunal assemblages by sampling sites rather than sampling period suggests that structural differences between habitats are important factors determining distribution patterns. The most obvious differences between major habitats are related to sediment composition, type and density of vegetation, amount of flooding and hydroperiod, and water circulation. Water-level manipulations in impoundments create a distinctive habitat that differs from the natural marsh by duration of flooding, vegetative diversity, and sediment chemistry. The creek environment, however, provides subtidal habitat with oyster beds and allocthonous debris and has diel tidal currents. Interestingly, the faunal assemblages of the natural marsh are more similar to those from the creek than the impoundments, which are dominated by insects and hydrobiid snails. Although diverse vegetation and long-term flooding in the impoundments appear to be conducive to habitation by insects, hydrobiid snails, oligochaetes and some polychaetes, the stressful conditions due to low water circulation and prolonged periods of oxygen depletion may have discouraged establishment by many intertidal invertebrates.

CONCLUSIONS

Major differences in faunal composition and community structure of macrobenthic invertebrates were observed between habitats in this study. The impoundments, which supported different faunal assemblages than the creek and marsh habitats, contained vegetated sites that were inhabited by fewer species than nonimpounded sites, whereas the perimeter ditch sites were comparatively depauperate. A primary reason for the low species richness observed in the perimeter ditches and most vegetated sites in the impoundments was the limited number of taxa that could adapt to stressful conditions of varying salinity, pH, and dissolved oxygen. Despite severe environmental stresses in the salt-marsh system, diel tidal inundation ensured that water was circulated and nutrient exchange occurred over that habitat twice daily. The impoundment represented a more stressful habitat, because water exchange was dependent on management objectives and water control. Water circulation was largely mediated by wind during the study. This was particularly true for the perimeter ditches, which received little vertical mixing because of water depth and, consequently, were anoxic for prolonged periods. Although water-management strategy influences abundance and occurrence of taxonomic groups such as fishes and birds, there was little evidence to support that the alternate strategy of tidal circulation in impoundment 2 during 1984 influenced macrobenthic species composition or density.

In a physically stressed environment such as that occurring in the impoundments, predation effects could be especially important in structuring the macrobenthic community. The effect of natant predators such as fish and shrimp would most likely be intensified in habitats that are shallowly inundated for prolonged periods rather than in the open marsh, where natant predators forage only at high tide. Increased predation by natant predators in warmer months when water quality is poor could so drastically reduce the density of some moderately common or rare species in impoundments that they may become rare or be eliminated altogether. Predation is probably an important regulator of macrobenthic densities in the marsh creek. Although predator refugia such as patches of subtidal oyster reefs and allocthonous debris exist in the creek, these may not offer as effective a refuge as dense vegetation. The influence of predation on the macrobenthos in the creek may be less important in structuring the community than the better water quality conditions, moderately coarse sediments, and lower amount of organic matter found there.

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SECTION VII

NEKTONIC COMMUNITY

GENERAL INTRODUCTION

Decapod crustaceans function both as metabolizers of energy and controllers of energy flow in the salt marsh. Particulate consumers such as fiddler crabs and shrimps feed on phytoplankton and benthic algae, as well as on detritus derived from Spartina and feces (Field, 1983). One of the most important particulate feeders is the grass shrimp, Palaemonetes pugio, which is a conspicuously abundant inhabitant of salt marshes (Kneib, 1984) and impoundments (this report). This species dampens organic pulses and fluctuations in detritus production through its feeding activities (Welsh, 1975). Large accumulations of macrophytic biomass are prevented from occurring, and the production of total consumables such as biomass, dissolved organic matter (DOM), and fecal pellets are converted to protein-rich material because of the grazing activity of grass shrimp. This conversion process is important not only for making detritus available to several different trophic levels, but also because the particles are processed in such a way that substrate is enhanced for accelerated growth by diatoms and bacteria.

As larvae, penaeid shrimps and blue crab are planktotrophs. Their diets in nature are not known, but survival and growth in the laboratory increases on a mixture of phytoplankters and zooplankters rather than on phytoplankton alone (Pearson, 1939; Ewald, 1965; Sulkin, 1978; Millikin, 1978). Thus as meroplankton, larvae of these species feed at the base of the food web on the primary producers and primary consumers. While planktonic, penaeid shrimps and blue crab are susceptible to predation by a large number of organisms such as filter-feeding fishes and possibly coelenterates and ctenophores (Van Engel, 1958).

Having reached the estuarine nursery areas, postlarval and juvenile penaeids and juvenile blue crab settle out of the plankton and adopt a benthonic existence. Here penaeid shrimps and blue crab are opportunistic omnivores, feeding on a wide variety of plant and animal materials. Penaeid shrimps consume algae, organic detritus, and small infaunal and epifaunal organisms (Perez-Farfante, 1969). As well as being scavengers, blue crabs are active predators on fish, mollusks, and other crustaceans

(Tagatz, 1968; Millikin and Williams, 1984). Smaller juveniles also consume detritus (Laughlin, 1982). Juvenile and adult penaeid shrimps are preyed on principally by fishes (Perez-Farfante, 1969). Blue crab, especially vulnerable in the softshell stage, are consumed by a large number of fish species and may be an important food item in some species such as the red drum, Sciaenops ocellatus, and black drum, Pogonias cromis (Jaworski, 1972; Millikin and Williams, 1984).

The transfer efficiency of carbon from particulate feeders to scavengers and carnivores such as blue crab, Callinectes sapidus, that are seasonally abundant in salt marshes (Kneib, 1984) is about 20% (Field, 1983). Day et al. (1973) noted that the total intake of organic matter by the blue crab population in a Louisiana salt marsh system must be 1.88 g/m^2 per year. Mud crabs are important consumers of detritus and were reported by Teal (1962) to consume 5.4 g/m^2 per year. Although there is an apparent surplus of carbon within the marsh system, much of it is refractory and poor in nitrogen. The widespread occurrence of omnivory among marsh inhabitants suggests that food does limit the population size of consumers (Montague et al., 1981).

Decapod crustaceans such as fiddler and mud crabs have an active role in controlling energy flow. These organisms aerate the sediments by burrowing or turning over the top layers of sediment, thereby allowing aerobic microorganisms to colonize the material. Large decapod crustaceans such as blue crab masticate food, reducing the particle size and making the egested material more accessible to utilization by microbes through increased surface area (Field, 1983).

Chapter 13

A. Recruitment Patterns Of Selected Decapod Crustaceans

E. J. Olmi, III

INTRODUCTION

Estuarine salt marshes not only support a diverse assemblage of permanent residents (Nixon and Oviatt, 1973; Subramanyam and Drake, 1975; Subramanyam et al., 1976; Bell, 1979; Knieb, 1984) but also harbor large numbers of transients, those natant species that utilize the inundated marsh for refuge and food availability (Herke, 1971; Bell and Coull, 1978; Minello and Zimmerman, 1983; Boesch and Turner, 1984). Mome transient species are permanent in that they utilize the marsh year round, even though access is restricted to periods of inundation (Kneib, 1984). Most, however, are seasonal in occurrence, utilizing the shallow estuarine areas (especially vegetated areas) as nursery grounds during postlarval and juvenile stages (Herke, 1971; Weinstein, 1979; Rogers et al., 1984; Rozas and Hackney, 1984), then moving as adults to deeper parts of the estuary or to the ocean. Although settlement of transient species on the nursery grounds is usually by postlarvae or juveniles, most have planktonic larval stages which risk being flushed out of the estuary by its net seaward flow. Larval and postlarval stages of many taxa exhibit behavioral patterns, however, that facilitate retention in the estuary (Bousfield, 1955; Sandifer, 1975; Cronin, 1982), expulsion from and later reinvasion of the estuary (Sandifer, 1975; McConaugha et al., 1981; Epifanio et al., 1984), or penetration of the estuary by marine-spawned species (Hughes, 1969; 1970; 1972; Weinstein et al., 1979). Typically, these meroplankters effect estuarine retention or penetration by vertical migration upward during flood tide and then downward to the level of no net motion (or inflowing bottom water of a layered system) during ebb tide (Sandifer, 1975; Weinstein et al., 1979).

Decapod crustacean larvae form a significant component of the spring-summer meroplankton, and their later-stage larvae and juveniles may dominate macroplankton collections (Holt and Strawn, 1983). Movements of penaeid shrimps through tidal passes have been monitored, but methods by which the young are transported from offshore spawning grounds to estuarine nurseries are not well understood. It is believed that larvae are transported landward by wind-driven currents in the surface layers (South Atlantic Fisheries Management Council, 1981). Hughes (1969, 1972) has shown behavioral aspects of postlarval pink shrimp, Penaeus duorarum, that facilitate movement into the estuary. The transport of penaeid postlarvae in the upper reaches of the estuary has received even less attention (Holt and Strawn, 1983), and the movement of shrimp into impoundments has been studied only circumstantially (Herke, 1971; Wengert 1972; Weaver and Holloway, 1974).

Recent studies (McConaugha et al., 1981; Provenzano et al., 1983; Epifanio et al., 1984) have done much to elucidate the methods by which blue crab repopulate estuaries. Dudley and Judy (1973) concluded that estuarine immigration is primarily by juveniles, but it now appears that megalopae often are responsible for the bulk of blue crab recruitment. The relative contribution of megalopae or juveniles that move into the estuary may depend on environmental conditions (Johnson, 1982). Blue crab megalopae may penetrate well into the estuary (Cargo, 1960; Tagatz, 1968; Holt and Strawn, 1983). The use of vegetated shallow estuarine zones by blue crab juveniles has been well documented (Tagatz, 1968; Weinstein, 1979; Heck and Thoman, 1984), but their movement into subhabitats (especially impoundments) has received little attention.

As part of the present study on decapod crustaceans in impounded and nonimpounded salt marsh, mesoplankton nets were fished in the creeks and at the water-control structures of the impoundments to elucidate the methods by which decapod crustaceans populate these systems. Penaeid shrimps and portunid crabs (of which the blue crab, Callinectus sapidus, is a member) are commercially important along the Atlantic and Gulf of Mexico coasts and were the focus of this study. Grass shrimps, Palaemonetes sp., are abundant in saltmarsh (Welsh, 1975; Subrahmanyam et al., 1976; Kneib, 1984) and impounded systems (Weaver and Holloway, 1974; present study) and were also considered in this study.

METHODS

Field Sampling

Five mesoplankton sampling stations were established to monitor the tidal transport of penaeid shrimps, portunid crabs, and grass shrimps, Palaemonetes sp. into, within, and out of the Chainey Creek - Paddy Field study area at Cat Island (Fig. 13.1). Two stations, CH01 (near surface) and CH02 (near bottom), were located at the same site in Chainey Creek, downstream of the Paddy Field (Impoundment) complex. At this site, Chainey Creek is approximately 16 m wide and 1.6 m deep at mean low water. Station SC01 was located in a small creek leading from Chainey Creek to an area of mud flats and Spartina marsh opposite the Paddy Field complex. At mean low water the width and depth of this creek (at station) are approximately 6.0 and 0.8 m, respectively. Movements of target species between Chainey Creek and impoundments 2 and 4 were monitored at the water-control structures (trunks) of these impoundments (stations I200 and I400).

Creek stations (CH01, CH02, and SC01) were sampled with 0.5-m diameter (1.5-m length) plankton nets of 0.5-mm mesh. Suspended in the mouth of each net was a General Oceanics Inc. model 2030 (torpedo-type) flowmeter with low-speed rotor. Nets were deployed from an anchored boat and were passively fished 0.5 m below the surface (Station CH01) and 0.5 m above the bottom (Station CH02) in Chainey Creek and 0.5 m above the bottom in the marsh creek (Station SC01). Passive nets are commonly used to collect planktonic organisms in tidal estuaries (King, 1971; Williams and Deubler, 1968; Weinstein et al., 1979; Herke et al., 1984). Flow-meter readings were recorded prior to net deployment and following net retrieval to determine the volume of water filtered for each collection.

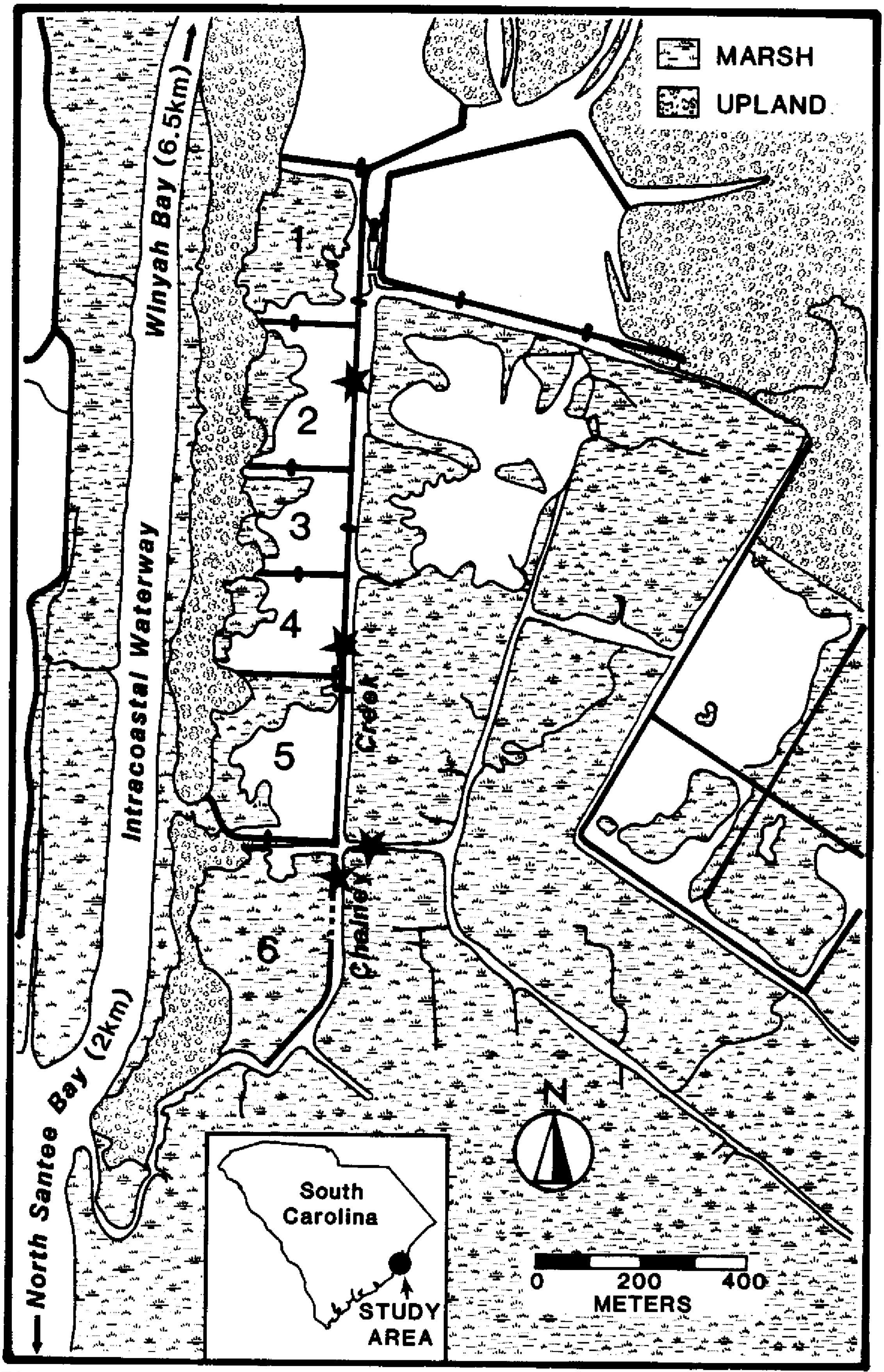


Figure 13.1 Mesoplankton sampling stations indicated by stars. These same stations, except the southern-most station, were also used for adult decapod crustacean collections with crab pot and cast net.

Stations I200 and I400 were sampled with 0.5-mm mesh plankton nets attached to rectangular frames designed to fit on top of the flashboards of the water-control structures (Fig. 13.2). Net frames were constructed of 0.94-cm galvanized rod and had mouth openings of 0.83 m width by 0.32 m height. By securing the inside tidal gate in a closed position, the nets filtered all incoming and outgoing water except leakage through the gate. Flow rates, for estimation of volumes filtered, were not initially obtained for trunk samples. From 23 March to 28 June 1983, flow rates were measured with a modified General Oceanics model 2030 flowmeter. After June 1983, a Montedoro-Whitney Corp. Model PVM-2 portable flowmeter was used to measure water velocity during sampling at the impoundment stations. Flow rate was recorded during the midpoint of sample collection.

Mesoplankton nets were fished for 20 min at all stations, during which time a water sample was recovered with a 1-liter Kemmerer bottle. Water temperature was read from an internally mounted stem thermometer, and a 275-ml sample was returned to the laboratory for salinity determination. Also recorded at the time of collection were tidal stage, water depth, time of collection, and light phase (dawn, day, dusk, or night). Water depth was measured to the nearest 0.1 m at creek stations and 0.01 m at impoundment stations. Samples were preserved in 10 to 20% seawater formalin and returned to the laboratory.

Mesoplankton samples were collected from January 1983 to December 1984 (Fig. 13.3). During year I (January 1983 to January 1984) two sampling schemes were employed. Intensive sampling was conducted monthly from February 1983 to January 1984 during the period of maximum tidal height (usually within a few days of the new moon), when water exchange between Chainey Creek and the impoundments was greatest. One sample was collected at each of the five stations during early, mid, and late ebb and flood tidal stages (approximately 1, 3, and 5 hr after slack water) over two consecutive tidal cycles (12 samples per station). Intensive sampling was conducted at impoundment 3 in February, March, and April in lieu of impoundment 4 prior to lowering of the impoundment 4 water-control structure, which increased the water exchange between that impoundment and Chainey Creek.

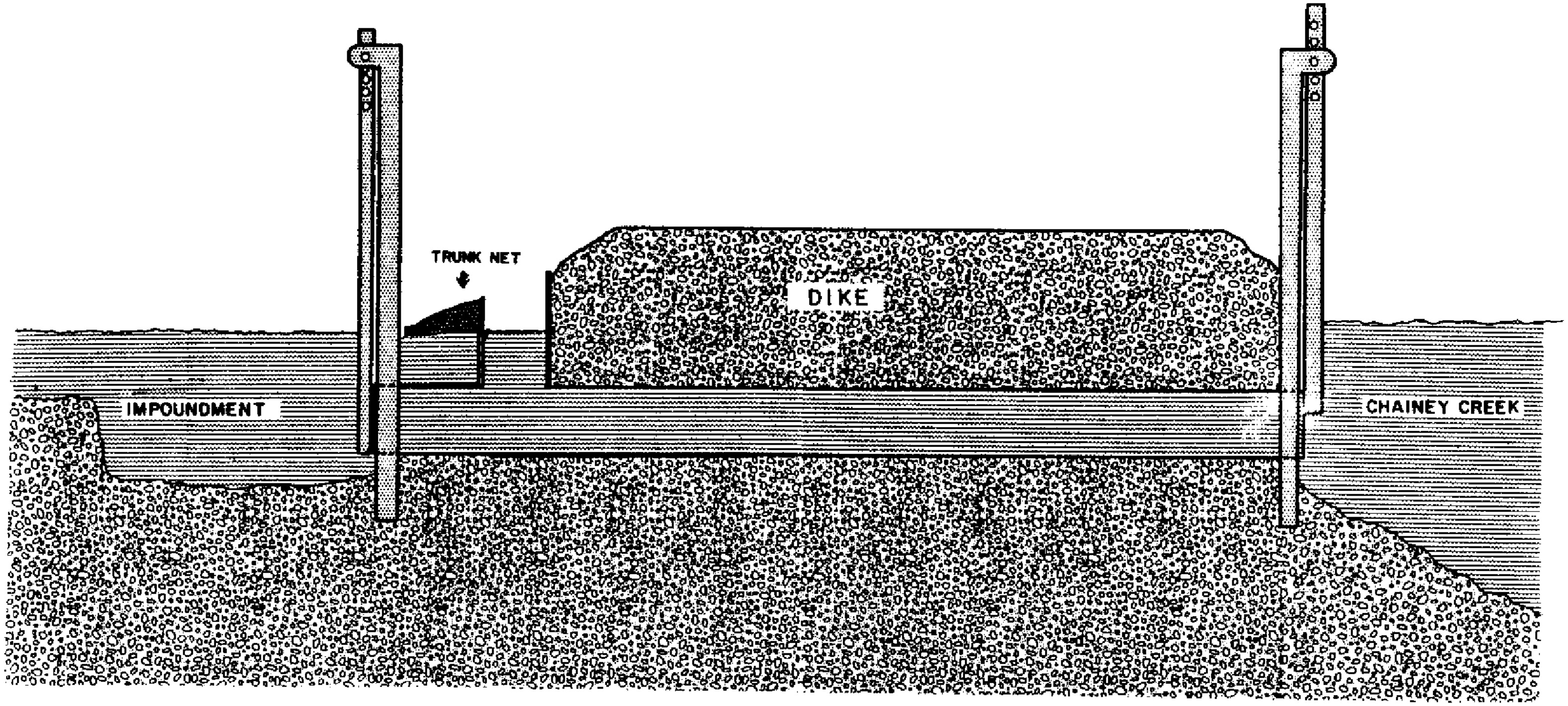
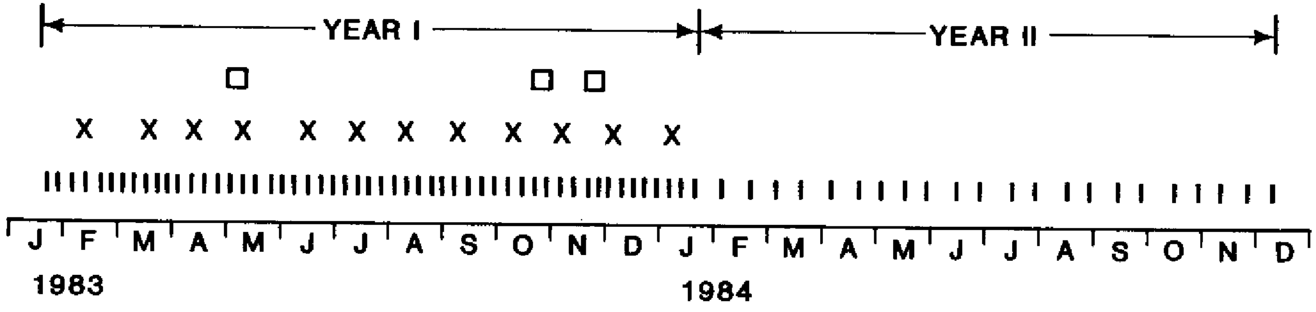


Figure 13.2 Cross-section schematic of impoundment water control structure with trunk net in place to sample flood waters.



X SAMPLES COLLECTED AT ALL FIVE STATIONS DURING EARLY, MID, AND LATE FLOOD AND EBB TIDAL STAGES OVER TWO COMPLETE TIDAL CYCLES.

I ONE SAMPLE COLLECTED AT EACH CHAINEY CREEK STATION (CH01 AND CH02) AND AT IMPOUNDMENT II (I200) AT NIGHT DURING MID-FLOOD TIDE.

☐ SAMPLES COLLECTED DURING MANIPULATION OF IMPOUNDMENT WATER LEVELS.

Figure 13.3 Mesoplankton sampling schedule during impoundment study.

Samples also were collected each week at stations CH01, CH02, and I200. These "extensive" samples were collected during darkness at mid-flood tide, and the method of collection was the same as for intensive samples at these stations.

Sampling during year II (January to December 1984) was a continuation of the year I extensive sampling program; however, samples were collected biweekly instead of weekly (Fig. 13.3).

In addition, events associated with the impoundment management strategy were monitored at stations I200 and I400. During the draining of the impoundments on 6-7 May 1983, nine samples were collected at I200 and eight samples were collected at I400. All except the last two draiw-down samples at each station were of 10-min duration and were collected similarly to the monthly ebb samples. The last two draiw-down samples at each impoundment were of 5-min duration and were collected at the creek-side opening of the trunk.

During the reflooding of the impoundments on 8 May 1983, two samples of 5-min duration each were collected at I200 and I400 in a manner similar to that of the last two draiw-down samples, except that the net was fished at the inside mouth of the trunk.

Impoundment water levels were lowered approximately 10 cm on 20 October 1983 and again on 21 November 1983. Three 20-min samples were collected at I200 and I400 during each of these events.

In summary, the intensive sampling program was conducted monthly during year I to observe spatial variability (5 stations) in abundance of organisms and variability over diel and tidal cycles. Extensive samples were collected at three stations weekly in year I and biweekly in year II to observe temporal variability in abundances. Events associated with impoundment management were sampled to determine the effect these events had on movement of target organisms between creek and impoundment systems.

Laboratory Procedures

Salinities of water samples were determined to the nearest 0.1 part per thousand (ppt) with a Beckman RS7B Induction Salinometer, and volumes filtered were calculated from flowmeter readings to the nearest 0.1 m^3.

Mesoplankton samples were rinsed and sorted under a lighted magnification loop. Year I samples were sorted for penaeid shrimps, portunid crabs (including megalopae but not zoeae), and Palaemonetes (excluding larval stages). Year II samples were sorted only for penaeid shrimps. Total number of penaeid shrimps per sample was established by direct count, and if exceeding 100 individuals, estimates of the total number of each species were based on the subsample of 100 that were identified. Total length (tip of rostrum to tip of telson) and rostral tooth count (number of dorsal and ventral teeth on the rostrum, including epigastric tooth) were recorded for up to 30 individuals of each species per sample. Total length was measured along the dorsal surface to the nearest 0.1 mm with an ocular micrometer (for individuals $\leq$40 mm) or with vernier calipers (for individuals >40 mm). Shrimps were considered to be postlarvae if the full complement of rostral teeth had yet to be achieved (Perez-Farfante, 1969).

Crab stages of portunids from each collection were identified to species, but portunid megalopae were not identified below the familial level. Crab stages and megalopae were enumerated by direct count. Crab total width (TW) was measured to 0.1 mm. Sex and maturity were determined (Van Engel, 1958) and recorded for each crab (sex was not determined for individuals <10 mm total width).

Grass shrimps, Palaemonetes sp., collected from all but station I200 were only enumerated. For station I200 samples, the total number of Palaemonetes was determined by count for each sample, and up to 50 individuals were identified to species. If more than 50 Palaemonetes were collected in a sample, total numbers of each species were estimated from the subsample composition. Total lengths (to the nearest 1 mm) were recorded for those Palaemonetes identified to species.

Analysis

To facilitate comparisons among samples and selected variables, numbers of target organisms were standardized on the basis of number per 100 m^3 of water filtered. Samples for which no volumes were recorded were omitted from density estimates but were included in values of absolute numbers collected. Density ($N/100\ m^3$) of each taxon was calculated for each sample.

Shrimp and crab densities in relation to certain variables (e.g., station, month, tide) were derived by summing the number of individuals (by taxon) and the sample volumes collected from all samples within the defined variable(s), and then calculating density (N/100 m^3) from the summed values [i.e., $(\Sigma N/\Sigma VOL) * 100$]. This method reduced bias introduced by calculating means from individual sample densities and provided an accurate density estimate for the variables considered. Because density values were reduced to a single observation (overall density for each variable), this method did not allow calculation of variances within or among the selected variables. Intensive samples were analyzed with regard to month, station, and tidal stage. Extensive samples were examined in relation to week, month, and station. Samples collected during the monthly intensive sampling effort that corresponded with the weekly extensive samples (i.e., collected at stations CH01, CH02, and I200 at night during mid-flood tide) were included in analysis of both intensive and extensive samples. Samples collected at impoundment 3 prior to utilization of impoundment 4 as a station (February to April, 1983) are included with impoundment 4 samples in the analysis.

RESULTS AND DISCUSSION

Physical Factors

Samples Collected and Volumes Filtered. During the two-year study 804 samples were collected and processed. An additional 148 collections were scheduled but could not be collected because of insufficient currents in the creeks (8 samples) or lack of flow at the impoundment stations (140 samples) (Appendix 13.1). During year I, 41% of the samples scheduled at impoundment stations could not be collected.

Exchange of water (and organisms) between impoundment and creek systems did not occur if: (1) the tidal gate sealed off water flow, (2) high tides in Chainey Creek did not exceed the water level in the impoundments (flood tides), or (3) the sill level of the flash board riser exceeded the impoundment water level on ebb tides. During late summer of year I, impoundment water levels exceeded 50 cm over the grass beds (see Table 4.1; Figs. 4.4 and 4.5), and water exchange was precluded except on extreme high tides. Consequently, few samples were collected at impoundment stations (Appendix 13.1). Dissolved oxygen depletion occurred in several impoundments during this time. During year I, relatively free exchange of water occurred only in May, June and July, when the tidal gates were open and the impoundment water levels were below approximately 50 cm (and also at I200 in October and anomalously at I400 in January) (Fig. 13.4). The tidal gate of impoundment 2 remained open during year II, and water exchange was restricted only by high water levels in the impoundments during late fall and early winter (see Fig. 4.4 and Appendix 13.1).

Intensive sampling efforts were scheduled to coincide with monthly maximum tidal heights and thus occurred at times of maximum water exchange. Even so, many scheduled mesoplankton samples from the impoundment stations could not be collected. The reduced, and at times non existent, water exchange was a result of the impoundment management scheme at Cat Island. Since impoundment management practices vary among landowners, the management scheme utilized at Cat Island may not be typical for other coastal waterfowl impoundments. It should be noted that although water exchange (and concurrent movement of organisms) between systems was restricted, those natant organisms that were able to invade the impoundments had nearly unlimited access to the grass bed areas. In contrast, availability of open Spartina marsh to natant macrofauna is tidally limited.

Estimates of water volume filtered were recorded for 746 samples. No volumes were recorded for impoundment trunk samples collected from January to mid-March 1983. During monthly intensive sampling, between 350 and 1060 m^3 of water were filtered at each creek station (Fig. 13.4). Only in June and July did the impoundment 2 station filter as much water as the creek stations. The maximum total volume filtered for a monthly sample at station I400 (315.5 m^3 in January) probably resulted from incomplete closure of the tidal gate, which should have been closed at this time.

Some leakage of water through the closed tidal gate often occurred, and if possible, samples were collected even during the period when the gates were closed (late fall to spring). Volumes filtered per sample during this period rarely exceeded 10 m^3 and were usually less than 5

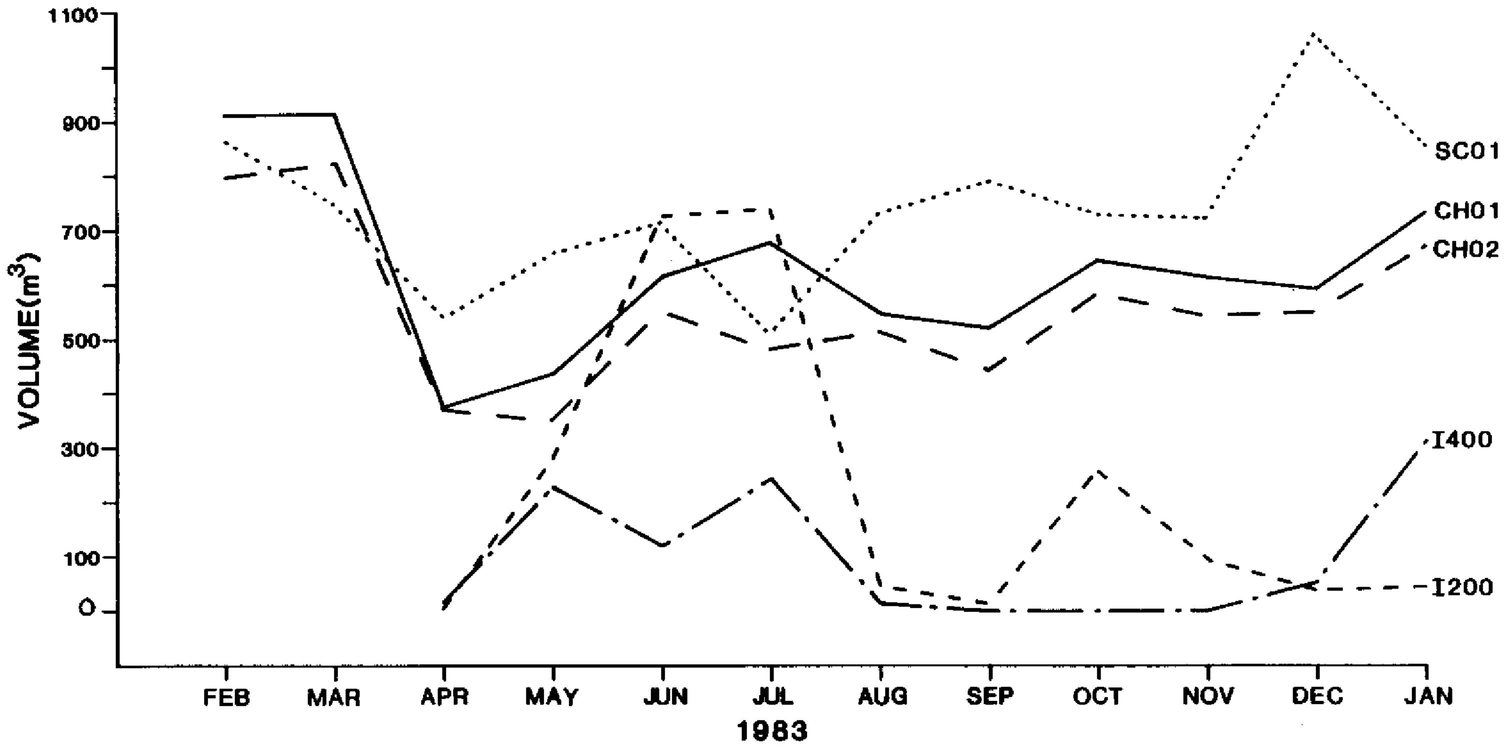


Figure 13.4 Total volume (m^3) of water filtered at each station during monthly Intensive sampling.

m3 (station I400 in January was an exception); thus samples were collected even though little water exchange took place between Chainey Creek and the impoundments (Fig. 13.4 and Appendix 13.1). Unfortunately, flow data for the impoundment stations in the early part of year I were limited.

Temperature and Salinity Regimes. During the two-year extensive sampling program (night; mid-flood collections), water temperatures and salinities in Chainey Creek (Station CH02) ranged from 4.0 to 32.4°C and 0.0 to 31.9 ppt, respectively. Patterns of temperature and salinity were similar for the two years; however, weekly (or biweekly) variation was often considerable (Fig. 13.5). Temperature changes of 10°C over a two-week period were observed in spring and fall of both years. Temperatures generally remained above 20°C from May to October and were below 10°C from December to February.

Low salinities (<3 ppt) encountered in spring of each year were followed by a rapid increase in salinity (~17 ppt in two weeks) during May. Salinities were generally >20 ppt from May to December. Salinity declined rapidly in December 1983. Sampling was terminated early in December 1984, and a similar decline was not observed. Mean monthly salinity in Chainey Creek was negatively correlated with discharge from the Santee River (Fig. 13.6; Santee River discharge data were provided by the U.S. Geological Survey, Water Resources Division). Seasonal (early spring) periods of high river discharge and associated low salinities in estuarine areas have also been reported for North Carolina (Weinstein et al., 1979; Laney and Copeland, 1981) and Georgia (Rogers et al., 1984).

Temperature and salinity ranges recorded for intensive samples were 4.1 to 33.8°C and 0.0 to 32.3 ppt. During intensive sampling each month, temperatures and salinities in Chainey Creek usually did not vary more than 5°C or 5 ppt, respectively. Temperature generally followed a diurnal cycle but was influenced by tidal stage, with the temperature of water moving off shallows during ebb tide being more extreme. Salinity varied with tidal stage and season. Salinity usually increased during flood stages; however, in early spring when the North and South Santee rivers became fresh, late flood stages were accompanied by decreasing salinities. An increase from 12.4 ppt at early flood to 23.3

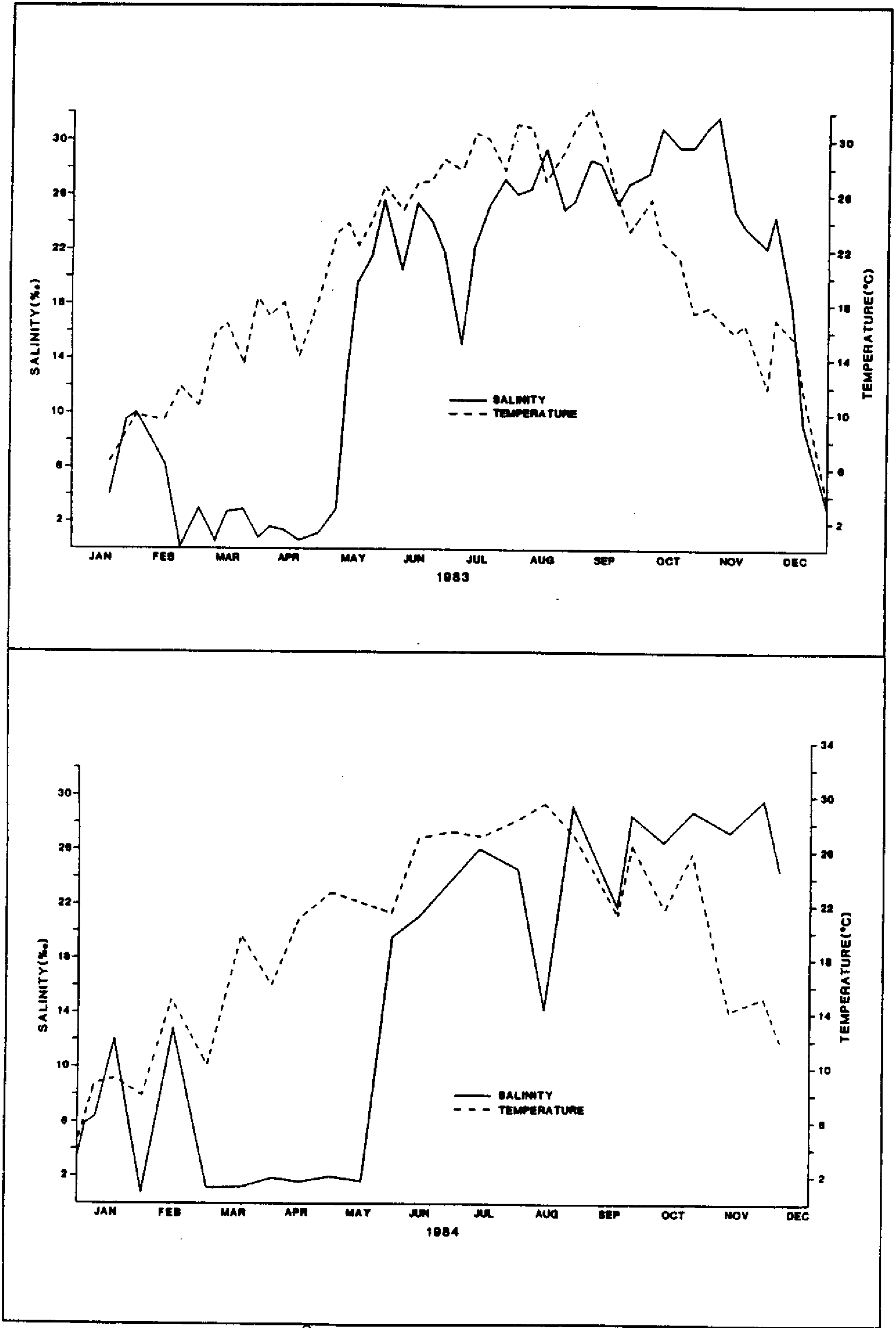


Figure 13.5 Temperature (^{o}C) and salinity (ppt) in Chainey Creek (Station CH02) recorded weekly in 1983 and biweekly in 1984.

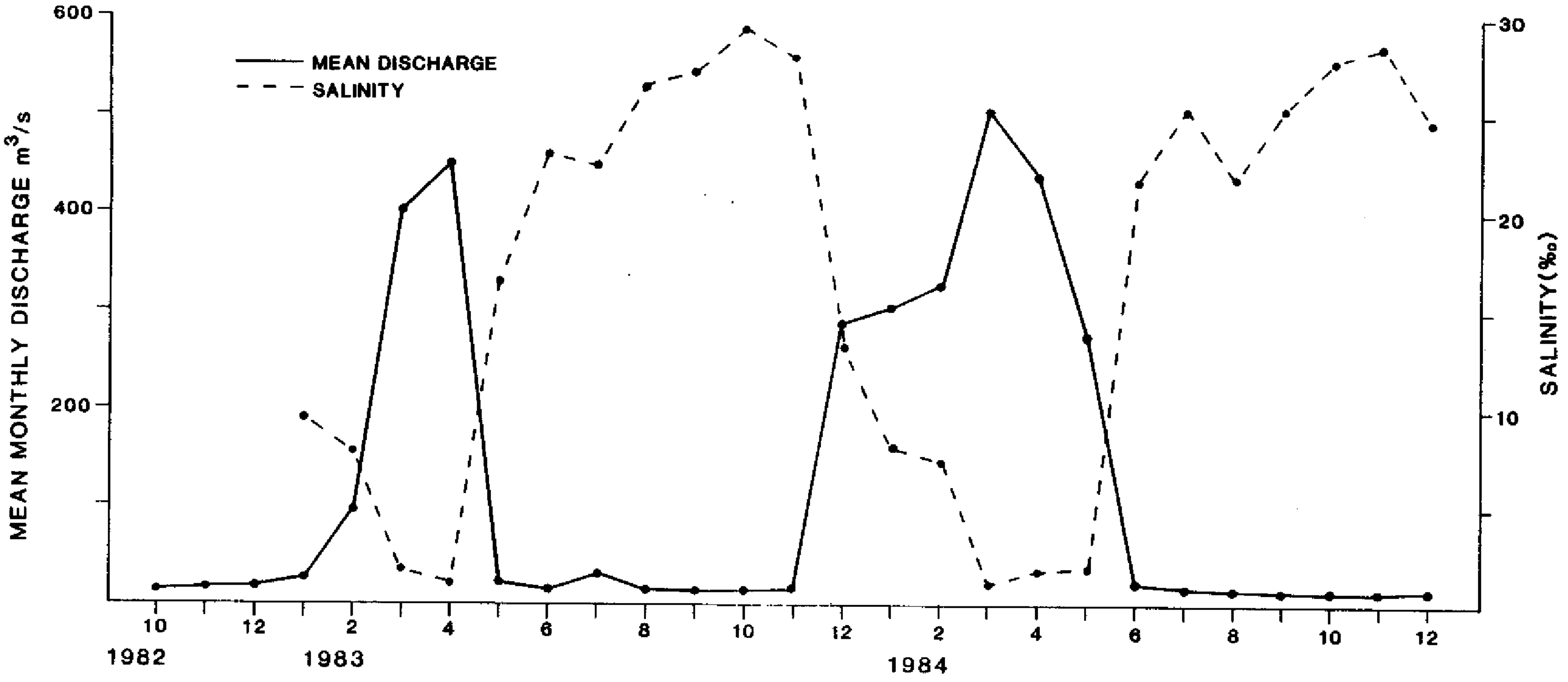


Figure 13.6 Monthly mean Santee River discharge (m^3/s) and monthly mean salinity (ppt) in Chainey Creek.

ppt at late flood in Chainey Creek represented the greatest salinity change during an intensive series (May). Because of its greater depth, variation of physical parameters was probably less at station CH02 than at the other four stations.

Penaeid Shrimps

Species Composition. During the two-year mesoplankton sampling program, 4204 penaeid shrimps were collected (Table 13.1). *Penaeus aztecus*, *P. duorarum*, *P. setiferus*, and *Trachypenaeus constrictus* constituted 10.9, 52.0, 28.9, and 6.9% of the total number, respectively. Fifty-one individuals (1.2% of total) were damaged and identified only as *Penaeus* sp. (most of these specimens were from two improperly preserved samples in May 1983; most, if not all, of these were probably *P. aztecus*). Species composition differed between the two years, mostly because of the decline in *P. setiferus* from 33% of the penaeids collected in year I to 0% in year II (Table 13.1). In the absence of *P. setiferus*, *P. duorarum* increased from 48.5% in year I to 75.0% of all penaeids collected in year II.

The dominance of pink shrimp, *P. duorarum*, in mesoplankton samples was notable because this species usually has contributed <0.5% of the state's annual commercial shrimp landings (South Atlantic Fisheries Management Council, 1981; Fish Statistics Section, S.C.M.R.D.) and was relatively uncommon in trawl collections (Bishop and Shealy, 1977) and plankton net collections of postlarvae (Bearden, 1961; Farmer and Boardman S.C.M.R.D., unpublished data report, hereafter cited as Farmer and Boardman, unpublished) in South Carolina. That *P. duorarum* was the most abundant penaeid in our samples probably reflects reduced recruitment of brown (*P. aztecus*) and white (*P. setiferus*) shrimp in Chainey Creek, as a result of local environmental conditions during their ingress. High freshwater discharge in the Santee River system during spring in both years may have negatively affected immigration of brown shrimp into the system. In contrast, salinities in Chainey Creek were >20 ppt during the summer and fall, and young white shrimp, which generally concentrate in areas of low salinity (Williams, 1959; Gunter et al., 1964; Joyce, 1965), may have followed salinity gradients in the Santee River to more upstream locations. The complete absence of white shrimp in 1984 reflects the loss of the overwintering spawning stock because of severely low water temperatures.

Table 13.1

Numbers of penaeid shrimp, by species, collected in mesoplankton samples during the two-year study.

Species	Year I		Year II		Total	
	N	%	N	%	N	%
Penaeus aztecus	371	10.2	88	15.7	459	10.9
Penaeus duorarum	1768	48.5	420	75.0	2188	52.1
Penaeus setiferus	1215	33.3	0	0	1215	28.9
Penaeus sp.	51	1.4	0	0	51	1.2
Trachypenaeus constrictus	239	6.6	52	9.3	291	6.9
All species	3544	100.0	560	100.0	4204	100.0

Trachypenaeus constrictus is a stenohaline species restricted in its penetration of estuaries (Williams, 1969). Consequently, it is the minor contributor to the total number of penaeids collected.

Temporal Abundance and Size Distribution. 1. *Penaeus aztecus*. Brown shrimp exhibited a bimodal pattern of recruitment in 1983, with maximum abundance in May and a smaller peak in December (Fig. 13.7 and Appendix 13.2). Postlarval brown shrimp were collected throughout May and measured 10 to 16 mm TL, with a modal size of 12 mm (Figs. 13.8 and 13.9). These shrimp accounted for 82% of all *P. aztecus* collected during year I. Samples from June and July indicated a cessation of postlarval recruitment and rapid growth of juveniles. The largest brown shrimp collected (124 mm TL) was taken in July. From August through November four postlarvae and no juveniles were collected (Figs. 13.7 and 13.9). A second period of abundance of postlarval (10 to 13 mm TL) brown shrimp was observed in December, when water temperatures were 10.6 to 15.4°C. Brown shrimp were collected during 1983 in temperatures of 10.6 to 31.6°C and salinities of 3.0 to 30.7 ppt, although most were collected

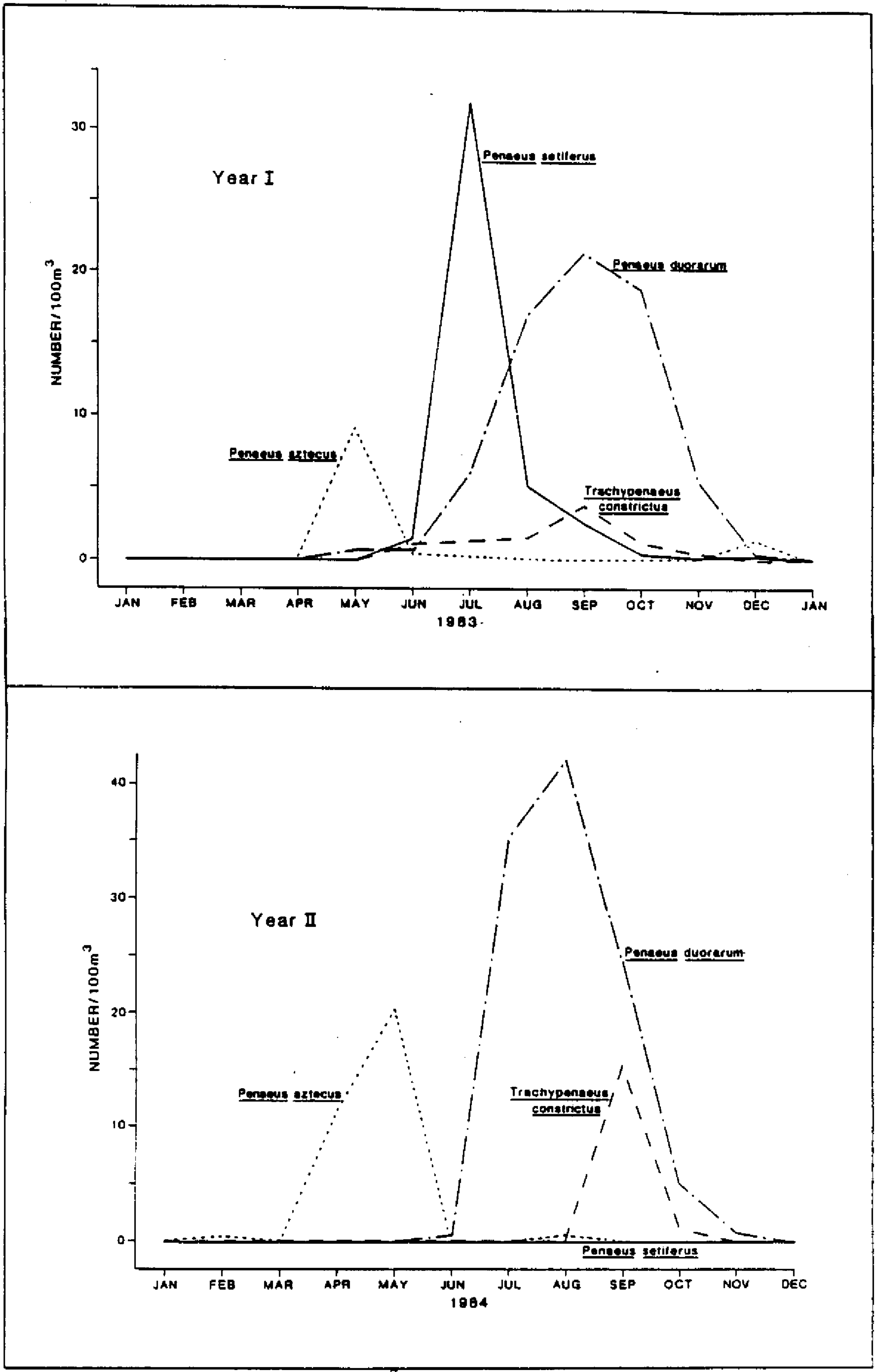


Figure 13.7 Densities (N/100 m^3) of penaeid shrimps by month from all samples (Extensive, Intensive, and event) collected during Year I and all samples (Extensive and event) collected during Year II.

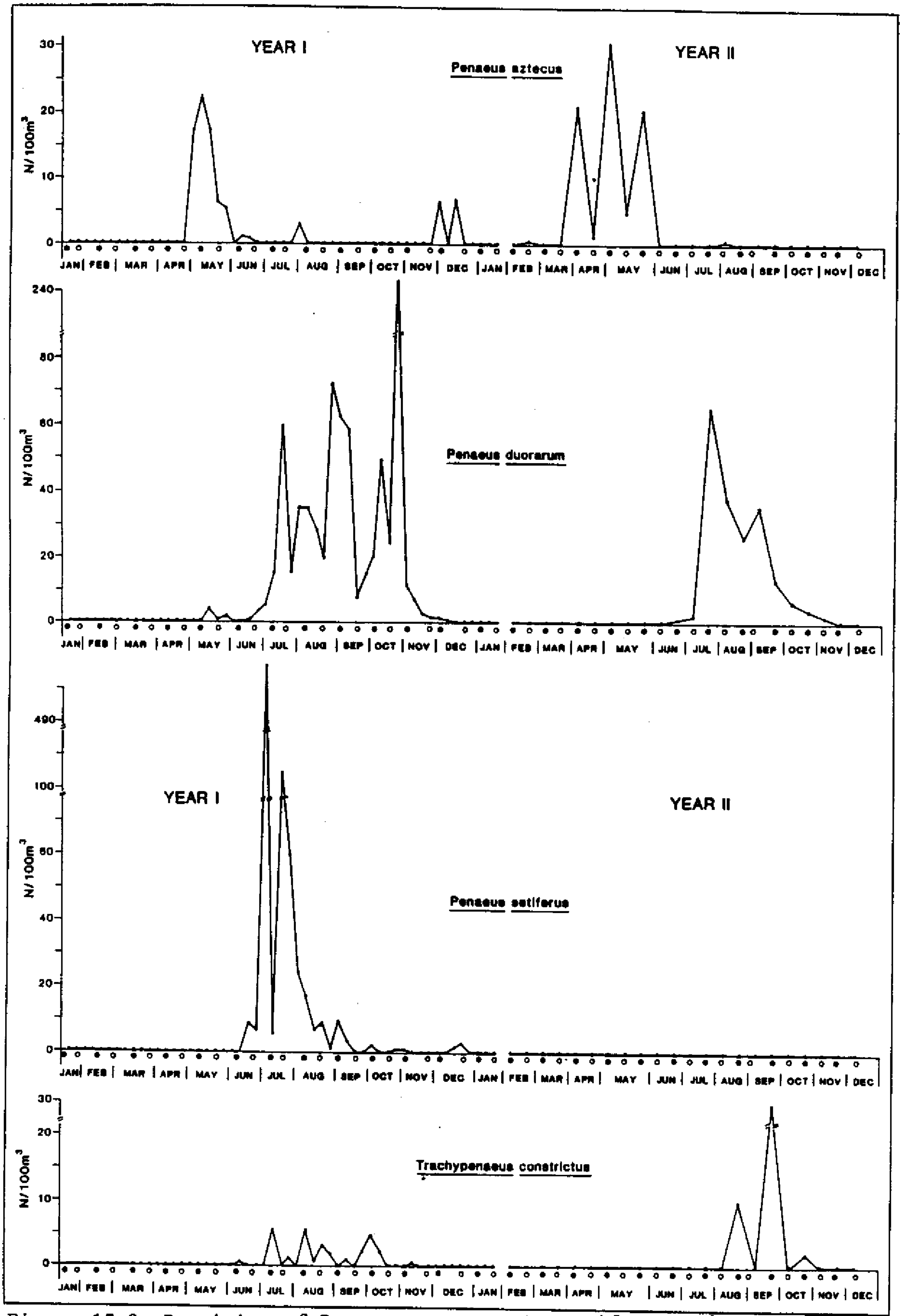


Figure 13.8 Densities of *Penaeus aztecus*, *P. setiferus* and *Trachypenaeus constrictus* collected during weekly (Year I) and biweekly (Year II) sampling.

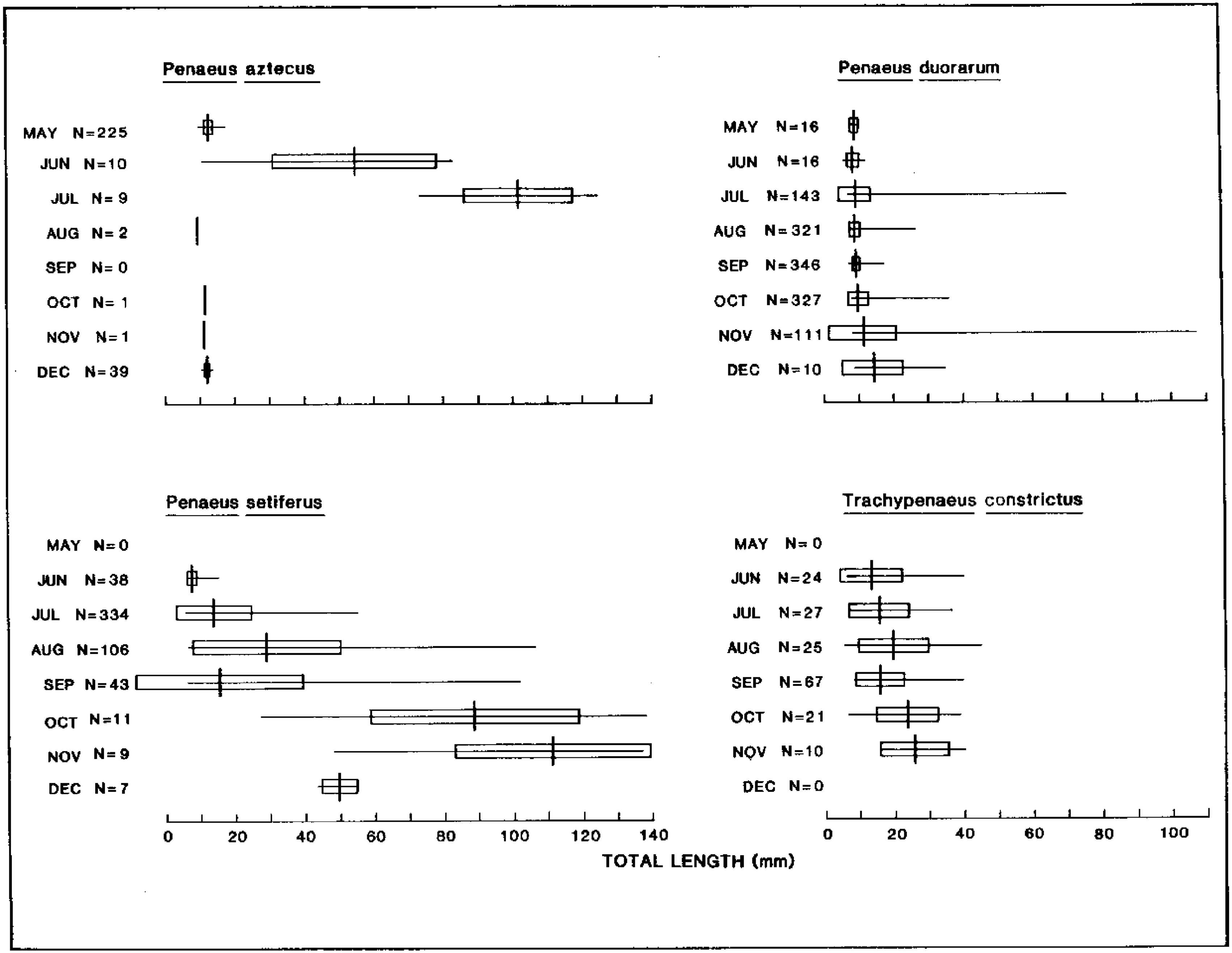


Figure 13.9 Total lengths of *Penaeus aztecus*, *P. duorarum*, *P. setiferus* and *Trachypenaeus constrictus* by months from all samples collected during Year I (vertical line = means, horizontal line = range, rectangle = ± one SD6).

in temperatures <25oC and salinities <20 ppt. Postlarval stages constituted 95% of all brown shrimp collected during year I.

During year II, one P. aztecus postlarva was collected in February and August, and the remainder of the 88 brown shrimp collected were caught in April and May (Fig. 13.7). Brown shrimp were collected in temperatures of 15.2 to 29.4°C and salinities of 1.1 to 19.9 ppt. Brown shrimp were abundant during April and May, although densities fluctuated considerably from week to week (Fig. 13.8). Similar to year I, immigration of postlarval brown shrimp was over by the end of May (18 of 19 P. aztecus collected 31 May were juveniles, and only one postlarva was collected after May). Sampling was terminated in early December, and the bimodal recruitment pattern observed in 1983 was not seen in 1984.

In the Carolinas, ingress of postlarval brown shrimp commences when water temperatures increase to ~11°C (usually in January or February) and continues through June (Williams, 1955; Bearden, 1961; Farmer and Boardman unpublished). In the present study, brown shrimp were not collected until May 1983, and with the exception of one postlarva in February, they were not collected until April 1984. The first occurrence of postlarvae in 1983 and 1984 coincided with rapid salinity increases (Figs. 13.5 and 13.8 and Appendix 13.3), suggesting that postlarvae may have avoided low salinities in Chainey Creek. However, their abundance in 1984 (April and May) occurred while salinities were <3 ppt, and other studies have found postlarval brown shrimp in salinities <2 ppt (Gunter et al., 1964; Christmas et al., 1966). Zein-Eldin and Aldrich (1965) reported that P. aztecus postlarvae had reduced tolerance to low salinities (<10 ppt) at temperatures <15°C. Brown shrimp may have avoided low salinity (<3 ppt) and low temperature (<20°C) conditions in Chainey Creek during spring of both years, or their immigration may have been impeded by the high discharge of the Santee River each spring. Our collection of brown shrimp postlarvae in December indicates that some fall-winter recruitment does occur, at least in some years. Water temperatures associated with these December samples were 10.6 to 13.2°C. Williams (1955) suggested that postlarvae recruited to North Carolina estuaries in late fall or early winter do not survive until spring. Initial occurrence of brown shrimp postlarvae may have been delayed by low salinity, low temperature, high river discharge, or a combination of these factors; however, within periods of abundance, fluctuations in concentrations of brown shrimp do not appear to be correlated with temperature or salinity.

Following a period of rapid growth, brown shrimp leave the estuary. In the Carolinas, brown shrimp usually begin to enter the fishery in June and the fishery reaches a peak in July and August (South Atlantic Fisheries Management Council, 1981). No juvenile or subadult _P. aztecus_ were collected in our samples after July (Fig. 13.9).

2. _Penaeus duorarum_. Pink shrimp were collected each week except one from 17 May to 5 December 1983 in water temperatures of 10.8 to 33.8°C and salinities of 3.0 to 30.7 ppt (Figs. 13.7 and 13.8 and Appendices 13.2 and 13.3). Seventy-nine percent of those collected were caught from August to October, and monthly density was highest in September. Pink shrimp were generally abundant while temperatures were >25°C and salinities were >25 ppt, but the highest density (244/100 m^3) was recorded in an extensive sample collected late October, when water temperature was declining (Figs. 13.5 and 13.8 and Appendix 13.3).

Postlarval stages (6 to 13 mm TL) of _P. duorarum_ were present in samples from May to December 1983, and for each month, the modal class was 9 to 10 mm TL (Fig. 13.9). Ninety-three percent of the pink shrimp collected in year I were postlarvae.

During 1984 pink shrimp were collected from 28 June to 8 November over a temperature range of 14.4 to 29.4°C and a salinity range of 14.4 to 29.4 ppt. Samples collected from July to September accounted for 95% of the pink shrimp collected in year II, and the highest density (65/100 m^3) was observed 30 July (Fig. 13.8). Densities of pink shrimp declined to <7/100 m^3 after mid-September. Ninety-six percent of the _P. duorarum_ collected in 1984 were postlarvae.

Spawning of pink shrimp is correlated with increasing water temperatures, and a minimum critical temperature for spawning may exist (Eldred et al., 1961). In Florida spawning may occur year-round (Eldred et al., 1961, 1965; Tabb et al., 1962), but on the Gulf of Mexico coast and in the Carolinas postlarval immigration occurs from late spring through the fall, with maximum ingress in late summer (Bearden, 1961; Christmas et al., 1966; Copeland and Truitt, 1966; Williams, 1969, 1984). Our samples also indicate a protracted spawning and recruitment period for

P. duorarum in South Carolina. Except for the late (27 October) peak in density in 1983, pink shrimp were most abundant when water temperatures were greater than 26°C. Williams (1955) suggested that late-summer and fall recruits in North Carolina remain in the estuary as an overwintering population. A similar situation in South Carolina is indicated from our collections of postlarval pink shrimp through the fall.

Salinities remained high in Chainey Creek from early July through mid-November 1983 (Fig. 13.5); therefore, few pink shrimp were collected in water <25 ppt. In year II, salinities generally were not as high as in the first year, but salinities were >20 ppt during the period of pink shrimp recruitment (June to November), except for one collection date (13 August). Fluctuations in shrimp abundance appeared to be independent of changes in salinity within the period of shrimp immigration each year.

The paucity of juvenile pink shrimp in our mesoplankton samples may indicate migration out of the area soon after recruitment, or it may show that a high mortality rate existed for postlarval and juvenile pink shrimp. In addition, greater burying behavior of juvenile pink shrimp may have reduced their vulnerability to our mesoplankton nets.

3. Penaeus setiferus. White shrimp were collected from June to December 1983, with peak abundance in July (Fig. 13.7 and Appendix 13.2). Postlarval white shrimp were first caught 22 June, when water temperature and salinity were 26.8°C and 24.2 ppt. Two weeks later (6 July) postlarval P. setiferus reached the maximum density (507/100 m^3) recorded during our study (Fig. 13.8 and Appendix 13.3). This peak was nearly four times greater than the next highest density of white shrimp (105/100 m^3) and coincided with a brief, marked drop in salinity (Fig. 13.5 and Appendix 13.3). Immigration of postlarval white shrimp (modal size class 7 to 8 mm TL) continued into September (Fig. 13.9), but densities did not exceed 10/100 m^3 after mid-August (Fig. 13.8). Almost all postlarval white shrimp were collected in temperatures >25°C, and except for the marked decline in salinity on 6 July, salinities generally remained above 25 ppt during the period of white shrimp immigration. Juvenile and subadult P. setiferus (maximum size 138 mm TL) were collected July to December (Fig. 13.9) and comprised 34% of all white shrimp collected. Subadult white shrimp were collected as late as 19 December,

when water temperature and salinity were 12.0oC and 9.4 ppt. No white shrimp were collected in 1984.

Temperature is a major factor controlling spawning in white shrimp (Perez-Farante, 1969), and postlarval immigration generally occurs during the summer months when water temperatures are high (Williams, 1955; Bearden, 1961; Christmas et al., 1966; Baxter and Renfro, 1967; Farmer and Boardman, unpublished). Nearly all postlarval white shrimp in our samples were collected in water temperatures >25°C (July to September), with a maximum temperature of 33.8°C.

Juvenile white shrimp were collected in larger numbers than were juveniles of other species, and their abundance during July and August indicates use of the study area as a nursery. Subadult white shrimp generally enter the fishery from July to October in this region (South Atlantic Fisheries Management Council, 1981), and most juvenile and subadult white shrimp appear to have moved out of the area by September (Fig. 13.9). Those collected after October probably represent part of the overwintering population (Farmer and Whitaker, 1978). Although postlarvae were collected only during high (>25°C) water temperatures, subadults were collected in temperatures down to 12.0°C in December. The absence of white shrimp in our samples during 1984 was probably influenced by a severe winter kill of the overwintering spawning stock in South Carolina waters.

White shrimp were collected in salinities of 9.4 to 31.7 ppt. Juvenile white shrimp are often concentrated in areas of low salinity (<10 ppt) (Williams, 1955; Gunter et al., 1964; Joyce, 1965), but are apparently not adversely affected by high salinity (Perez-Farfante, 1969). Because our sampling was confined to one creek system, shrimp abundance in relation to salinity reflects the salinity regime present during shrimp ingress more than any salinity preferences of the species. Interestingly, the dramatic peak in white shrimp abundance observed on 6 July coincided with the lowest salinity recorded during the period of white shrimp recruitment. Nevertheless, weekly fluctuations in white shrimp density did not appear to be related to temperature or salinity.

4. Trachypenaeus constrictus. Roughneck shrimp were collected from June to November 1983 and August to October 1984. Peak abundance in September (Figs. 13.7 and 13.8 and Appendices 13.2 and 13.3) accounted for

33 and 79% of roughneck shrimp collected in year I and year II, respectively. T. constrictus was collected in temperatures of 17.1 to 31.1°C and salinities of 21.4 to 31.9 ppt, but most were collected when temperatures were >25°C. During year II, T. constrictus was caught on only three nights (25.8 to 27.2°C, 28.7 to 29.1 ppt), but densities were generally greater than had been observed in 1983 (Fig. 13.8). Specimens collected during 1983 were 5 to 40 mm TL, and specimens <10 mm TL were collected June to October (Fig. 13.9).

Trachypenaeus constrictus is a stenohaline marine species generally restricted to coastal waters and lower estuarine areas where salinities remain high (Williams, 1969; Wenner et al., 1982). Mean salinities in Chainey Creek were greater than 20 ppt during all months in which T. constrictus was collected and exceeded 25 ppt during months of peak abundance (September of both years).

Peak spawning of T. constrictus along the South Atlantic coast is in May and June (Joyce, 1965; Anderson, 1970); however, spawning appears to extend through much of the summer (Williams, 1969) and may be year-round in the Gulf of Mexico (Williams, 1984). Our data supported the belief that spawning of T. constrictus in this area occurs at least throughout the summer. Decreased salinities (<20 ppt) may have influenced their absence during other months.

Spatial Variability in Shrimp Abundance. Densities of penaeid shrimp (species pooled) in intensive samples were greater at impoundment stations than at creek stations, although fewer individuals were collected at impoundment stations (Fig. 13.10). Several factors may have contributed to greater densities at I200 and I400 than at creek stations. Because volumes filtered were not recorded for samples collected from impoundments from February to April, these collections were not included in estimation of overall densities of shrimp at impoundment stations in year I. Samples collected during this period at creek stations, however, were included in estimates of overall density and were void of shrimp. Thus, overall shrimp densities at creek stations were depressed by zero catches during this period, whereas densities at impoundment stations were unaffected. Although overall densities for creek and impoundment stations may have been affected differently because these samples, penaeid shrimp densities were generally greater at impoundment stations when shrimp were present.

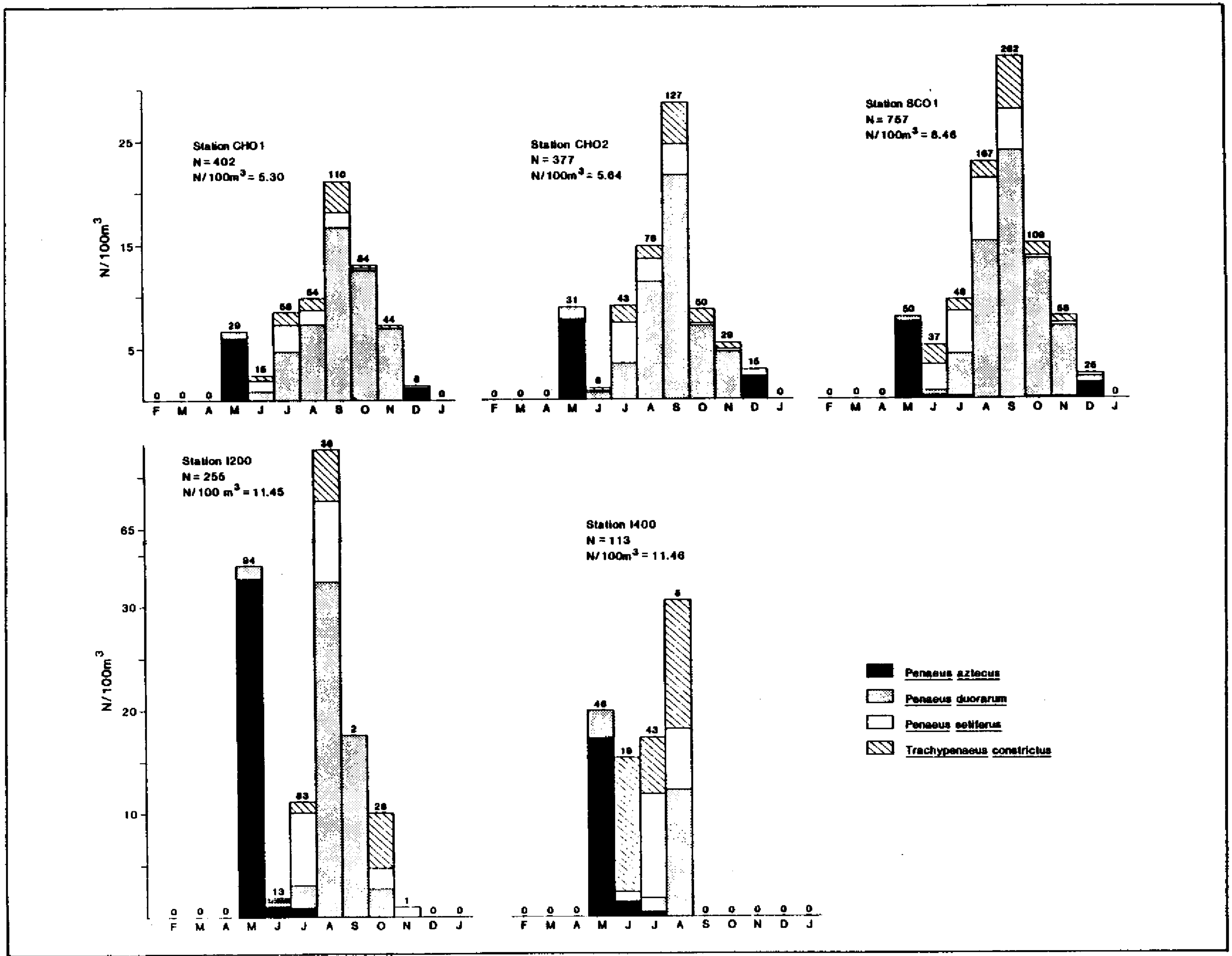


Figure 13.10 Densities (N/100 m^3) of penaeid shrimps in relation to station and month. The number of individuals collected each month is displayed above each monthly histogram. Each monthly histogram is subdivided to indicate the relative contrigution of each species. Number of samples: CHO1 = 141; CHO2 = 141; SCO1 = 142; 1200 = 82; 1400 = 68).

Net avoidance by shrimp may also have affected shrimp densities. The likelihood of net avoidance at impoundment stations was remote, because trunk nets filtered all inflowing and outflowing water, but avoidance of nets in creeks was possible, especially in weak currents of late tidal stages. Avoidance by postlarval shrimp was probably insignificant, but avoidance by juveniles and subadults may have been a factor (proportionately more shrimp collected in trunk nets were juveniles or subadults). Because the vast majority of shrimp collected were postlarvae, the effect of net avoidance on overall densities was assumed to be minor. It then appears that shrimp were more concentrated moving through impoundment trunks than in the creeks, but because water exchange was restricted, the number of individuals collected at impoundments was less than at creek stations.

Among creek stations, densities of shrimp were greatest at the marsh creek station, SC01 (Fig. 13.10). This suggests that the marshes and tidal flats fed by this creek are well utilized by young penaeid shrimps. Juvenile shrimps concentrate in shallows along edges of estuarine systems (Tagatz, 1968; Parker, 1970; Truesdale, 1970; Weinstein, 1979), and densities of shrimp were greater at the peripheral stations (SC01, I200, I400) in the present study. Densities of shrimp differed little between the two Chainey Creek stations.

Densities of shrimp were similar at the two impoundment stations, but less than half as many individuals were collected at I400 because less water was exchanged at impoundment 4 (Fig. 13.4).

Densities of shrimp collected by month at creek stations reflect general patterns of abundance and varied similarly among stations (Fig. 13.10). At impoundment stations, however, monthly catches of shrimp were influenced more by the water management regime than by natural patterns of abundance (i.e., during the period of shrimp availibility, regulation of water exchange had a greater effect on numbers of shrimp collected at impoundment stations than did general abundance).

Spatial patterns of shrimp abundance in intensive samples differed among species (Fig. 13.11 and Appendix 13.4). The general pattern of greater density but fewer individuals at impoundment stations was exhibited by white shrimp and roughneck shrimp. Brown shrimp were collected in greater densities and greater numbers at impoundment stations. In contrast, pink shrimp were collected in greater numbers and densities at creek stations.

These differences relate to temporal variations in abundances of each species in regard to creek-impoundment water exchange. The mean number of brown shrimp collected at impoundment stations was greater than at creek stations during intensive sampling in May, June, and July, the months of maximum water exchange. During the December period of minor brown shrimp abundance, the tidal gates were closed, and no brown shrimp were collected at impoundment stations. Numbers of brown shrimp collected in December were few relative to the spring collections, however (Fig. 13.10).

Numbers and densities of pink shrimp were comparable at all stations from May to July, but few shrimp were collected relative to later months (Fig. 13.10). Pink shrimp abundance increased considerably in intensive samples during August and was greatest in September. Water exchange at the impoundment trunks was slight by August, and mean number of shrimp per station was greater at creek stations by a factor of 13. The greater number of individuals and greater densities of pink shrimp at creek stations than at impoundment stations resulted from low availability of pink shrimp during the months of good flow into impoundments and large numbers of shrimp available to creek nets but not impoundment nets in late summer (Figs. 13.10 and 13.11).

White shrimp densities were greater at impoundment stations than at creek stations, and more white shrimp were collected at station I200 than at either of the Chainey Creek stations (Fig. 13.11). The average number of white shrimp collected per station was greater at creek stations, however, because of the large number of white shrimp collected at SC01 (Appendix 13.4). In July, when water exchange was good and white shrimp were abundant, both impoundment stations collected white shrimp in greater numbers and densities than creek stations. Very little flow occurred at impoundment stations in August, but more white shrimp were collected at I200 than at either Chainey Creek station. As with the other species, overall densities of white shrimp at creek stations were depressed by the months of sampling when shrimp were absent.

Overall densities of roughneck shrimp were greater at impoundment stations than at creek stations, but mean number collected per station was greater at creek stations (Figs. 13.10 and 13.11 and Appendix 13.4). In

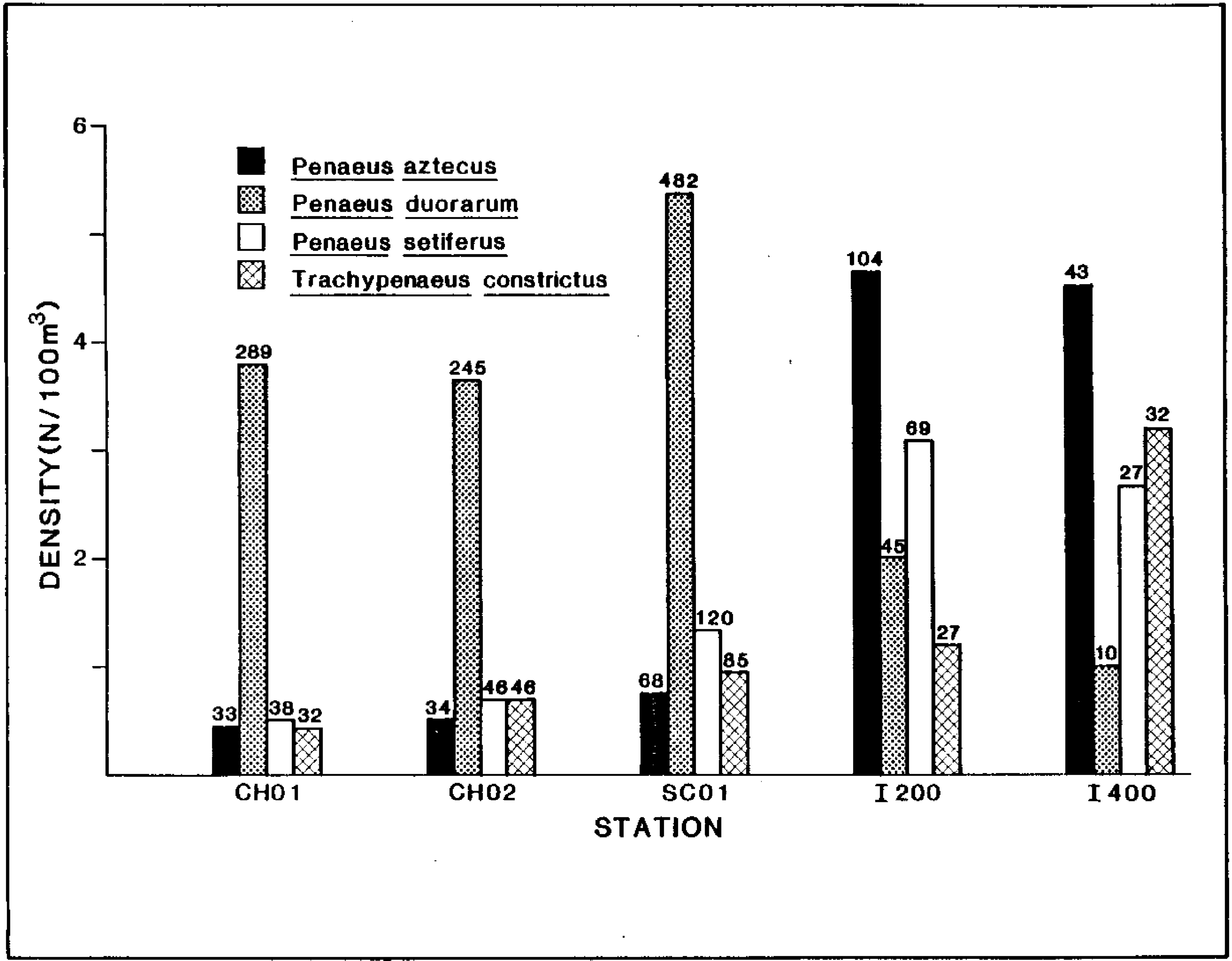


Figure 13.11 Densities (N/100 m^3) of *Penaeus aztecus*, *Penaeus duorarum*, *Penaeus setiferus* and *Trachypenaeus constrictus* in relation to station from Intensive samples. Number of samples: CH01 = 141; CH02 = 141; SC01 = 142; 1200 = 82; 1400 = 68.

June, July, and October roughneck shrimp were collected in greater numbers (mean per station) at impoundment stations; however, peak abundance of the species occurred in September, when creek-impoundment water exchange was virtually absent, and none was collected at impoundment stations that month (Fig. 13.11).

Among creek stations, number of individuals and density was greatest for each species at the marsh creek station (Fig. 13.11 and Appendix 13.4). In Chainey Creek pink shrimp were slightly more concentrated near the surface (3.81/100 m^3) than near the bottom (3.66/100m^3), whereas other species were slightly more concentrated near the bottom. Brown shrimp, white shrimp, and pink shrimp were collected in greater numbers and densities at I200 than at I400, but roughneck shrimp were more abundant at I400 (Fig. 13.11).

Patterns of shrimp abundance in relation to tidal stage differed among stations (Table 13.2). Penaeid shrimp were collected in greater densities during flood than during ebb at all stations except the marsh creek station. Ebb and flood densities at creek stations differed by less than 1.5 shrimp/100 m^3, but at impoundment stations shrimp densities on flood tide exceeded those on ebb by 12/100 m^3 (I400) and 17/100 m^3 (I200). Nearly six times as many penaeid shrimp were collected at impoundment stations on flood tides (314) as on ebb tides (54).

During flood at creek stations, maximum shrimp densities were collected at mid-flood (Table 13.2). Shrimp densities varied little (4.20 to 5.82/100 m^3) among ebb stages at the Chainey Creek stations, but at the marsh creek station densities declined during mid-ebb and then increased dramatically during late ebb. At station I200, shrimp abundance was greatest during early flood, and maximum abundance at I400 was at mid-flood (Table 13.2). Because the collection of impoundment samples was delayed, the maximum abundance recorded during early- and mid-flood at these stations corresponds to mid- and late-flood densities at creek stations. In contrast to the other species, brown shrimp were most abundant in early-flood samples. This difference is explained by the predominance of brown shrimp in impoundment samples. Less than half of the late-flood samples and less than half of all ebb samples scheduled were collected at the impoundment stations because of insufficient flow.

Table 13.2 Catches of penaeid shrimps (all species) from Year I intensive samples in relation to tidal stage and station (SMP = number of samples, N = number of individuals, N/100 m^3 = number of individuals collected per 100 m^3 of water filtered).

	STATION														
	CH01			CH02			SC01			I200			I400		
Tidal Stage	SMP	N	N/100 m^3	SMP	N	N/100 m^3	SMP	N	N/100 m^3	SMP	N	N/100 m^3	SMP	N	N/100 m^3
Early flood	24	35	3.72	24	35	3.94	24	37	2.90	17	114	36.77	14	17	6.91
Mid flood	24	106	7.60	24	90	8.02	24	183	11.90	21	81	15.23	13	71	23.10
Late flood	22	42	4.17	22	58	6.66	22	88	8.04	12	23	11.14	7	8	22.10
All flood	70	183	5.47	70	183	6.35	70	308	7.88	50	218	20.80	34	96	16.28
Early ebb	24	101	4.95	24	94	5.34	24	147	7.58	13	30	6.80	14	12	6.57
Mid ebb	24	88	5.82	24	69	5.25	24	44	3.36	12	7	1.62	13	4	2.80
Late ebb	23	30	4.34	23	31	4.20	24	258	14.45	7	0	0.00	7	1	1.15
All ebb	71	219	5.16	71	194	5.09	72	449	8.92	32	37	3.08	34	17	4.12

Of the 54 shrimp collected during ebb at impoundment stations, 42 were collected at the early-ebb stage (Table 13.2).

Mean sizes of each species collected during flood or ebb from creek stations (all year I samples) differed little (≤4 mm), and interestingly, only white shrimp were larger in ebb samples than in flood (Table 13.3). Roughneck shrimp were not collected during ebb from impoundment stations, but mean lengths of the three Penaeus species were 15.1 to 59.5 mm greater during ebb than during flood (Table 13.3).

Few studies have investigated the movements of organisms between impounded and nonimpounded marshes, and these have addressed impoundments created by weir systems in Louisiana (Herke, 1968; 1971; Wengert, 1972; Rose et al., 1975; Herke et al., 1984). Although weirs and the tidal-gate structures at Cat Island achieve the same result, the method by which water level is controlled differs between the two systems. Water exchange between weir impoundments and the open system is determined by the difference between the weir crest level and the high-water level. Weirs are usually built such that their crests are approximately 15 cm below the soil supporting the emergent vegetation, and water exchange occurs on most tidal cycles (Herke, 1979). In contrast to the weir system, water exchange at tidal-gate impoundments can be controlled. Also, inflowing water does not pass over a weir crest, but instead passes through the subsurface trunk. Only during outflow must the water pass over a weirlike structure, the flashboard riser.

In studies of weir impoundments in Louisiana, Herke (1971) found that weirs act as barriers to the movements of various species of fish and shellfish. During periods of low water the weirs are physical barriers preventing passage of any species, and when water levels exceed the weir crest, the weir continues to act as an "ethological" barrier to bottom-oriented species, inhibiting their immigration into and subsequent emigration from the impoundment area. Also in Louisiana, Wengert (1972) observed that weirs interfere with the natural tidal processes that carry shrimp postlarvae into the marsh. Few shrimp <25 mm total length were collected inside the weir, and the peak abundance of larger (>25 mm) shrimp occurred three weeks later inside the weir than in the adjacent creek.

Table 13.3 Mean total lengths of penaeid shrimps collected in all Year I samples from creek or impoundment stations during flood or ebb tide. (N = number of shrimp measured; TL = mean total length [mm]; SD = standard deviation).

	Creek Stations						Impoundment Stations					
	Flood			Ebb			Flood			Ebb		
Species	N	TL	SD	N	TL	SD	N	TL	SD	N	TL	SD
P. aztecus	78	3.7	11.4	68	12.5	1.2	114	16.4	13.4	27	39.2	42.0
P. duorarum	798	9.8	4.1	445	9.7	2.2	46	9.6	3.4	4	24.7	30.4
P. setiferus	313	15.1	16.9	103	19.1	18.8	118	24.7	22.4	16	4.2	42.4
T. constrictus	65	18.6	9.0	79	16.5	8.8	30	16.9	9.5	0	--	--

Whereas movements of penaeid shrimps into weir impoundments were apparently inhibited by the presence of the weir, densities of shrimp moving into Cat Island impoundments were equivalent to or greater than shrimp densities in the creeks. However, the flow of water between Chainey Creek and the impoundments was severely restricted except for three months of the year. Peak abundance of brown shrimp occured during the time of good water exchange, and more were collected at impoundment stations than at creek stations. In contrast, pink shrimp were virtually restricted from the impoundments, because their period of abundance coincides with greatly reduced water exchange between systems (because of high water levels in impoundments). Weirs deny access to impoundments by shrimp and other species only when tidal heights do not exceed weir crest level (see Herke, 1979). Recruitment of penaeid shrimp to Cat Island impoundments was mostly by postlarvae, whereas Wengert (1972) collected few shrimp <25 mm TL inside weired impoundments.

In addition to delaying immigration, weirs also delay shrimp emigration relative to the open creeks (Herke, 1971). Shrimp emigration from Cat Island impoundments is probably also delayed, as evidenced by the large animals collected during outflow (Table 13.3). More important though is the fact that few shrimp were collected leaving the impoundments. Only 7.6% as many shrimp were collected during ebb as during flood at the impoundment stations.

Shallow estuarine areas are heavily utilized by postlarval and juvenile penaeid shrimps (Parker, 1970; Truesdale, 1970; Weinstein, 1979; Zimmerman and Minello, 1984), but their movement into and within these nursery grounds have received little attention (Herke, 1971). Herke et al. (1984) collected penaeid shrimps in stationary traps set in a Louisiana saltmarsh canal. They found that penaeid shrimps of "a similar size" tend to "slosh" back and forth with the tide and that, generally, there is a net movement of smaller individuals toward the marshes and larger individuals seaward. Findings were similar for creek stations in the present study, in that shrimp densities and mean total lengths differed little between flood and ebb samples. In fact, at each station, shrimp densities varied considerably more among flood stages or among ebb stages than between flood and ebb tides. The slightly greater ($\leq 1.26/100$ m^3) densities during flood in Chainey Creek suggest a net movement of shrimp toward the headwaters. At the small marsh creek station, however, shrimp density was greater during ebb than during flood, and densities at the late ebb stage were particularly high (Table 13.2). This creek feeds an expansive area of Spartina saltmarsh and mud flats that, as indicated by the high densities recorded at this station, are extensively used by postlarval, juvenile, and some subadult shrimp. The high density observed at late ebb indicates that shrimp remain in this creek until late in the ebb, when water depth in the creek has decreased to <1m. Interestingly, several large (>100 mm TL) shrimps were collected moving toward the marsh-tidal flat area, indicating that utilization of the shallow "nursery zone" is not restricted to postlarvae and juveniles.

The higher shrimp densities recorded at peripheral stations (SC01, I200, I400) suggest that shrimp may have been more concentrated near the creek banks than near the center in Chainey Creek. Such a distribution is consistent with the premise that young penaeid shrimp seek out a shallow vegetated habitat for the protection and food it provides (Williams, 1955; Parker, 1970; Herke, 1971; Giles and Zamora, 1973; Weinstein, 1979; Minello and Zimmerman, 1983; Zimmerman et al., 1984).

Spatial distribution of penaeid shrimp in the present study was unaffected by day/night differences. Penaeid shrimp are typically nocturnal (P. setiferus to a lesser degree) (Williams, 1958; Perez-Farfante, 1969), and postlarvae adjust their distribution in the water column in response to light. Generally, postlarvae are found closer to the surface at night and are either closer to the bottom or distributed throughout the water column in the day (Bearden, 1961; Duronslet et al., 1972); however, this pattern is not always apparent (Eldred et al., 1965). Our near-surface and near-bottom nets in Chainey Creek usually fished no more than 1.5 m apart, and shrimp densities differed little (<1/100 m^3) between stations during day or night.

Penaeid Shrimp Occurrence in "Event" Samples. During the draiwdown of the impoundments 6-7 May 1983, nine samples collected at station I200 contained eight P. aztecus postlarvae (mean total length 12.7 mm), and eight samples from station I400 contained no penaeid shrimps. Total volumes of water filtered during draiwdown sampling at I200 and I400 were 272.5 and 411.3 m^3, respectively (Table 13.4).

Table 13.4 Occurrences of penaeid shrimp in "event" samples associated with impoundment management procedures.

Event	Date	Station	No. of Samples	Total Volume Filtered	Shrimp Collected	Mean Total Length
Draindown	6-7 May	I200	9	272.5	8 *P. aztecus*	12.7 mm
Draindown	6-7 May	I400	8	411.3	0	
Reflood	8 May	I200	2	109.2	4 *P. aztecus*	12.4 mm
Reflood	8 May	I400	2	96.7	15 *P. aztecus*	12.0 mm
Drop water level	20 Oct	I200	3	362.6	3 *P. setiferus*	118.5 mm
Drop water level	20 Oct	I400	3	94.4	0	--
Drop water level	21 Nov	I200	3	67.2	0	--
Drop water level	21 Nov	I400	3	24.3	0	--

Two samples were collected at each impoundment station during reflooding on 8 May 1983. Two samples at I200 filtered 109.2 m^3 and contained four P. aztecus postlarvae (mean total length 12.4 mm). Two reflood samples from I400 filtered 96.7 m^3 of water and collected 15 P. aztecus postlarvae (mean total length 12.0 mm).

The water levels in the impoundments were lowered by approximately 10 cm (by removing one board from the flashboard riser) on 20 October 1983 and 21 November 1983. Three samples were collected at each station during each of these events. Three large (mean total length 118.5 mm) P. setiferus were collected from I200 in October. No other penaeid shrimp were collected during the lowering of impoundment water levels.

Of the impoundment management events monitored, only the reflooding of the impoundments appeared to move large numbers of shrimp between systems. Sampling this event was extremely difficult, and only two samples were collected at each station. The water volume filtered at each station (about 100 m^3) was certainly small in relation to the total volume that flowed into the impoundments. Although shrimp densities were not great, the total number of individuals recruited may have been considerable (no attempt was made to estimate total numbers recruited).

Portunid Crabs

Species Composition. During year I of the mesoplankton survey, 432 juvenile and adult portunid crabs and 2836 portunid megalopae were collected. Two juveniles were identified to the genus Portunus, but the specimens were small (<6 mm TW) and damaged, and specific identification was not possible. All other juvenile and adult portunid crabs were identified as blue crabs, Callinectes sapidus. The results of the decapod population studies (Chapter 13B), in which seven C. similis and 1509 C. sapidus were collected, also emphasizes the dominance of C. sapidus in the study area.

Portunid megalopae (the final larval stage) were not identified below the familial level; however, most, if not all, were probably C. sapidus. Megalopae of other portunid species are generally restricted to more oceanic salinities (Williams, 1971; Stuck and Perry, 1981), and the periods of abundance in our samples were similar to those observed for C. sapidus megalopae on the Atlantic (Tagatz, 1968; Dudley and Judy, 1971;

Meredith, 1982) and Gulf of Mexico coasts (King, 1971; Stuck and Perry, 1981). Throughout this section on portunid crabs, use of the word megalopae implies portunid megalopae and, most probably, those of *C. sapidus*.

The large number of megalopae collected during year I of the study suggests that recruitment to the study area by blue crab was largely by the megalopal stage. Johnson (1982) found maximum concentration of megalopae in the neuston layer more than 25 km offshore and concluded that reinvasion of the estuary by the megalopal stage occurs only during years of predominantly onshore winds during September and October; otherwise, reinvasion is by juveniles. Tagatz (1968) and Dudley and Judy (1971, 1973) also concluded that recruitment of blue crab is largely by juveniles. Other investigators (King, 1971; Williams, 1971; Meredith, 1982; McConaugha et al., 1983; Epifanio et al., 1984), however, have collected large numbers of megalopae invading estuaries, and megalopae have been collected at considerable distances (40 to 170 km) inshore from inlets (Cargo, 1960; Tagatz, 1968; Williams, 1971).

Results from the present study are similar to those of Meredith (1982), in that recruitment to a marsh/creek population appeared to be largely by megalopae, but recently metamorphosed juveniles remained in the plankton and also contributed to recruitment.

Temporal Abundance and Size Distribution. Portunid megalopae were collected in February and May to December 1983 (Fig. 13.12). From all samples collected, densities exceeded four megalopae per 100 m^3 of water in each of these months except in February and June. Megalopae were abundant (>20/100 m^3) from September to November, and maximum monthly density was observed in November. Peak densities occurred during extensive sampling on 8 and 16 November (Fig. 13.13 and Appendix 13.5). Megalopae were collected in waters with temperature and salinity ranges of 10.6 to 33.8°C and 3.0 to 31.9 ppt, but the vast majority were collected in temperatures >16°C and salinities >22 ppt.

Crab stages (juveniles and adults) of *C. Sapidus* were collected in all months except January 1983 (when only six samples were collected), but monthly densities never exceeded three crabs per 100 m^3 of water (Fig. 13.12). Maximum densities of blue crabs were observed in May (2.68/100 m^3) and September (2.59/100 m^3). Crab stages were collected over

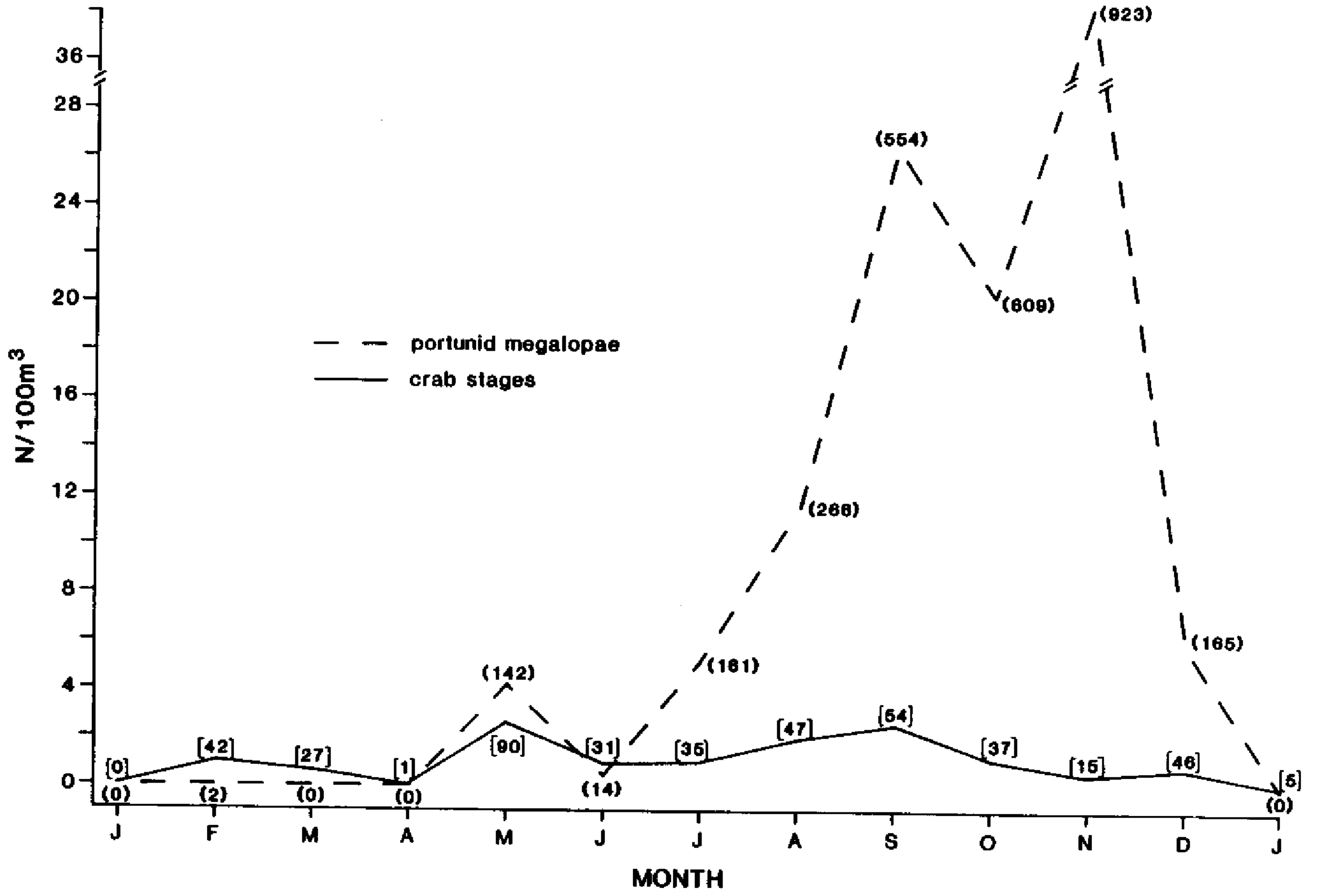


Figure 13.12 Densities of portunid megalopae and crab stages of Callinectes sapidus by month from all samples collected in Year I. Numbers of individual megalopae ( ) and crabs [ ] collected each month are indicated.

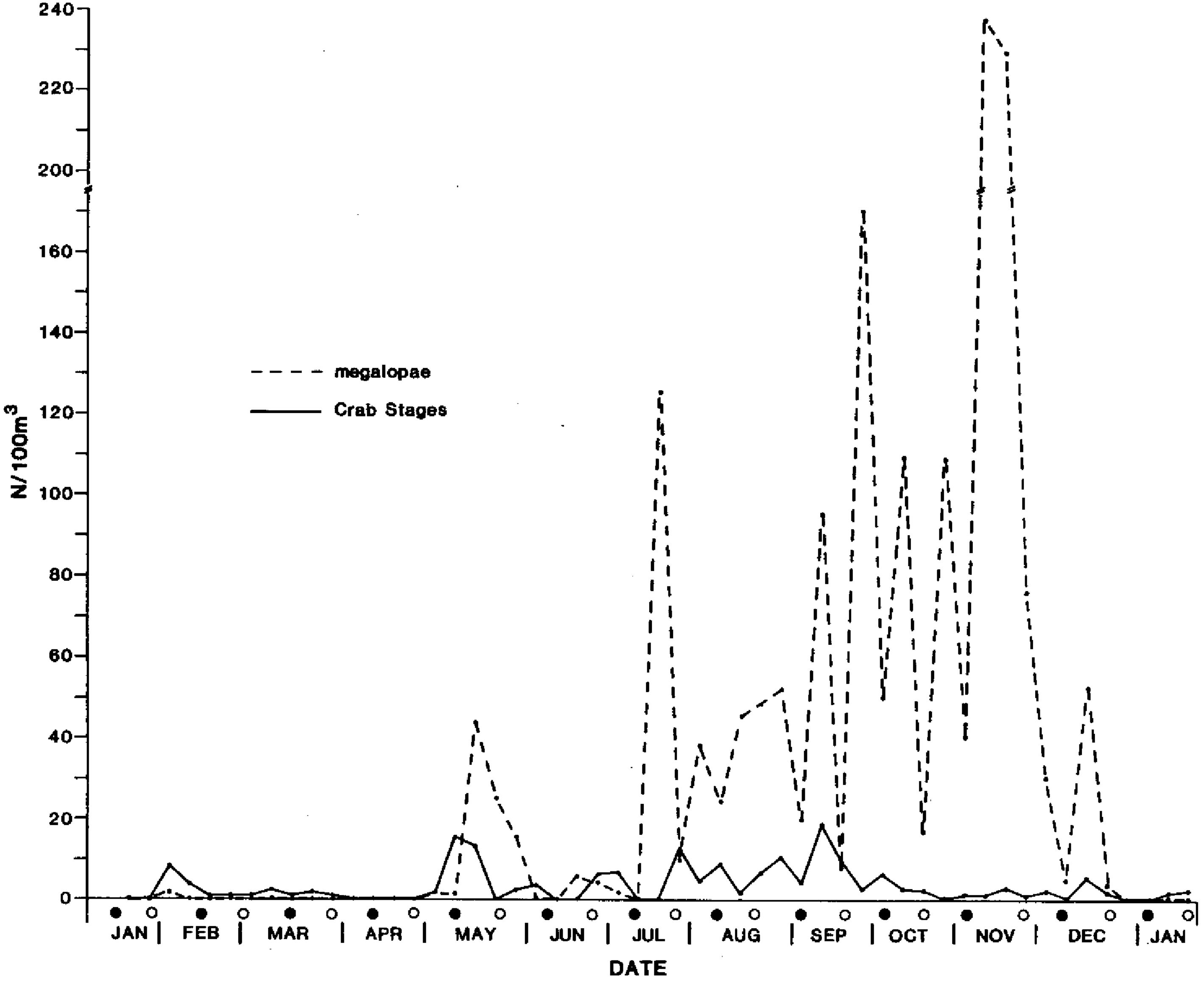


Figure 13.13 Densities (N/100 m^3) of portunid megalopae and crab stages of <u>Callinectes sapidus</u> during weekly (Extensive) sampling in Year I.

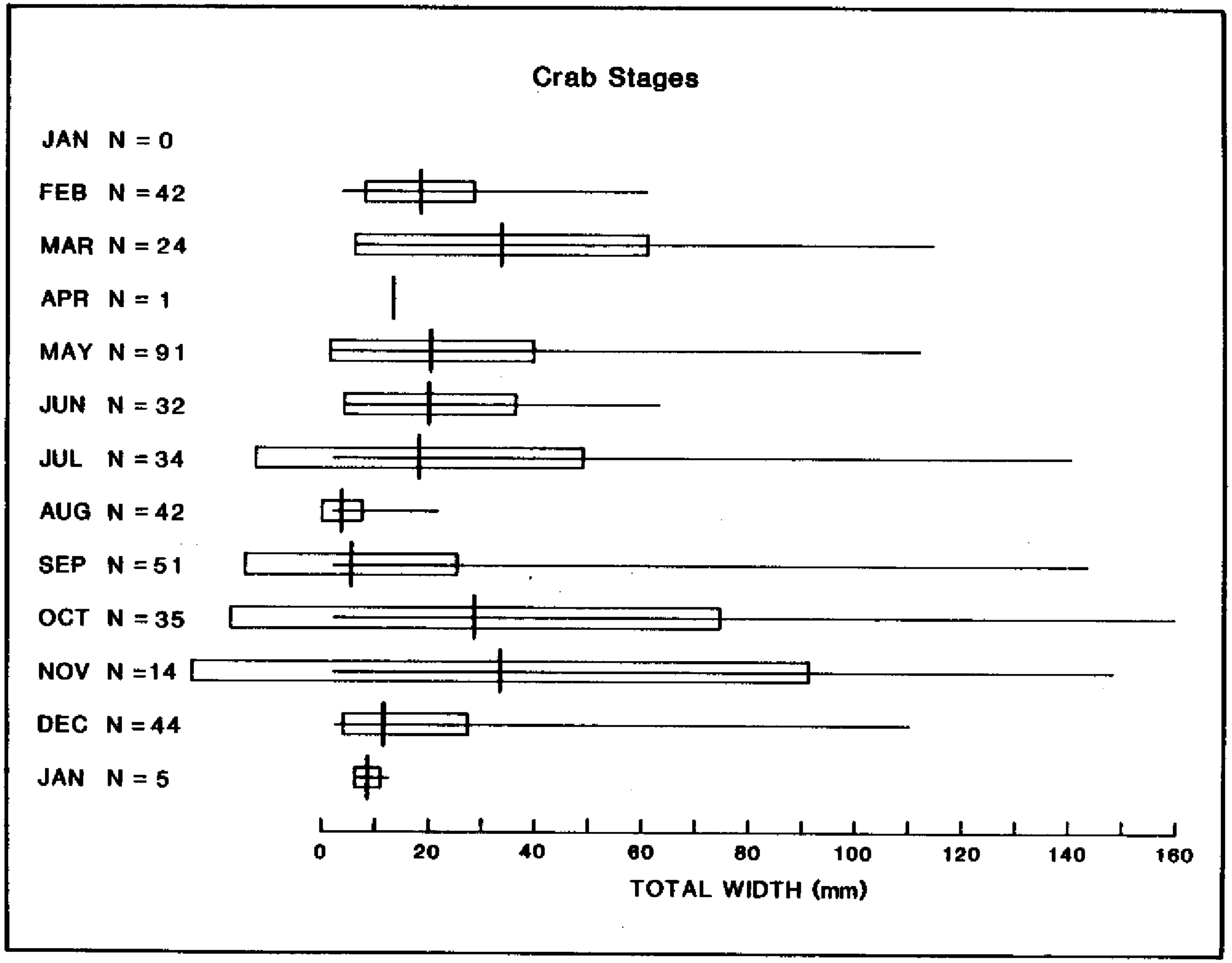


Figure 13.14 Total widths (mm) of crab stages of Callinectes sapidus by month from all samples collected during Year I (vertical line = mean, horizontal line = range, rectangle = ± one SD).

temperature and salinity ranges of 8.4 to 32.4oC and 0.0 to 31.9 ppt, respectively. The majority of the crabs collected February to June were 8 to 40 mm total width (TW) juveniles (Fig. 13.14). From July through November, crab catches were dominated by early stage (≤5 mm TW) juveniles, most of which were first or second crab stages. In December and January, concurrent with the decrease of megalopal influx, crab modal size again exceeded 5 mm TW. Ninety-four percent of the crabs collected in the mescoplankton samples were less than 50 mm TW, and only eight individuals (1.9%) were mature.

The period of recruitment of megalopae and early stage juveniles in the present study was generally similar to those observed in other investigations; however, we observed peak concentrations in November, whereas other investigators observed maximum concentrations from July to October (Tagatz, 1968; Williams, 1971; Meredith, 1982). In Mississippi coastal waters *C. sapidus* megalopae were collected all months except January and February, with two peaks of abundance occurring, one in late spring/early summer and the other larger peak during late summer/early fall (Stuck and Perry, 1981). Low salinities in the Santee River system during spring may have negatively influenced immigration of blue crab megalopae in the present study.

The two megalopae collected from Chainey Creek in February appear anomalous to the general recruitment patterns of *C. sapidus*. King (1971) suggested that late winter (January to March) concentrations of megalopae that he observed were *C. sapidus* larvae spawned the previous fall, but Stuck and Perry (1981) collected large numbers of *C. similis* and almost no *C. sapidus* megalopae during February and March.

Juveniles 10 to 50 mm TW were most abundant from February to June. These individuals represent the previous fall hatch. Dudley and Judy (1973) reported that young-of-the-year juveniles arrive in the creeks in large numbers in November and December, reach a peak from January to March, and move out into the sound in the spring. Meredith (1982) did not observe a similar spring exodus, however. Lower numbers of juveniles in our March and April samples were more likely the result of low-salinity conditions than a general migration. By late June and July these juveniles were probably too large to be collected efficiently by plankton nets. Peak blue crab concentration in May was comprised of 8 to 50 mm juveniles, whereas the September abundance was almost exclusively early stage (<5 mm) crabs. In view of the large number of megalopae collected from late September through November, relatively few recently metamorphosed individuals were collected.

Spatial Variability in Abundance. Densities of megalopae at creek stations were almost twice that at impoundment stations, and numbers of megalopae collected were nearly eight times greater at creek stations than at impoundment stations (Fig. 13.15 and Appendix 13.6). This situation was similar to that observed for pink shrimp, which recruited at similar times; that is, numbers of megalopae collected at impoundment stations were far fewer than at creek stations, because peak abundance of megalopae occurred when little water was exchanged between creek and impoundment systems (late summer). Megalopal densities were not proportionately smaller at impoundment stations, because fewer samples were collected at impoundments (tidal gates closed) during the winter, when megalopae were absent.

During the May intensive sample, megalopae were most abundant (numbers of individuals and density) at the impoundment 2 station (Fig. 13.15 and Appendix 13.6). Similar numbers of megalopae were collected at I200 as at the creek stations through August, and although densities remained relatively high, the relative numbers of megalopae collected at I200 dropped dramatically after the August intensive sample because of high water levels in the impoundment, which decreased circulation. No water exchange into impoundment 4 occurred during the period of maximum megalopal concentrations (September to November), and only five megalopae were collected at this station. Among creek stations, overall density of megalopae was greatest at CH02, but maximum densities varied among stations and months (Fig. 13.15 and Appendix 13.6).

In contrast to the pattern observed for megalopae, crab stages were more abundant at impoundment 2 than at creek stations (Fig. 13.15 and Appendix 13.6). Overall crab density was also greater at station I400 than at creek stations, but the number collected (25) was less as a result of reduced volumes filtered. Crabs collected February to April at I200 (N = 5) and I400 (N = 7) were not included in density estimates, because flow velocities were not measured during that time. Greater efficiency of the trunk nets in capturing juvenile and adult blue crabs probably contributed

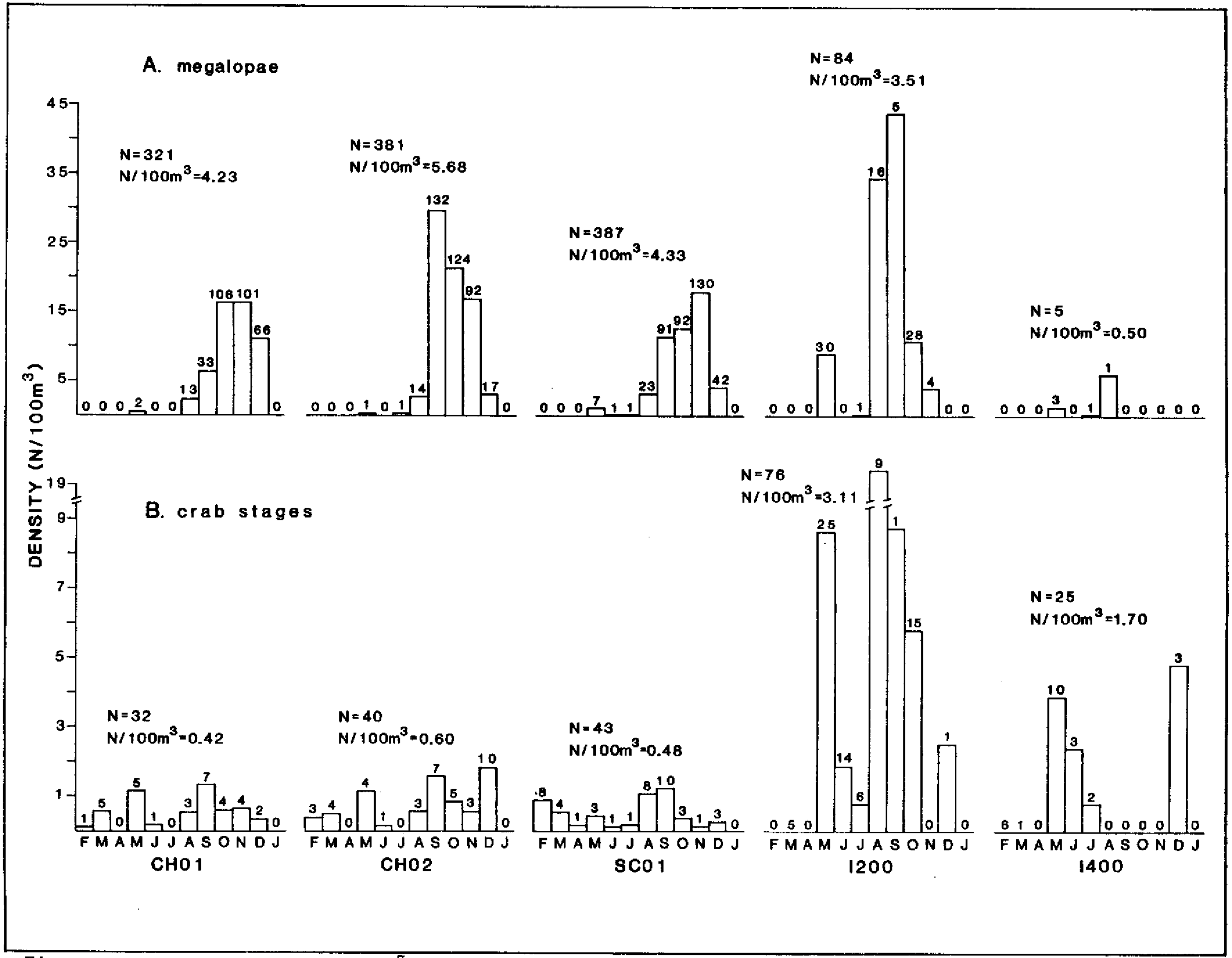


Figure 13.15 Densities (N/100 m^3) of portunid megalopae and crab stages of Callinectes sapidus by station and month from intensive samples.

to the observed differences in densities between creek stations and impoundment stations. Densities of crab stages were low ($\leq$0.60/100 m^3) at all creek sites (Fig. 13.15 and Appendix 13.6).

Crab catches at creek stations were lowest during April (N = 1), June (N = 3), July (N = 1), and January (N = 0). The maximum crab density recorded at a creek station during monthly sampling was 1.82/100 m^3. At station I200 and I400 the maximum numbers of crabs collected during monthly intensive sampling was in May, but crab density was greatest in August at I200 and December at I400 (Fig. 13.15 and Appendix 13.6). No crabs were collected from August to November at the impoundment 4 station.

Effect of Tidal Stage on Portunid Abundance. Overall, the density of megalopae in flood-tide collections (8.09/100 m^3) was more than five times the megalopal concentration in ebb collections (1.50/100 m^3). This pattern was reflected at all five stations (Fig. 13.16) and indicates a substantial directed movement of megalopae toward the marshes and upper reaches of Chainey Creek. Predation upon megalopae in the upper creeks and marsh may have contributed to the observed differences between the number of megalopae collected on flood or ebb, but it seems unlikely that predation alone accounted for this difference. Meredith (1982) observed an even greater difference between flood and ebb densities of megalopae and stated, "It is probable that recruitment into the marsh via megalopal stages is an important mechanism for maintaining marsh populations...." Almost without exception, megalopae have been collected in greater abundance during flood than during ebb (Stuck and Perry, 1981; Epifanio et al., 1984; Brookins and Epifanio, 1985). Sulkin and Van Heukelem (1982) have shown possible mechanisms by which *C. sapidus* megalopae are able to control their vertical position in the water column to facilitate transport into estuarine systems.

Densities of megalopae were greater during flood than during ebb at all stations, but patterns of megalopal density in relation to tidal stage differed among stations (Fig. 13.16A). At stations CH01 and SC01 maximum density of megalopae occurred during mid-flood. At CH02, however, densities of megalopae increased markedly during late flood (the maximum density of megalopae recorded during the study, 390.5/100 m^3, was collected at station CH02 during late flood). High concentrations of megalopae at SC01 during late ebb probably relates to complete (or near

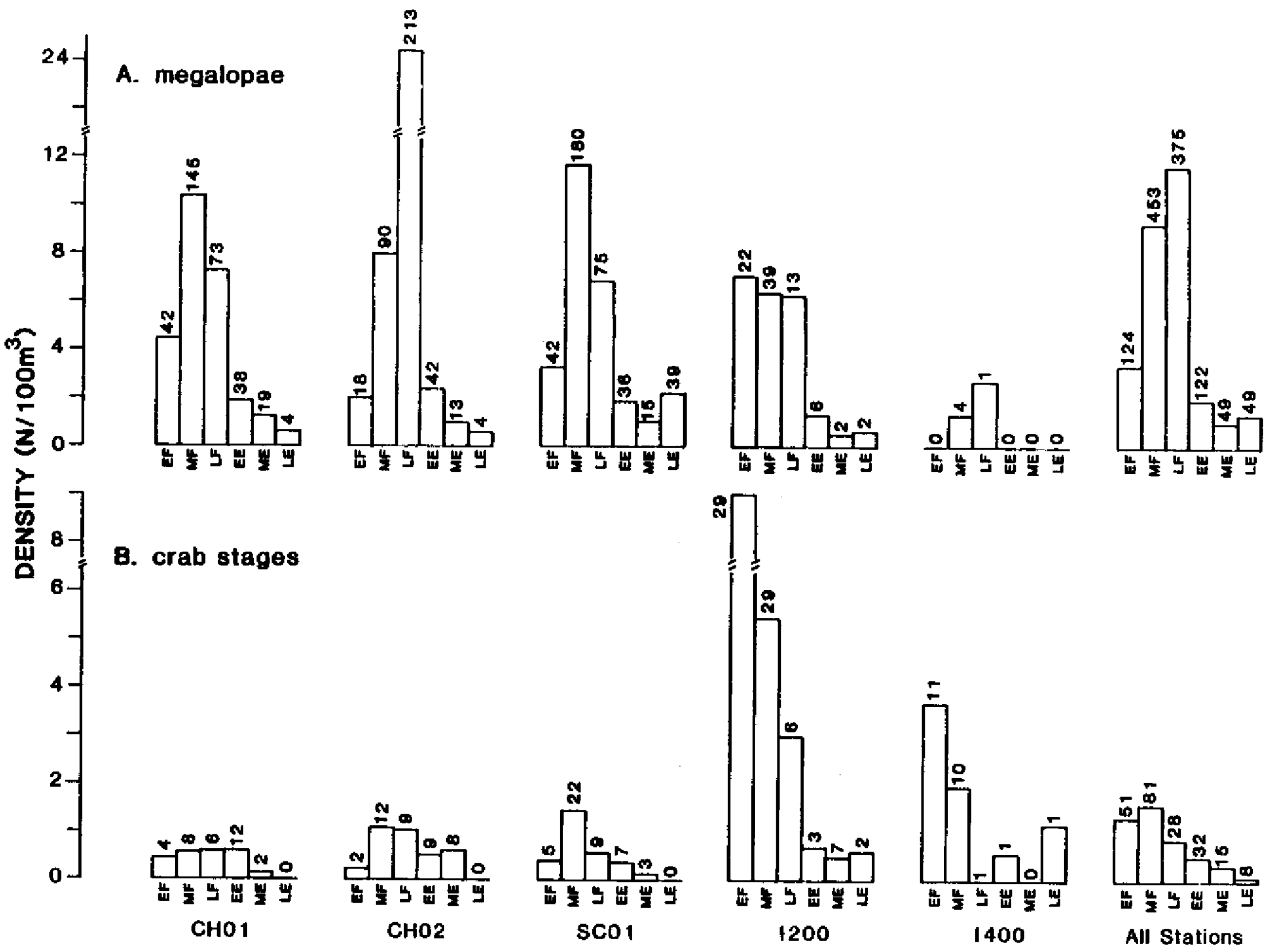


Figure 13.16 Densities (N/100 m^3) of portunid megalopae and crab stages of Callinectes sapidus by station and tidal stage from Intensive samples (EF = early flood, MF = mid-flood, LF = late flood, EE = early ebb, ME = mid-ebb, LE = late ebb).

complete) drainage of the tidal flats by the marsh creek, a pattern also observed for penaeid shrimp.

At station I200, concentrations of megalopae were similar among flood stages and among ebb stages (Fig. 13.16). The five megalopae collected at station I400 were taken during mid- and late-flood stages.

Crab stages also were more abundant during flood than ebb at all stations (Fig. 13.16B). Overall, crab densities during flood and ebb were 1.29 and 0.34/100 m^3, respectively. The greater abundance of juvenile blue crabs in flood than in ebb waters suggests that juveniles also contribute to recruitment, but to a lesser degree than megalopae. Crab stages were six times more abundant during flood ($N = 86$) than ebb ($N = 14$) at impoundment stations. Dudley and Judy (1973) reported that juveniles move from creeks into the sounds in spring, but Meredith (1982) did not observe such an exodus. In the present study, crabs were more abundant during flood than ebb collections in all months except December. The December data may indicate a movement out of the shallows in response to declining water temperatures. Herke et al. (1984) observed increased emigrations of blue crabs from marsh areas following the passage of cold fronts. Our plankton-net collections, however, may not be good indicators of movement of juveniles older than the first few crab stages. The pattern of crab density in relation to tidal stage differed among stations (Fig. 13.16B).

Blue crabs collected during ebb samples had a greater mean size (TW) than crabs collected during flood at creek stations (flood, 9.2 mm; ebb, 15.5 mm) and at impoundment stations (flood, 16.7 mm; ebb, 72.7 mm). Crabs were larger at impoundment stations than at creek stations on either tide (Table 13.5). Early-stage crabs ($\leq$5mm) comprised 60, 30, 14, and 0% of crabs collected in creek-flood, creek-ebb, impoundment-flood, and impoundment-ebb samples, respectively. Fewer early-stage crabs at impoundment stations probably resulted from reduced water exchange during the major period of ingress of megalopae and early crab stages. These data indicate that the majority of the small crabs that move into the upper creeks and impoundments are not immediately flushed back out, but rather utilize these areas during early juvenile development. The larger mean size of crabs at impoundment stations was probably influenced by greater capture efficiency of larger crabs by trunk nets. Seven of the eight mature blue crabs collected in mesoplankton samples were from impoundment stations, and all but one of these were collected in outflow samples.

Table 13.5

Mean total width of blue crabs from creek and impoundment stations collected during flood or ebb. (N = number of crabs, TW = mean total width (mm), SD = standard deviation of mean total width).

Station, Tide	N	TW	SD
Creek, flood	169	9.2	12.4
Creek, ebb	39	15.5	23.2
Impoundment, flood	179	16.7	17.7
Impoundment, ebb	28	72.8	51.4

Event Samples. Six blue crabs were collected from station I200 (2.20/100 m^3) and none from I400 during draining of the impoundment 6-7 May (Table 13.6). During reflooding of impoundments on 8 May, 13 crabs were collected at station I200 (11.90/100 m^3) and 4 crabs were collected at I400 (4.14/100 m^3). This event could have moved considerable numbers of crabs from Chainey Creek into the impoundments. The water level in the impoundments was lowered 20 October and again 21 November. At station I200, five crabs were caught during the October event (1.38/100 m^3), and three were collected during the November event (4.46/100 m^3). No crabs were collected from I400 during lowering of the water levels. No megalopae were collected in event samples.

Grass Shrimp (Palaemonetes)

Total Number and Species Composition. During year I of the mesoplankton survey, 230,771 juvenile and adult Palaemonetes were collected. Although juveniles as small as 6 mm TL were recovered from the plankton samples, probably not all small juveniles (<10 mm) were recovered. Therefore, the numbers of Palaemonetes reported in this section represent minimum numbers collected.

Table 13.6 Number of individuals (N), density (N/100 m^3) and mean total width (mm) of blue crabs collected during "event" samples in Year I.

Event	Date	Station	No. of Samples	Volume Filtered	N	N/100 m^3	Mean Total Width
Draindown	6-7 May	I200	9	272.5	6	2.20	94.9
Draindown	6-7 May	I400	8	411.3	0	0.00	--
Reflood	8 May	I200	2	109.2	13	11.90	13.0
Reflood	8 May	I400	2	96.7	4	4.14	23.8
Drop water level	20 Oct	I200	3	362.6	5	1.38	134.3
Drop water level	20 Oct	I400	3	94.4	0	0.00	--
Drop water level	21 Nov	I200	3	67.2	3	4.46	139.7
Drop water level	21 Nov	I400	3	24.3	0	0.00	--

Only those grass shrimp collected at impoundment 2 (N = 95,525) during intensive and extensive sampling were identified to species. Of these, 99.97% were P. pugio. P. vulgaris (N = 292) was collected only from October to January at I200, and its greatest contribution to the monthly total Palaemonetes at I200 was 13.6% in October. All P. vulgaris collected during intensive sampling were in flood samples; however, 221 P. vulgaris were collected during the lowering of the impoundment water levels (event sampling) in October and November. The ratio of P. pugio to P. vulgaris observed at station I200 may not be representative of the other stations. During the population studies, the P. pugio/P. vulgaris ratio was greater in the impoundments than in the creeks (see Chapter 13B).

Spatial Variability. Overall, numbers of individuals and densities of grass shrimp were 8.6 to 30.9 times greater at impoundment stations than at creek stations during intensive sampling. Greatest numbers of Palaemonetes were collected at station I200 (N = 35,270), but grass shrimp density was greatest at station I400 (Fig. 13.17). Among creek stations, the density of grass shrimp at the marsh creek station (SC01) was greater than twice that at either Chainey Creek Station (Fig. 13.17). As was the case with the penaeid shrimp, Palaemonetes were more concentrated at the peripheral stations than in Chainey Creek, suggesting an affinity for shallow, vegetated areas.

Temporal Variation in Abundance. Grass shrimp were collected every week during extensive sampling in year I (Appendix 13.7), and they were collected at each station during each monthly intensive sample except September to November at station I400, when no water was exchanged between Chainey Creek and impoundment 4 (Fig. 13.17 and Appendix 13.1). Except for May, densities of grass shrimp were greatest at station I400 for every month that samples and flow volumes were collected at that station. Densities of grass shrimps at impoundment 2 exceeded those at Chainey Creek stations all months except April and January, when the tidal gates were closed. Maximum numbers and densities of Palaemonetes were collected at the impoundment stations during May, when the tidal gates were open and impoundment water levels were low. Even during the months in which the tidal gates were closed (February to April and November to January),

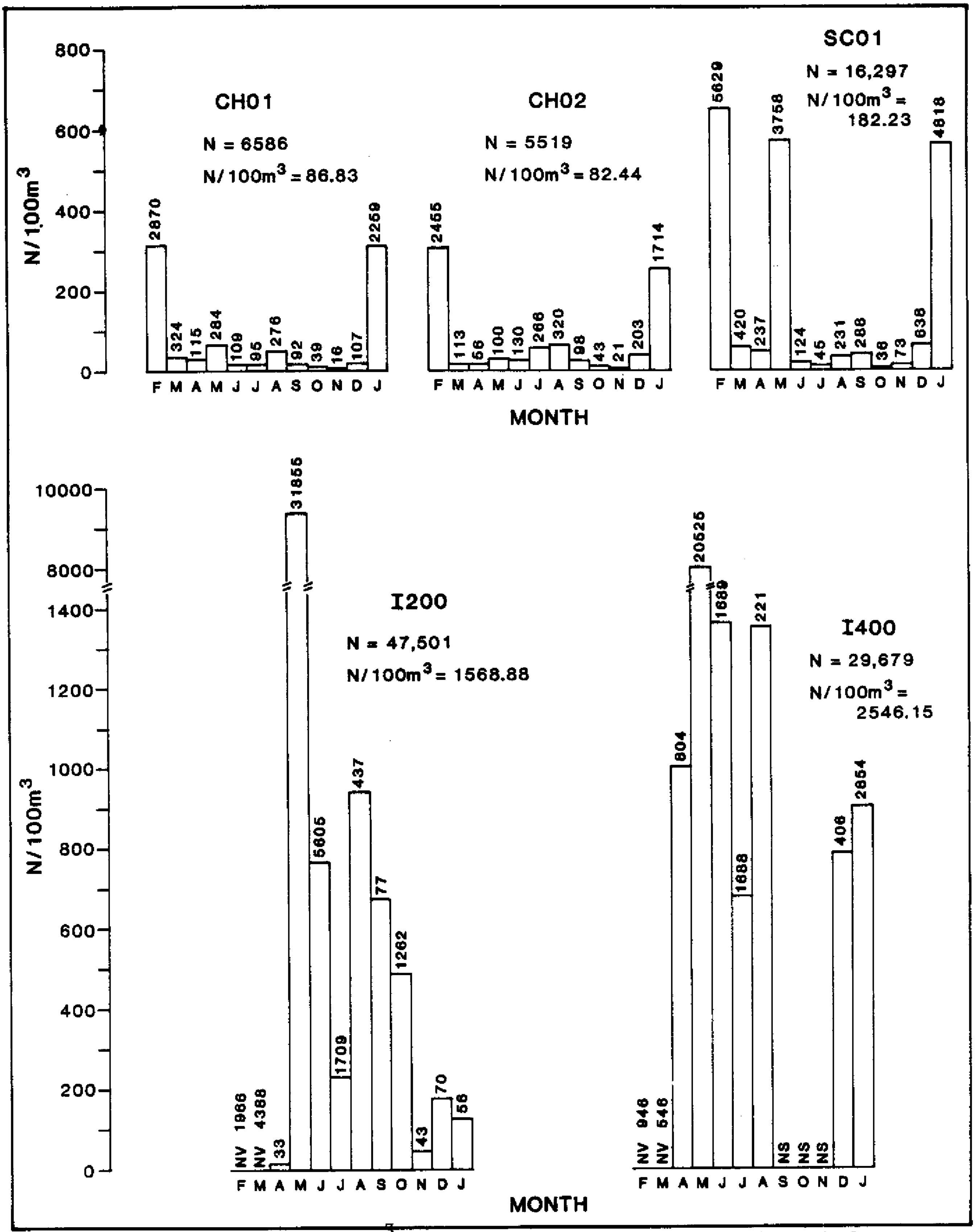


Figure 13.17 Densities (N/100 m^3) of *Palaemonetes* by station and month from Intensive samples. (NV = no value estimate, NS = no sample collected).

Palaemonetes were collected in the trunk nets, often in numbers greater than were collected at creek stations.

Grass shrimp were most abundant at creek stations in February and January. At station SC01, densities were also high in May; however, only slight increases in grass shrimp density were noted at the Chainey Creek stations that month (Fig. 13.17). Alon and Stancyk, (1982) reported that new generation grass shrimp entered the Minim Creek (South Carolina) population in mid-June and reached peak abundance in September and October. A second, smaller wave of recruitment lasted from December to mid-March, with a peak in January (Alon and Stancyk 1982). Although grass shrimp densities at our creek stations increased during the July to September period, their abundance during summer was minor compared to that observed in February and January. Welsh (1975) reported that the standing crop of *Palaemonetes* in a salt marsh embayment of Narraganset Bay was lowest during the summer.

Variation in Abundance among Stations and Tidal Stages. At all three creek stations, grass shrimp showed a clear pattern of being more concentrated in the creeks during periods of low water (late ebb, early flood), becoming less dense with increased tidal height and inundation of the *Spartina* marsh (Table 13.7). Lowest *Palaemonetes* densities were during late flood at all three creek sites.

Densities of grass shrimp at impoundment stations were greatest at early-flood and early-ebb tidal stages, then generally decreased during the later stages (Table 13.7). This pattern was not related to mean volume filtered per tidal stage, and it suggests that grass shrimp may have congregated around the impoundment trunk structures during slack tide and then been carried into the net by the changing flow (grass shrimp were observed in great numbers around the trunk structures at night).

Mean total lengths of *P. pugio* and *P. vulgaris* in outflow (ebb) samples were equal to or greater than mean lengths in flood samples at station I200 for all months in which they were represented (Table 13.8). Overall, *P. pugio* had mean total lengths of 23.7 mm in flood samples and 25.3 mm in ebb samples. For *P. vulgaris*, mean size was 23.9 mm in flood samples and 24.8 mm in ebb samples.

At all five stations, grass shrimp densities were greater during ebb than during flood (Table 13.7). The relative difference was greatest at

Table 13.7 Number of individuals (N) and density (N/100 m^3) of *Palaemonetes* from intensive samples in relation to station and tidal stage.

	CHO1		CHO2		SCO1		I200		I400	
Tidal Stage	N	N/100 m^3	N	N/100 m^3	N	N/100 m^3	N	N/100 m^3	N	N/100 m^3
Early flood	1,946	206.76	988	111.15	3,255	255.09	11,341	1946.45	9,795	3727.53
Mid flood	575	41.21	327	29.14	2,245	145.84	5,666	955.81	6,511	1485.04
Late flood	249	24.71	144	16.53	257	23.48	1,043	484.75	1,157	3135.36
Early ebb	824	40.42	818	46.47	997	51.39	17,816	3193.61	7,451	3789.27
Mid ebb	1,662	109.94	1,506	114.63	2,275	173.92	10,456	1823.77	4,207	2216.93
Late ebb	1,330	192.53	1,736	235.26	7,268	407.17	1,179	361.32	558	641.38
All flood	2,770	82.83	1,459	50.61	5,757	147.25	18,050	1155.97	17,463	2521.80
All ebb	3,816	89.98	4,060	106.50	10,540	209.41	29,451	1929.65	12,216	2580.95

	Creek Stations		Impoundment Stations	
	N	N/100 m^3	N	N/100m^3
All flood	9,986	98.51	35,513 (26,984)	1647.58
All ebb	18,416	140.73	41,667 (33,801)	2096.32

Table 13.8 Size and range (total length [mm]) of *Palaemonetes* by species, month, and tide (inflow or outflow) from all samples collected at Station I200 (N = number of individuals measured).

	P. pugio						*P. vulgaris*					
	FLOOD			EBB			FLOOD			EBB		
Month	N	Mean Size	Range	N	Mean Size	Range	N	Mean Size	Range	N	Mean Size	Range
Feb	147	22.7	14-35	170	23.7	12-23	0	--	--	0	--	--
Mar	143	24.7	13-35	200	24.8	18-35	0	—	--	0	--	--
Apr	67	24.4	14-38	1	28.0	--	0	—	--	0	--	--
May	473	25.2	15-38	714	25.4	13-38	0	--	--	0	--	--
Jun	307	27.2	13-38	136	27.9	17-37	0	--	--	0	--	--
Jul	246	25.4	10-35	55	25.4	14-35	0	--	--	0	--	--
Aug	50	21.4	9-32	0	--	--	0	--	--	0	--	--
Sep	80	16.4	8-31	0	—	—	0	--	--	0	--	--
Oct	141	17.4	10-33	2	23.0	21-25	19	22.3	12-29	8	25.3	19-30
Nov	66	19.6	6-32	26	25.3	21-32	22	24.2	15-31	90	24.8	18-34
Dec	117	22.0	9-34	0	--	--	44	24.5	18-30	0	--	--
Jan	206	22.4	12-35	0	--	--	1	20.0	--	0	--	--
TOTAL	2043	23.7	6-38	1304	25.3	12-38	86	23.9	12-31	98	24.8	18-34

CH02 (where ebb densities were more than twice as great as densities during flood), and was least at I400 (where densities during ebb were less than 3% greater than during flood). These data suggest that *Palaemonetes* are exported from the Chainey Creek study area; however, Alon and Stancyk (1982) suggested that larval development does not take place within this area. Also, the mean size of grass shrimp at station I200 was greater during ebb than flood. It is not known whether *Palaemonetes* are more vulnerable to nets during ebb than flood, whether recruitment is by larval stages that were not sorted from samples and, hence, not included in the analysis, or whether these data accurately represent a net movement of *Palaemonetes* out of the study area. In any case, it is apparent that great numbers of *Palaemonetes* move between Chainey Creek and the impoundments, even during periods when exchange is reduced. In contrast to an apparent export of *Palaemonetes* observed in this study, Nixon and Oviatt (1973) found that movement of *Palaemonetes* through a culvert and into a marsh embayment was almost always substantially greater than movement out of the embayment.

Event Samples. At the two impoundment stations, 71,466 *Palaemonetes* were collected during sampling of impoundment management events. These samples accounted for 24 and 58% of the grass shrimp collected at I200 and I400, respectively.

From each impoundment station, over 20,000 *Palaemonetes* were collected during impoundment draining on 6-7 May. Grass shrimp densities at stations I200 and I400 during the draiw-down were estimated at 7965/100 m^3 and 5442/100 m^3, respectively (Table 13.9). Density estimates for grass shrimp in reflood samples were 7656/100 m^3 at I200 and 17,263/100 m^3 at I400. It is apparent that enormous numbers of *Palaemonetes* were exchanged during draiwdown and flooding operations in May, but these data were insufficient to allow an estimate of net gain or loss of *Palaemonetes* in the impoundment systems.

Densities of *Palaemonetes* collected during sampling of the fall (October and November) lowering of impoundment water levels ranged from 2.8 to 4794/100 m^3 (Table 13.9). The numbers of *Palaemonetes* collected were similar to or less than numbers collected during intensive samples, when tidal exchange was not impeded by closed tidal gates or high impoundment water levels. These October samples marked the first movement

Table 13.9

Number of individuals (N) and density (N/100 m^3) of *Palaemonetes* collected during "event" samples.

Event	Date	Station	No. of Samples	Total Volume Filtered	N/100 m^3	N
Drawdown	6-7 May	I200	9	272.5	7965.14	21,705
Drawdown	6-7 May	I400	8	411.3	5442.01	22,383
Reflood	8 May	I200	2	109.2	7656.59	8,361
Reflood	8 May	I400	2	96.7	17263.70	16,694
Lower water level	20 Oct	I200	3	362.6	2.76	10
Lower water level	20 Oct	I400	3	94.4	944.92	892
Lower water level	21 Nov	I200	3	67.2	380.95	256
Lower water level	21 Nov	I400	3	24.3	4794.24	1,165

of organisms between impoundment 4 and Chainey Creek since August, when a single sample was collected.

CONCLUSIONS

Meroplanktonic decapod crustaceans formed a conspicuous segment of the plankton population in the Chainey Creek complex from May to November. Penaeid shrimps reached the study area as postlarvae and, of the four species collected (*Penaeus aztecus*, *P. duorarum*, *P. setiferus*, and *Trachypenaeus constrictus*), *P. duoraram* was the most abundant during both years of our survey. Periods of abundance differed among the penaeid species. Recruitment of the blue crab, *Callinectes sapidus*, to the study area was primarily by the megalopal stage, which was most abundant from July to November. Juvenile *C. sapidus* were collected throughout the year, but densities of juveniles in mesoplankton samples were low. Juvenile and adult grass shrimp, *Palaemonetes* sp., were collected throughout the year, with greatest abundance in the winter.

Utilization of the impoundments by target organisms was dependent on water exchange between Chainey Creek and the impoundments to provide access to the impounded area. The management strategy used to promote impoundment utilization by waterfowl severely restricted water exchange between systems during all but a few months of the year. The degree to which a particular species was able to inhabit the impounded areas depended on the timing of recruitment of that species and periods of water exchange between Chainey Creek and the impoundments.

Among penaeid shrimps, *P. aztecus* occurred almost exclusively during the May to July period of adequate water exchange between systems and was collected in greater numbers and greater densities at the impoundment water-control structures than at the creek stations. In contrast, *P. duorarum*, which was most abundant during late summer-fall period, was more abundant in creek samples than impoundment trunk samples, because little water exchange occurred at this time. Juvenile blue crabs were almost always more abundant at impoundment stations; however, megalopae were virtually precluded from entering the impoundments, because their recruitment coincided with the late summer-fall period of little water exchange. Grass shrimp were collected throughout the year and were nearly always more abundant at impoundment stations, with densities often exceeding $10/m^3$. Grass shrimp moved between systems even during periods of slight water exchange.

Grass shrimp appeared to be exported from the impoundment-Chainey Creek study area; however, it is questionable whether larval development of Palaemonetes was completed within the impoundments. If not, then the apparant export of Palaemonetes from the area was likely to not be a consistent pattern. In contrast, penaeid shrimp and portunid crabs appeared to be imported to the study area, particularly in impoundments. The water-control structures probably acted as barriers to emigration of these species.

Chapter 13

B. Decapod Crustacean Community

E. L. Wenner

INTRODUCTION

Decapod crustaceans are an important natant component of salt marsh habitats in the southeastern United States (Weinstein, 1979; Teal, 1962; Kneib, 1984) which they utilize as a refuge from predators during flood tides (Giles and Zamora, 1973; Minello and Zimmerman, 1983) and as a source of food (Montague et al., 1981; Welsh, 1975; Morgan, 1980; Bell and Coull, 1978). Over an annual cycle, marsh habitats are exploited by year-round resident estuarine species such as grass shrimp, *Palaemonetes pugio* and *P. vulgaris*, or seasonally-abundant species such as blue crab, *Callinectes sapidus*, and the penaeid shrimps, *Penaeus setiferus*, *P. aztecus*, and *P. duorarum* (Kneib, 1984, Weinstein, 1979).

A number of recent studies have addressed the interrelationships of macroinvertebrate species, including decapod crustaceans, in the salt-marsh system (e.g., Day et al., 1973; Nixon and Oviatt, 1973; Teal, 1962; Subrahmanyam and Drake, 1975; Subrahmanyam and Coultas, 1980; Weinstein, 1979; Rozas and Hackney, 1984; Parker et al., 1971); however, few have made comparisons in large-scale distributional patterns of invertebrates between subhabitats of the marsh ecosystem (Kneib, 1984; Subrahmanyam and Coultas, 1980). Man-made alterations to wetlands have provided yet another dimension to consideration of invertebrate community structure. Artificial alterations to salt-marsh habitat through construction of weirs and impoundments may be beneficial, detrimental, or relatively inconsequential for a particular species (Weaver and Holloway, 1974). Impounding wetlands, however, produces changes in vegetation (Daiber, 1974; Springer and Darsie, 1956) that may affect the well-established relationship between the natural distribution of salt-marsh plant communities and associated animal populations. Despite the implied consequences of impounding wetlands, little specific information exists on the effects of impoundments on invertebrates. Herke (1968) suggested that semi-impoundment of marshland may influence the distribution of certain estuarine species. Parker et al. (1971) conducted a survey of the macroinvertebrate fauna of a marsh adjacent to West Galveston Bay and speculated on changes that might result from impoundment of large areas of marsh for shrimp culture. Weaver and Holloway (1974) identified two communities of macrocrustaceans that occupied distinct habitats in a Louisiana tidal marsh influenced by weirs. These studies suggest that habitat management through impounding of wetlands alters the structure of the ecological community. Because tidal flooding expands the surface area of the marsh and its utility for natant macrofauna, predator-prey interactions, competition, disturbance, and physical stresses may be intensified in a closed system such as an impoundment that is subject to prolonged flooding.

This study focused on characterizing the community of decapod crustaceans from natural and impounded wetland habitats in South Carolina. The approach was to compare the community composition, diversity, and abundance of dominant species between the two habitats over a two-year period to determine whether impoundments prevent access to the habitat areas and nursery grounds that they replace.

METHODS

Field Sampling and Laboratory Analysis

Decapod crustaceans were collected from the perimeter ditch of impoundments in the Paddy Field complex and from Chainey Creek by seine, trawl, crab pot, and cast net. Decapods were taken along with fishes from seine collections in perimeter ditches of the impoundments and trawl collections in the creek to determine species composition, abundance, and community structure. Seine collections were made every other month from

March 1983 to December 1984 at three sites in the perimeter ditch of each of the study impoundments. Block nets with 0.8-mm mesh were used to isolate the sides of each site the day before sampling. Immediately prior to sampling, additional 0.8-mm mesh block nets were set across the perimeter ditch to partition the site into three equal areas (186 m^2). After closure of the sites and a delay of 11 to 15 hours three pulls were made with a 6-mm mesh bag seine. This was followed by a single haul of an 0.8-mm mesh bag seine. Otter trawl collections were made along a 1-km length of Chainey Creek. This portion of the creek was divided into 100-m lengths, of which three were randomly selected and sampled during late ebb or early flood tide by towing a 0.6-cm bar mesh flat trawl against the tidal current for a distance of 100 m. Detailed methodology for their collection is described in Chapter 14.

Attempts to collect decapod crustaceans from the vegetated flats of the impoundments by epibenthic sled were unsuccessful because of destruction of grassbeds and excessive clogging. Collecting with this gear, begun in June 1983, was discontinued after two months, and data are not included in this report.

Crab-pot and cast-net collections were made at 16 locations in the impoundments and adjacent creek system from April through November 1983 and March through November 1984. Five of the sixteen sampling sites were consistently sampled each month: inside and outside the water-control gates of impoundments 2 and 4 and at the mouth of a small feeder creek (designated SC) which branches off Chainey Creek diagonally across from impoundment 5 of the impoundment complex (Fig. 13.1). One of the remaining three impoundments (unit 1, 3, or 5) was randomly selected each month and sampled with crab pot and cast net inside and outside the water-control gate. In addition, three perimeter ditch locations were randomly selected from 14 equally divided lengths of the ditch and sampled in both impoundments 2 and 4. Similarly, the portion of Chainey Creek immediately adjacent to the impoundment complex was divided into ten segments of equal length, of which three were randomly selected each month for sampling.

Five casts with a 0.95-cm bar (1.9-cm stretch) mesh monofiliment cast net having a 1.5-m radius were made at each random site during daylight hours and pooled to form a sample. Casts that hung or those in which the net did not open were repeated. A vinyl-coated crab pot constructed of 1-in. (2.54-cm) wire mesh with two entrance holes was baited with herring, set at each location near dusk, and fished overnight for approximately 14 hr ($\bar{y} = 13.9$ hr, $s_{\bar{y}} = 10.1$, $n = 209$). Bait was measured so that equal amounts were placed in each trap. Temperature was recorded at the surface near the dike of each sampled impoundment, from Chainey Creek, and from the small feeder creek near impoundment 5. A salinity sample was taken at these sites and returned to the laboratory for analysis with an induction salinometer (Beckman RS 7B).

Decapod crustaceans collected by seine and trawl were preserved in 10% seawater formalin and returned to the laboratory, where they were sorted and identified to species. Data were collected on crabs and shrimp collected by crab pot and cast net immediately after capture.

To determine growth rates and movement of blue crab in the study area, 915 male and female crabs collected monthly by crab pot and cast net were tagged with numbered external spaghetti tags (Floy Mfg., Inc., Seattle, WA) having a t-shaped anchor. Tagging was begun in September 1983 and continued through October 1984. A tag was inserted through the membrane into the musculature at the dorso-posterior articulation of the fifth pereopod with the carapace. An attempt was made to tag all crabs collected inside the impoundments, whereas a representative number was tagged for other sites. Malfunctioning of the tagging gear in June 1984 prevented tagging of all crabs from impoundment sites that month. Individuals taken from inside the impoundments were returned to the impoundment from which they were collected, and all tagged crabs were returned to their initial capture location.

Observations recorded for shrimp species included the total weight and number of individuals in a collection. In addition, the total length (measured from tip of rostrum to tip of telson) and sex were noted for each specimen of all penaeoid species. It was often necessary to estimate numbers of individuals of the caridean shrimps, *Palaemonetes* spp. If the total weight of *Palaemonetes* spp. in a sample was less than 60 g, the number of individuals of each species was counted; however, when mass exceeded 60 g, then 10% by weight was removed, counted, and an estimated total number computed. Fifty randomly selected specimens from the 10% subsample were identified to species, enumerated, and weighed. The ratio of number and weight of species in the subsample to weight of the total sample was used to compute estimates of total number and weight for each species in the sample. Total length was noted for 50 subsampled specimens, as was presence of eggs on the pleopods. Crab species, except for C. sapidus, were enumerated but not weighed. Total weights were not recorded for blue crab prior to March 1984. Therefore, estimates of biomass were computed for monthly collections from March 1983 through January 1984 by using equations of weight regressed on total width as reported by Olmi and Bishop (1983). Measurements recorded for each blue crab specimen collected included carapace length (measured from the notch on the frontal margin to the posterior margin of the carapace), short carapace width (measured across the carapace from base of the posteriormost anterolateral spines), and total width (measured across the carapace from the tips of the posteriormost anterolateral spines). Sex, maturity as determined from abdominal shape, presence of eggs, and molt stage (Passano, 1960) were also noted. Carapace length, total width, sex, and presence of eggs were noted for other specimens of Brachyura.

Data Analysis

Community diversity was estimated for pooled seine and trawl collections of decapod crustaceans by the Shannon index (H') (Pielou, 1975) and the diversity components of species richness (SR) (Margalef, 1958) and evenness (J') (Pielou, 1975). Data from the three selected sites sampled by trawl in Chainey Creek were pooled by sampling trip. For seine collections, diversity indices were calculated from data pooled for the three sites sampled within each impoundment.

Numerical classification was used to determine patterns of similarity among pooled seine and trawl collections, as described above, and among decapod species. Species and collections were classified using a flexible sorting strategy (Lance and Williams, 1967) with a cluster intensity coefficient (β) of -0.25. The Jaccard similarity coefficient (Clifford and Stephenson, 1975) was used with presence/absence data collected by the two gear types. Subsequent to cluster analysis, species and site groups were chosen using a variable stopping rule. Nodal analysis was then used to express the degree of species/site group coincidence in terms of ecological constancy and fidelity (Boesch, 1977).

The chi-square test for goodness of fit was used to determine whether the ratio of male to female penaeid shrimps and blue crab significantly deviated from 1:1. Yates correction for continuity was used when sample size was <200 (Woolf, 1968).

The summation of the number of individuals and weight of species collected by three hauls with a 6-mm seine and one haul with a 1-mm seine was used to give an estimate of the number and weight of individuals at each of the three sites sampled within an impoundment. Catch per unit effort was then calculated as the mean total number of individuals and total weight for species per site for each impoundment. For trawl collections, catch per unit effort was expressed as the mean number and weight of individuals for the three trawl tows each month.

RESULTS AND DISCUSSION

Trawl and Seine Collections

Physical Variables, Community Structure, and Species Assemblages. Hydrographic conditions within the impoundments and Chainey Creek are discussed in Chapter 12. Additional information on hydrographic variables during bimonthly sampling with seine and trawl is presented in the assessment of the fish community (Chapter 14). The management scheme used to control water depth on the vegetated flats within the impoundments over the 2-year study period is presented in Chapter 4.

The composition and number of species was similar between the creek and impoundments, with 13 and 17 decapod crustaceans collected from these habitats, respectively (Table 13.10). The most-abundant species (*Palaemonetes pugio*, *P. vulgaris*, *Penaeus aztecus*, *P. setiferus*, *P. duorarum*, *Callinectes sapidus*, and *Palaemonetes* spp.), which collectively composed 99.5% of the total number of individuals collected by trawl and 99.9% of the total collected by seine, were essentially the same between the major habitats sampled. The only exception was the collection of large numbers of larval and juvenile *Palaemonetes* sp. in the impoundments but not the creek. The differences observed in order of abundance may reflect real differences in abundance of the numerical dominants between sites or differences with respect to efficiency and selectivity of the sampling gear.

Table 13.10 Total numbers and total weights of decapod crustaceans collected by trawl in Chainey Creek and by seine in impoundments.

	TRAWL COLLECTIONS				SEINE COLLECTIONS			
	Number		Weight		Number		Weight	
Species	Total	%	Total (kg)	%	Total	%	Total (kg)	%
Palaemonetes pugio	39,763	89.93	5.666	29.04	655,372	79.43	63.420	46.36
Palaemonetes sp.	--	--	--	--	164,531	19.24	0.185	0.14
Palaemonetes vulgaris	2,410	5.45	0.410	2.10	1,953	0.24	0.305	0.22
Penaeus aztecus	1,102	2.49	2.644	13.55	1,139	0.14	6.599	4.82
Callinectes sapidus	329	0.74	9.906	50.78	1,180	0.14	61.779	45.16
Penaeus setiferus	231	0.52	0.720	3.69	260	<0.1	3.334	2.44
Penaeus duorarum	162	0.37	0.131	0.67	310	<0.1	1.134	0.83
Acetes americanus	--	--	--	--	299	<0.1	--	--
Eurypanopeus depressus	101	0.23	0.009	<0.1	--	--	--	--
Rhithopanpopeus harrisii	35	<0.1	0.010	>0.1	1	--	0.001	<0.1
Uca minax	--	--	--	--	34	<0.1	0.026	<0.1
Trachypenaeus constrictus	25	<0.1	0.001	<0.1	3	<0.1	<0.001	<0.1
Panopeus herbstii	23	<0.1	0.008	<0.1	--	--	--	--
Neopanope sayi	20	<0.1	0.001	<0.1	1	<0.1	--	--
Callinectes similis	6	<0.1	--	--	1	<0.1	--	--
Sesarma reticulatum	--	--	--	--	6	<0.1	0.002	<0.1
Alpheus heteroclitus	5	<0.1	<0.001	<0.1	1	<0.1	0.001	<0.1
Sesarma cinereum	--	--	--	--	5	<0.1	<0.001	<0.1
Uca pugnax	--	--	--	--	5	<0.1	--	--
TOTAL	44,212		19.507		825,101		136.786	

Of the six most-abundant species, the grass shrimp, Palaemonetes pugio, dominated catches from both the impoundment and creek in terms of numbers (Table 13.10). Palaemonetes pugio also outranked other species in biomass within the impoundments. Only three other numerically abundant species, Callinectes sapidus, Penaeus aztecus, and P. setiferus, were important contributors to total biomass of decapod crustaceans in the study area.

Both the number of species and magnitude of the catch were highly seasonal and influenced measures of community structure, such as diversity and evenness. Over the two-year sampling period, increased species richness and total number of species in impoundments occurred in summer and early fall, whereas lowest values were noted in winter (Fig. 13.18). There was a magnitude of difference annually, however, in number of species from the same season, because considerably fewer species were collected in summer 1983 than summer 1984 (Fig. 13.18). The average number of species collected was greatest in impoundments during August 1984 (Fig. 13.19). A similar pattern of increased species richness in summer and fall also occurred in Chainey Creek; however, the annual pattern was different, with more species collected in 1983 (Figs. 13.19 and 13.20).

Temporal changes in abundance of dominant species had the greatest effect on species diversity (H') and evenness (J') in the study area. Mean abundance of decapod species increased from late summer (August) through fall to a peak during January 1984 in impoundments 3 and 4 and in Chainey Creek (Fig. 13.19). Impoundment 3 also showed a second peak in August 1984. The annual peaks in abundance primarily coincided with increased catches of P. pugio (Fig. 13.21), whose overwhelming dominance in catches coincided with periods of low species diversity and evenness. In impoundments, H' decreased in 1983 from a high in June to low values in August that continued until August 1984 (Fig. 13.18). Overwhelming numerical dominance by P. pugio was responsible for low evenness and diversity indices during that period (Fig. 13.21). Variation in H' and J' observed after June 1984 reflected variable catches of P. pugio and larval Palaemonetes sp. between impoundments. Diversity indices calculated for data from Chainey Creek also reflected dominance by P. pugio; but low J' and H' associated with large catches of this species were limited to

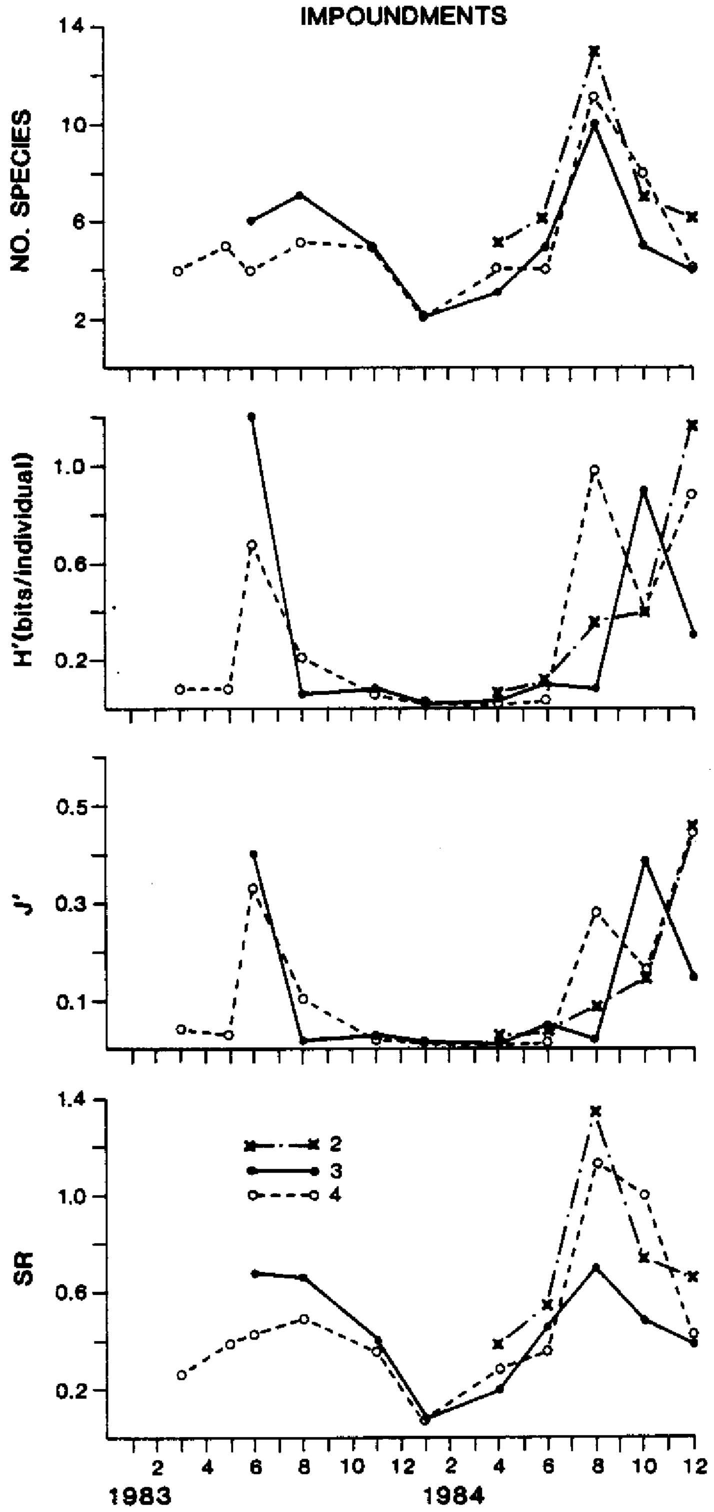


Figure 13.18 Temporal variation in number of species, diversity (H'), evenness (J') and species richness (SR) observed in impoundments sampled by seine.

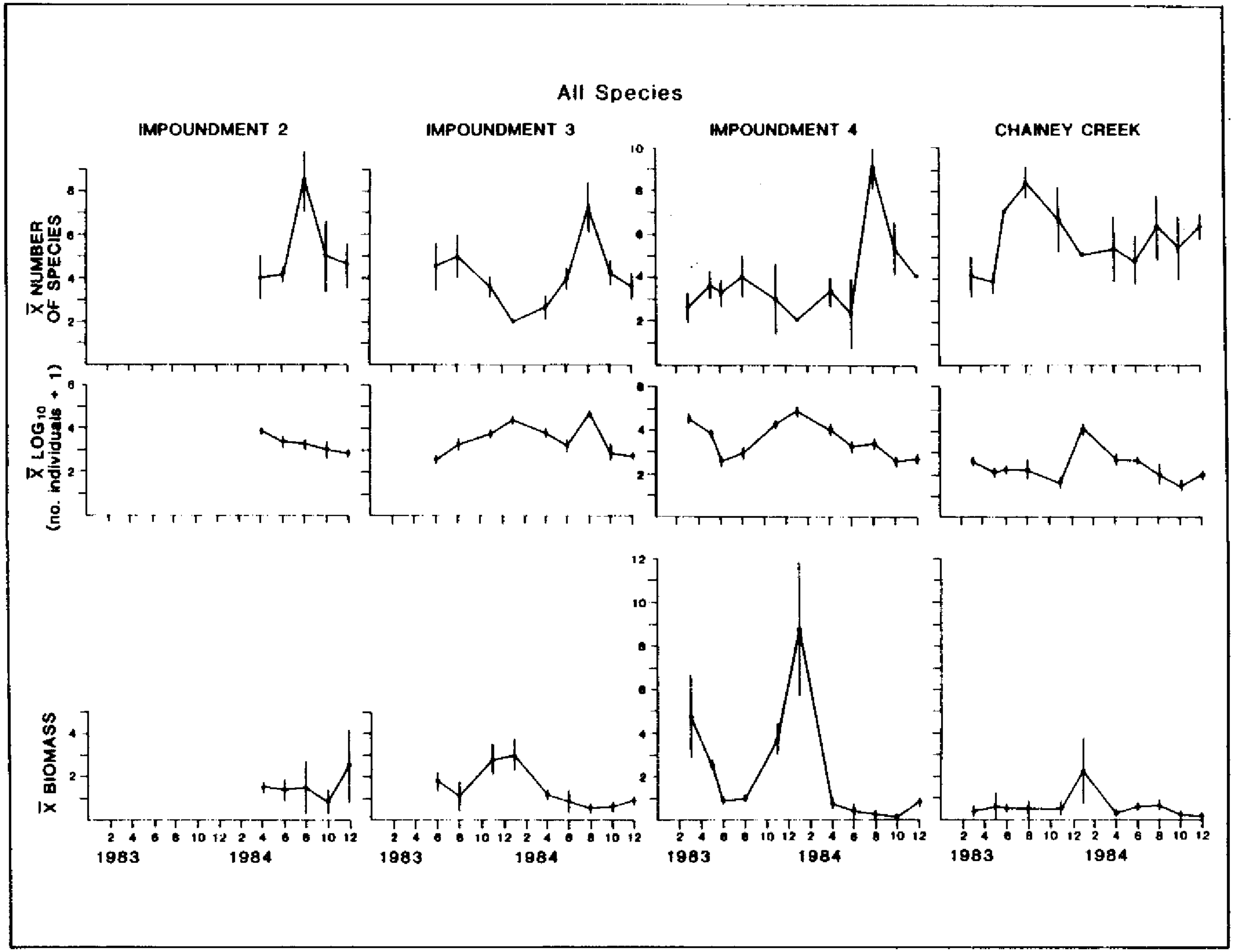


Figure 13.19 Mean bimonthly values of number of decapod crustacean species, transformed number of individuals, and biomass (kg) at sites sampled by seine and trawl. Vertical lines represent the standard deviation. Calculations are based on three collections by seine and trawl bimonthly.

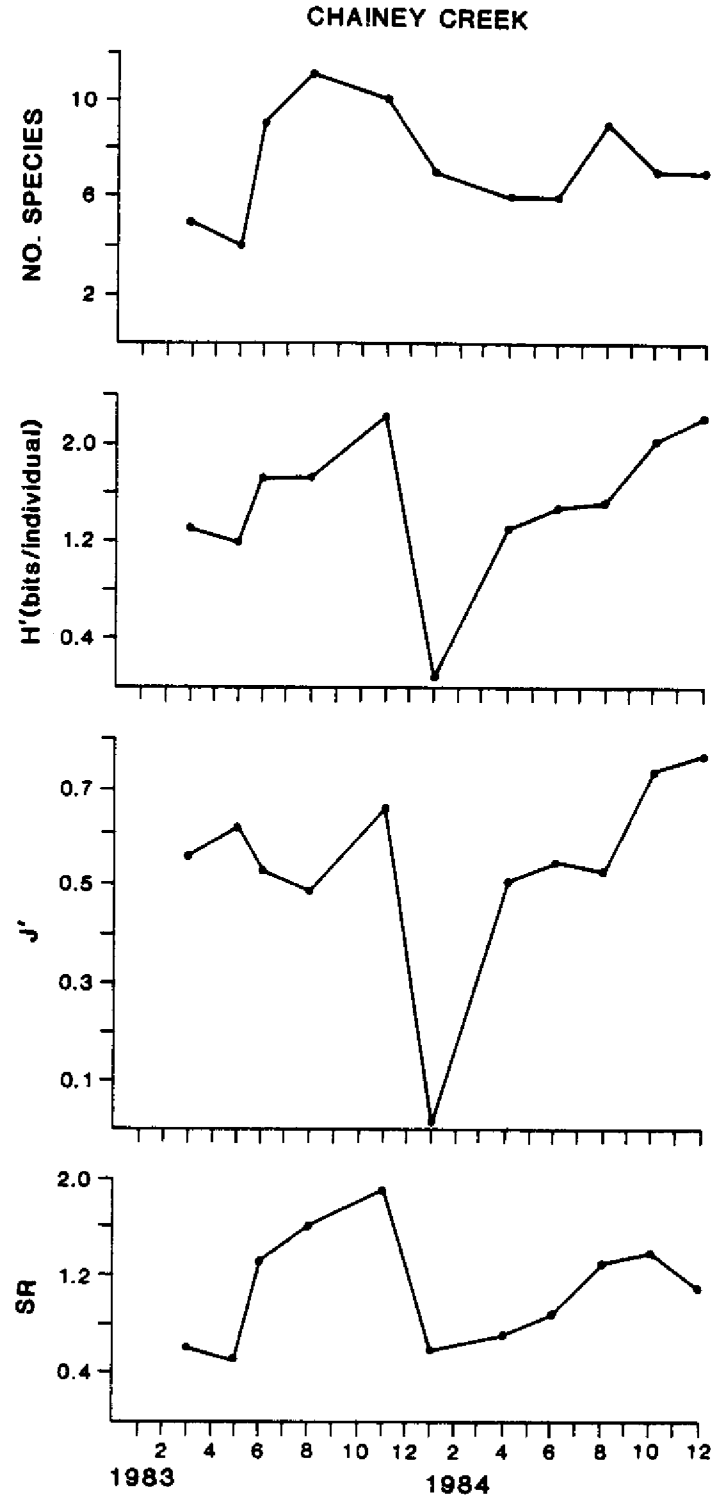


Figure 13.20 Temporal variation in number of decapod species, diversity (H'), eveness (J'), and species richness (SR) observed for trawl collections from Chainey Creek.

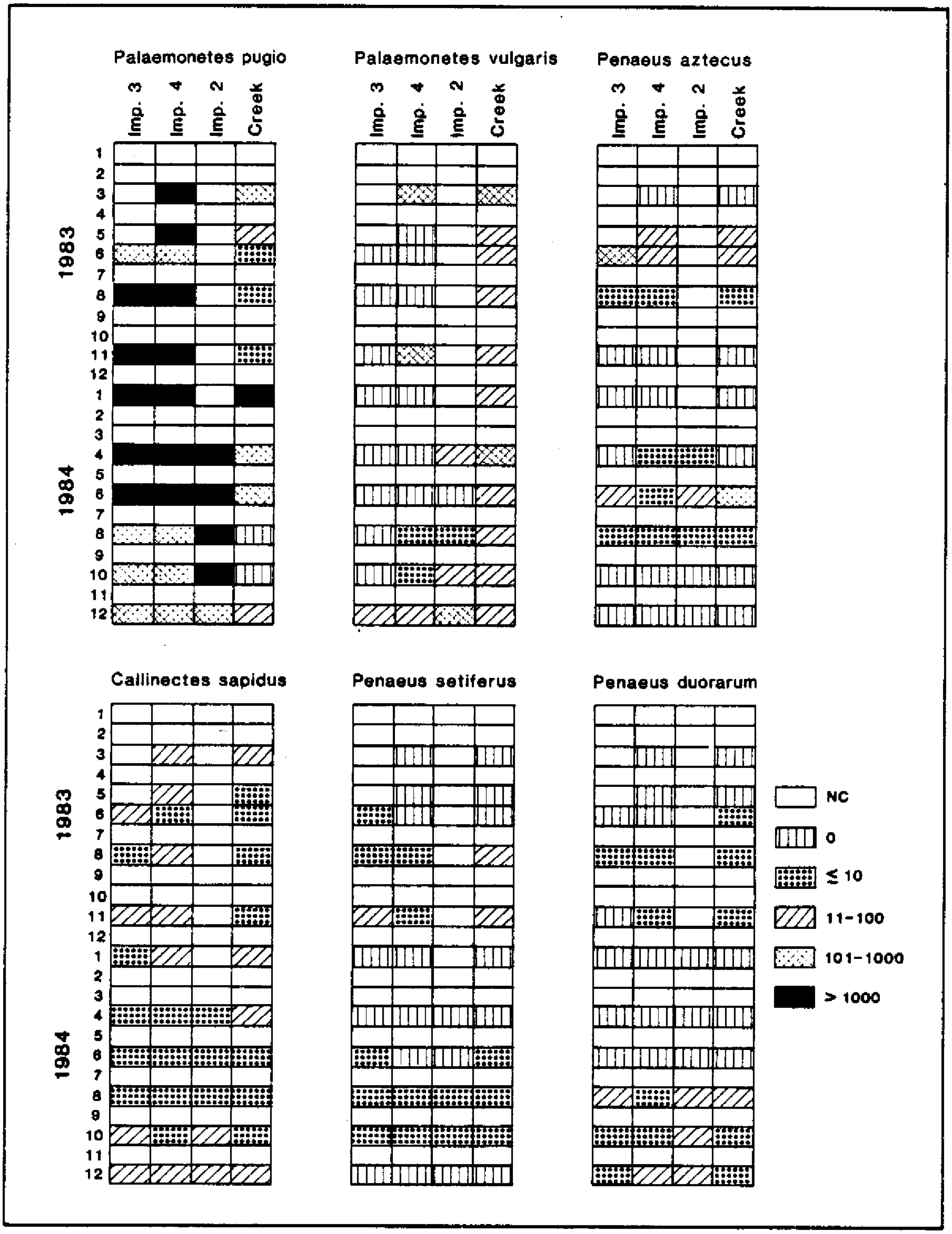


Figure 13.21 Abundance, expressed as mean number of individuals per site, of six numerically important decapod species collected from impoundments and Chainey Creek. Legend indicates five arbitrary levels of abundance from absent (0) to maximum abundance (1000). N.C. indicates no collection.

January 1984 (Fig. 13.20), when P. pugio constituted 99% of the total catch.

The temporal patterns in community structure observed during the two-year study were influenced by hydrographic conditions within the impoundments and by life history of individual species. Increased species richness during summer and fall was probably related to high salinities in the impoundments and Chainey Creek, which allowed penetration by stenohaline marine species; e.g., the lesser blue crab, Callinectes similis; the penaeid shrimp, Trachypenaeus constrictus; and the sergestid shrimp, Acetes americanus. These species, generally found in high-salinity coastal waters or inlets, penetrate upriver estuarine areas as salinity conditions allow (Williams, 1984). Furthermore, the penaeid shrimps, Penaeus aztecus and P. setiferus, which are seasonal inhabitants of marsh systems (Weinstein, 1979) were mainly collected in summer and fall, with peak recruitment of postlarvae in May and July, respectively (see Chapter 13A).

A summer peak in species richness has previously been reported for fishes and decapod crustaceans in marshes and estuarine systems of the southeastern Atlantic and Gulf coasts of the United States. The major explanation for temporal patterns of species richness is physical factors that mediate movement of species. In a study of seasonal fluctuations of macroinvertebrates in two North Florida salt marshes, Subrahmanyan and Coultas (1980) noted that the number of species increases in warmer months, which the authors attributed to differential dispersal of resident and transient species. Similarly, Rozas and Hackney (1984) collected the greatest number of fishes and macrofaunal crustaceans during summer in oligohaline marshes of North Carolina. They found that species richness is best predicted by temperature and dissolved oxygen and that salinity is not as important a factor in controlling species entry into low-salinity marshes. Salinity, however, never rose above 17.9 ppt at their sampling sites and was less than 5 ppt during the summer. Day et al. (1973) felt that movement of migratory species into the marsh system during spring is in response to the pulse of detritus and increased food availability at that time. In the Santee River system, maximum richness of fishes and decapod crustaceans consistently occurs during summer (Wenner et al., 1982). Livingston (1976) noted a tendency for increased numbers of invertebrate species, including decapod crustaceans, largely in relation to increased temperature and salinity during summer and fall in Apalachicola Bay.

The average biomass of decapods collected in impoundments and Chainey Creek followed an annual pattern similar to that observed for number of individuals (Fig. 13.19). Increased biomass in Chainey Creek and impoundments 3 and 4 during January 1984 was attributed to large catches of *P. pugio*. Although a peak in mean number of individuals was also observed in impoundment 3 during August 1984, average biomass of the catch was not great, because approximately 99% of the individuals collected were larval *Palaemonetes* sp. Peak biomass observed in impoundment 2 during December 1984 was attributed to *Callinectes sapidus*, which constituted 90% of the total catch by weight for that month in the impoundment.

Seasonal changes in total abundance and biomass of invertebrates have commonly been observed in other marsh and estuarine habitats (Nixon and Oviatt, 1973; Day et al., 1973; Livingston, 1976; Rozas and Hackney, 1984; Subrahmanyam and Coultas, 1980); however, the temporal pattern of abundance and biomass differed among the various studies. Reduced abundance of invertebrates in winter has been reported by Livingston (1976), who noted a relationship between abundance of estuarine organisms and seasonal changes in temperature and salinity. Similarly, Rozas and Hackney (1984) found three seasonal peaks (spring, summer, and fall) in numbers of macrofaunal crustaceans and fishes from oligohaline marshes. They noted, however, that the physical and chemical properties of the water do not explain the variability in abundance of organisms, which apparently is influenced more by life cycles of the numerically dominant species. Subrahmanyan and Coultas (1980), on the other hand, found that invertebrate density is influenced by temperature and recruitment patterns. They noted that higher temperature has a negative effect on abundance, whereas recruitment increases the number of individuals. It appears that a similar situation existed in the present study. Decreased summer and early fall abundance and biomass coincided with high temperatures, high salinity, and low dissolved oxygen conditions in the impoundments and Chainey Creek. These conditions probably stressed spring recruits such as *Penaeus* spp. and *C. sapidus*, which are sensitive to low dissolved oxygen (Carpenter and Cargo, 1957). *Palaemonetes* spp. which are relatively tolerant of low dissolved oxygen (Welsh, 1975) were probably not stressed by environmental conditions of the study sites. Instead, large numbers of individuals were recruited to the study areas during late fall and winter, thereby markedly increasing abundance. Furthermore, increased abundance of predatory fishes during late spring and early summer (see Chapter 14) may have reduced the population of grass shrimp in the system at that time. Alon and Stancyk (1982) hypothesized that the grass shrimp population in nearby Minim Creek may be heavily cropped during summer months.

Normal cluster analysis indicated that the impoundment sites were faunistically least similar to those in Chainey Creek (Fig. 13.22). Furthermore, the impoundment sites constituting groups 1 to 4 were not very similar to each other. Groups 1 and 2, which primarily consisted of collections made in impoundments during April to June and January, were more similar to each other than to groups 3 and 4, which consisted of August and October to December collections. Month of collection and, hence, seasonality appeared to be a major basis for differentiation between these groups, largely because of trends in species richness noted previously. Groups 1 and 2 contained collections taken when species richness was low. Collections in groups 3 and 4, on the other hand, were characterized by a comparatively high number of species (Figs. 13.19 and 13.22).

Four characteristic species assemblages were identified by inverse cluster analysis (Table 13.11). Members of group A were the most abundant and ubiquitous species collected by seine and trawl. Species group B consisted of species that occurred predominantly in collections from Chainey Creek. Two species in this group, the xanthid crabs, *Panopeus herbstii* and *Eurypanopeus depressus*, were collected only in Chainey Creek during the study period. The fiddler crabs, *Uca pugnax* and *Uca* sp., in group C were infrequently collected, while species in Group D were collected only in impoundments. These included the fiddler crab, *Uca minax*, the wharf crabs, *Sesarma cinereum*, *Sesarma* sp., *S. reticulatum*, and the shrimps, *Acetes americanus* and *Palaemonetes* sp.

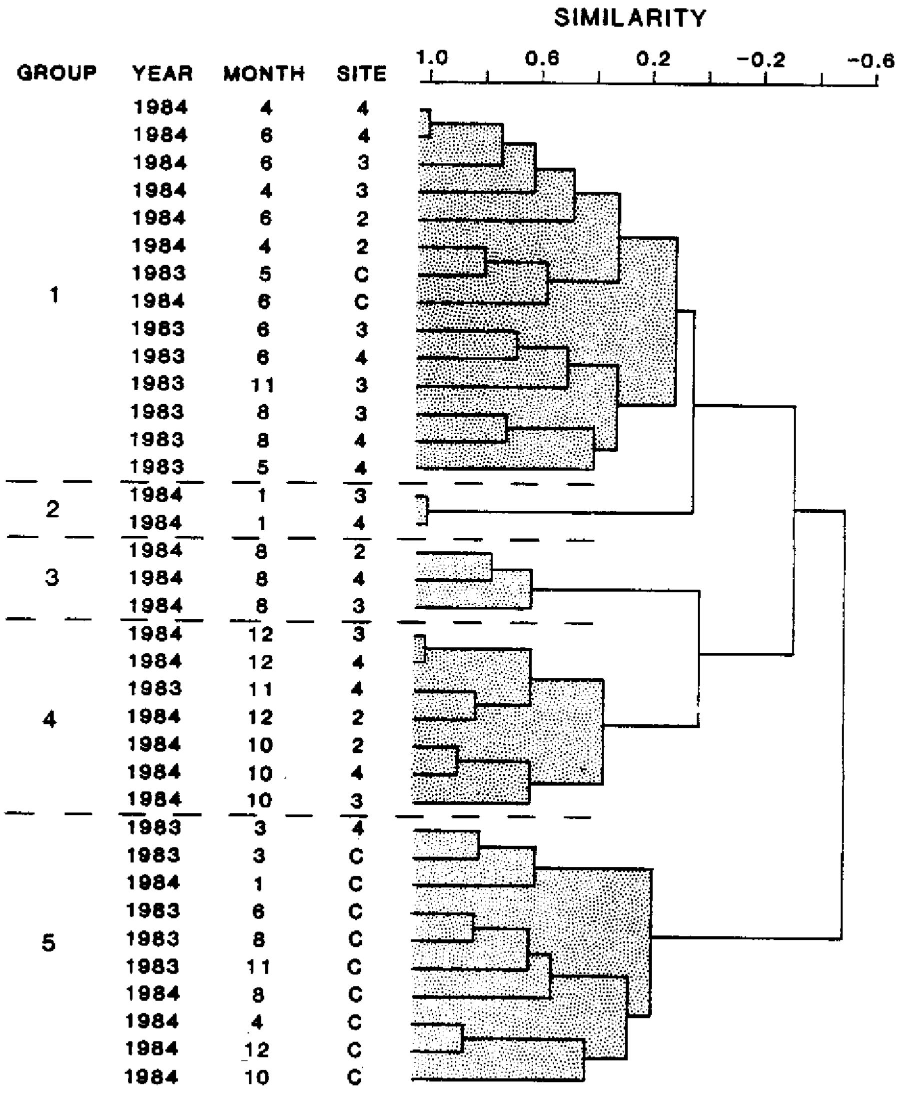


Figure 13.22 Normal cluster dendrogram of site groups formed using the Jaccard similarity coefficient and flexible sorting. Data from the three randomly selected sites sampled by trawl in Chainey Creek (C) were pooled by sampling trip, as were three sites sampled by seine within each impoundment (units 2 to 4).

Table 13.11

Species groups resulting from numerical classification of data from samples collected by seine and trawl during 1983 and 1984.

Group A

- *Palaemonetes pugio*
- *Callincetes sapidus*
- *Palaemonetes vulgaris*
- *Penaeus duorarum*
- *Penaeus setiferus*

Group B

- *Callinectes similis*
- *Trachypenaeus constrictus*
- *Eurypanopeus depressus*
- *Panopeus herbstii*
- *Neopanope sayi*
- *Alpheus heterochaelis*

Group C

- *Uca pugnax*
- *Uca* sp.

Group D

- *Penaeus aztecus*
- *Uca minax*
- *Acetes americanus*
- *Palaemonetes* sp.
- *Sesarma cinereum*
- *Sesarma* sp.
- *Sesarma reticulatum*
- *Rhithropanopeus harrisii*

The distinctiveness in species assemblages between Chainey Creek and the impoundments may reflect biased catches by the two different nets used to sample these sites, or it may be due to real differences in the habitats themselves. Stenohaline species such as *C. similis* and *T. constrictus* which were members of the creek assemblage (group B) were collected only during summer and fall, when salinity was highest. Although similar salinity conditions were found in the impoundments, low dissolved oxygen conditions at those sites may have limited their occurrence in impoundments. Other decapod crustaceans in this assemblage are commonly associated with sand bottom or structured habitats, such as oyster shells (Williams, 1984). The presence of live *Crassostrea virginica*, as well as broken shell, in grab collections from Chainey Creek (Chapter 12) suggests that bottom type was more suitable for frequent occurrence of these species in the creek than in impoundments. These results, however, are not intended to imply the exclusivity of assemblages to a particular habitat. For example, species such as *Uca pugnax*, *U.*

minax, and Sesarma cinereum, which constitute assemblages whose distribution was primarily associated with impoundments, are common inhabitants of open-marsh habitats as well (Williams, 1984). Therefore, the formation of assemblages based on distributional patterns from actual collections of the organism is an artificial attempt at forcing species into designated groups. It is probable that species will co-occur with others outside their group and that their occurrence at sites is primarily influenced by seasonal physiochemical conditions.

Temporal and Spatial Distribution of Dominant Species.

1. Palaemonetes spp. Caridean shrimps of the genus Palaemonetes were the most-abundant decapod crustaceans collected during the two-year sampling period. Of the Palaemonetes identified to species, P. pugio was by far the most abundant, constituting 99.7% and 94.3% of the total taken from impoundments and creek sites, respectively.

The annual abundance pattern of P. pugio largely reflected seasonal recruitment (Fig. 13.23). Large numbers of ovigerous females occurred from April through August (Fig. 13.24), suggesting maximum recruitment from summer through fall. Abundance of P. pugio in impoundment 4 was high in March 1983, declined to a low point in June, and increased again by August, when late summer recruitment began. By November 1983 catch per site was over an order of magnitude greater than during the August sampling, and by January 1984 the catch had more than tripled (Fig. 13.23). Sampling in impoundment 3 began in June 1983 and followed the same trends seen in impoundment 4 but with generally lower catches (Fig. 13.23). Beginning in April 1984, impoundments 2, 3, and 4 were sampled during each sampling period. Abundance of P. pugio declined from January to April in impoundments 3 and 4 and at all three sites from April to June, following a pattern similar to that observed in 1983. Abundances through December remained lower than expected for summer recruitment.

Temporal abundance patterns of P. pugio in Chainey Creek closely followed those in the impoundments (Fig. 13.23). Numbers declined from the end of the recruitment period in early spring to a low point prior to the beginning of summer recruitment. Catches then continued to increase throughout the fall to a peak in winter. The exception to this pattern occurred in August and October 1984, when no P. pugio were collected.

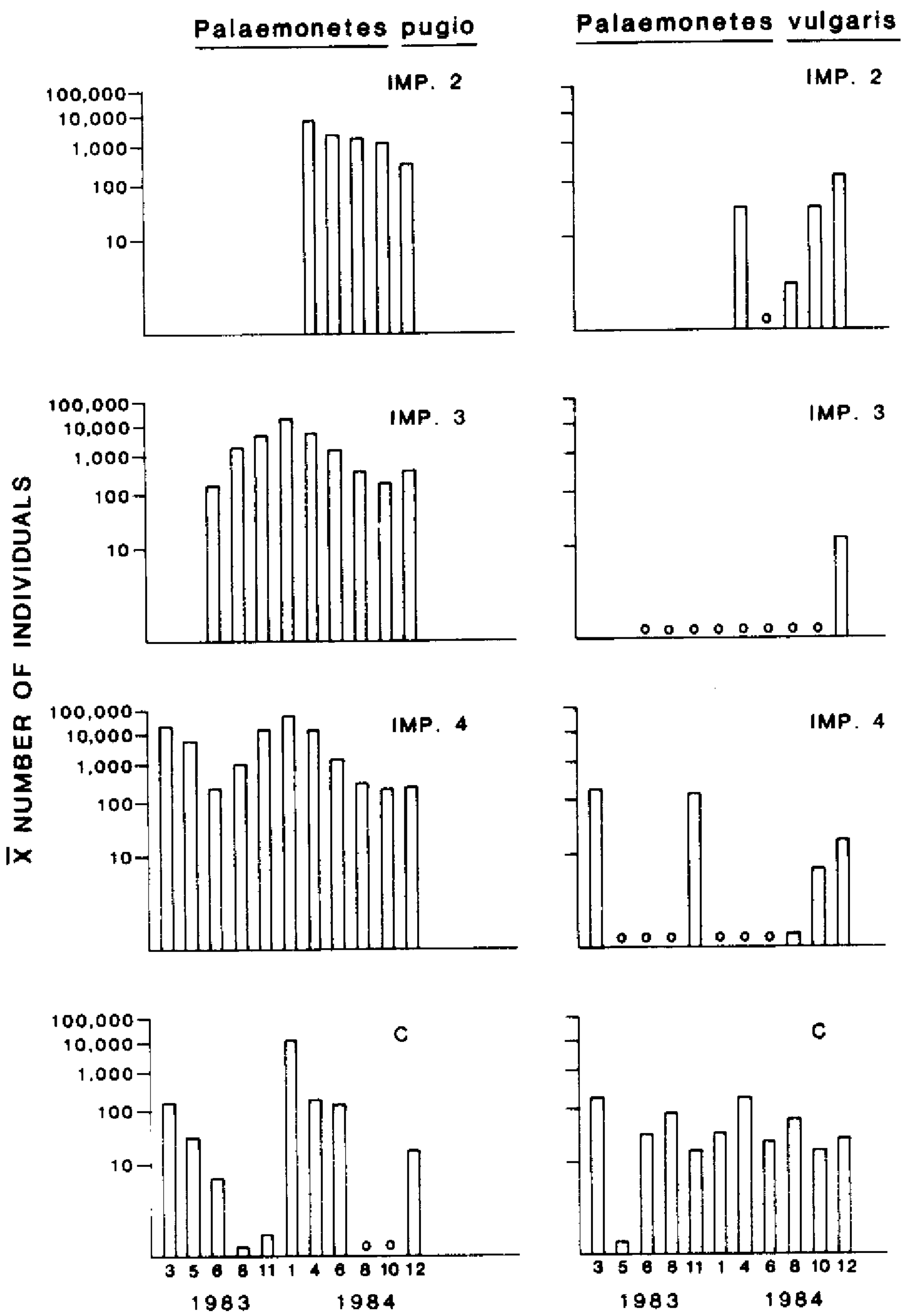


Figure 13.23 Mean abundance of P. pugio and P. vulgaris at sites sampled by seine and trawl. Means were computed from 3 samples in the creek and for 3 sites in each sampled impoundment.

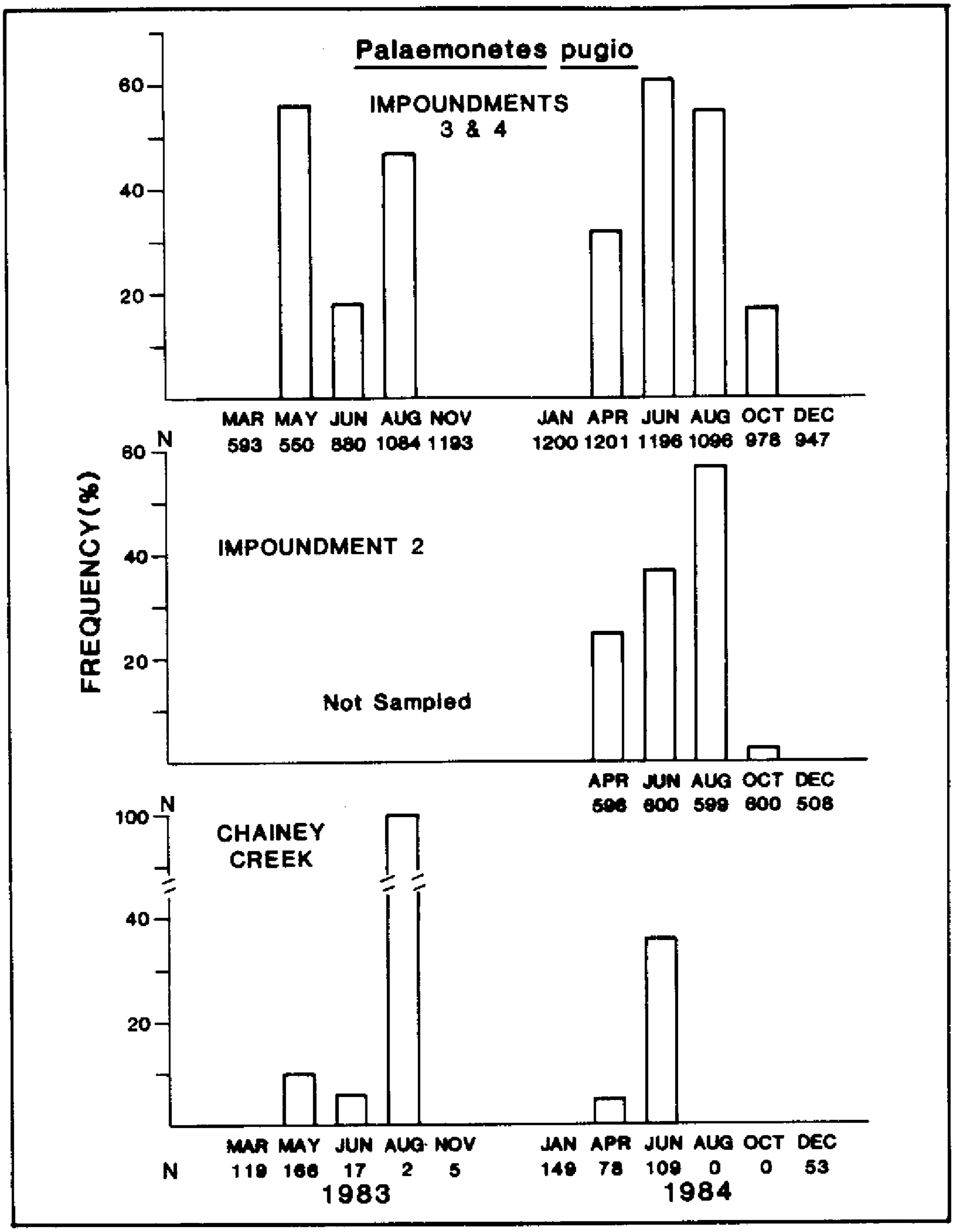


Figure 13.24 Incidence of gravid P. pugio in subsampled population from impoundments and Chainey Creek. N indicates total number of individuals in subsample.

Maximum catches of *P. vulgaris* in the impoundments generally occurred at similar times as observed for *P. pugio* (Fig. 13.23), with catches highest for both species in March and November 1983. The exception occurred during summer 1983, when no *P. vulgaris* were collected. Absence of *P. vulgaris* during the recruitment period in 1983 suggests either heavy mortality or migration from the area. During 1984 abundance of *P. vulgaris* was low in the impoundments but reflected the recruitment periods reported for the species in the Carolinas (Williams, 1984). In Chainey Creek, catches of *P. vulgaris* were high in spring of 1983 and 1984 following winter recruitment. Catches decreased during early summer and then increased when recruitment began in late summer. Decreased abundance in the fall of both years deviated from the expected abundance pattern; however, recovery did occur by winter (Fig. 13.23). The number of ovigerous females collected was high from May through August 1983, but in 1984 most were collected in October (Fig. 13.25).

The much greater abundance of *P. pugio* in the impoundments and *P. vulgaris* in Chainey Creek is explained by the physiological tolerance of the species and their habitat specificity. Although basically sympatric, *P. pugio* has a broader salinity tolerance and occurs more commonly in low-energy, highly organic habitats, such as was found in the impoundments. Zimmerman and Minello (1984) confirmed the broad tolerance of this species for variable water-quality conditions by finding no strong relationship between densities of *P. pugio* and temperature, salinity, or water level in a Texas salt marsh. *P. vulgaris*, on the other hand, is most common in areas having more current and fewer organic substrates (Boeston, 1971; Conte and Parker, 1971). Welsh (1975) reports that *P. pugio* is better adapted for survival in low oxygen conditions than *P. vulgaris* and that the ability of *P. pugio* to compensate at combinations of low oxygen and high temperature is more important in distribution of the species than salinity preferences. Nixon and Oviatt (1973) noted that large populations of *P. pugio* occur in New England salt marshes because of their tolerance for very low oxygen concentrations that effectively minimizes competition and predation by other species.

Length-frequency distributions verified that recruitment was an important factor in determining annual abundance patterns in the study area. For impoundments sampled during 1983, a mature overwintering

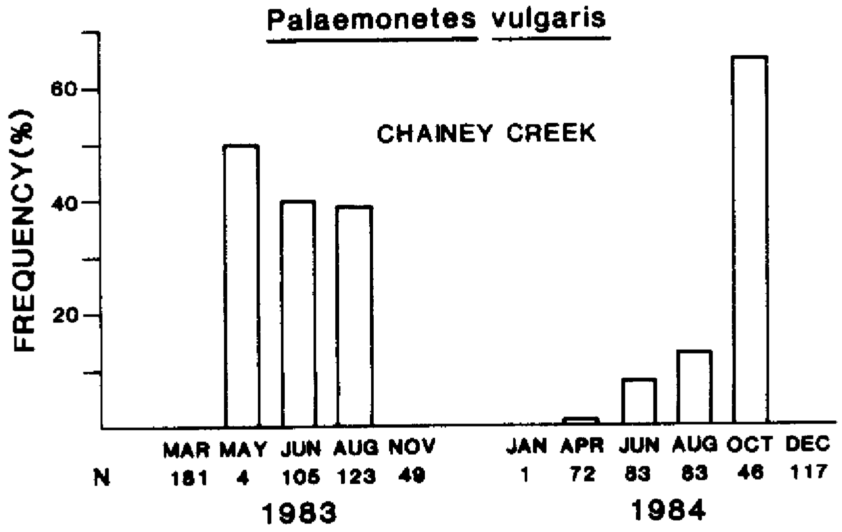


Figure 13.25 Incidence of gravid *P. vulgaris* in the subsampled population from Chainey Creek. N indicates total number of individuals in subsample.

population of P. pugio and a winter recruitment class were evident in March (Fig. 13.26). By May, the mean length of P. pugio had increased, indicating that most of the winter recruits had attained a size similar to that of the overwintering population. The distribution observed in May and June was probably due to differences in size and abundance between the sexes. Female P. pugio and P. vulgaris attain a larger size than males (Knowlton and Williams, 1970; Alon and Stancyk, 1982; Welsh, 1975; Wood, 1967) and are generally more abundant, although males may outnumber females in early summer (Welsh, 1975; Alon and Stancyk, 1982). The bimodal distribution observed in August probably reflects size differences between the sexes, as well as new recruits which formed a distinct mode in November. Mean size of the sampled population decreased until January 1984, when three distinct modes were present representing early summer, late summer, and winter recruits in impoundments 3 and 4 (Fig. 13.27). By April, three modes were visible in the impoundments, with the middle mode probably being a combination of males from the previous late summer recruitment period and winter-recruited females. The frequency distribution in June 1984 was similar to that for 1983, with a skewed distribution of larger females. Beginning in August 1984, larger females were not as numerous. Welsh (1975) suggested that decreased abundance of females in summer may result from selective predation of gravid females by fishes. Although gravid females are a component of the diet of fishes that consume Palaemonetes, there is no apparent selective predation of this group (R. Martore, College of Charleston, pers. comm.). Recruitment also began in August and was most noticeable in October, when mean size decreased. By December a bimodal distribution occurred with reduction of larger-sized individuals. Recruitment was still apparent in December.

Size-frequency distributions of individuals collected in Chainey Creek were similar to those described for shrimp in the impoundments. Samples from both years showed that individuals increased in size after winter recruitment through June, after which few individuals were collected in Chainey Creek.

Palaemonetes vulgaris was collected too infrequently in the impoundments to establish any reliable trends in size distribution over time. December 1984 was the only month during which enough specimens were examined to establish a valid size frequency. The population at that time

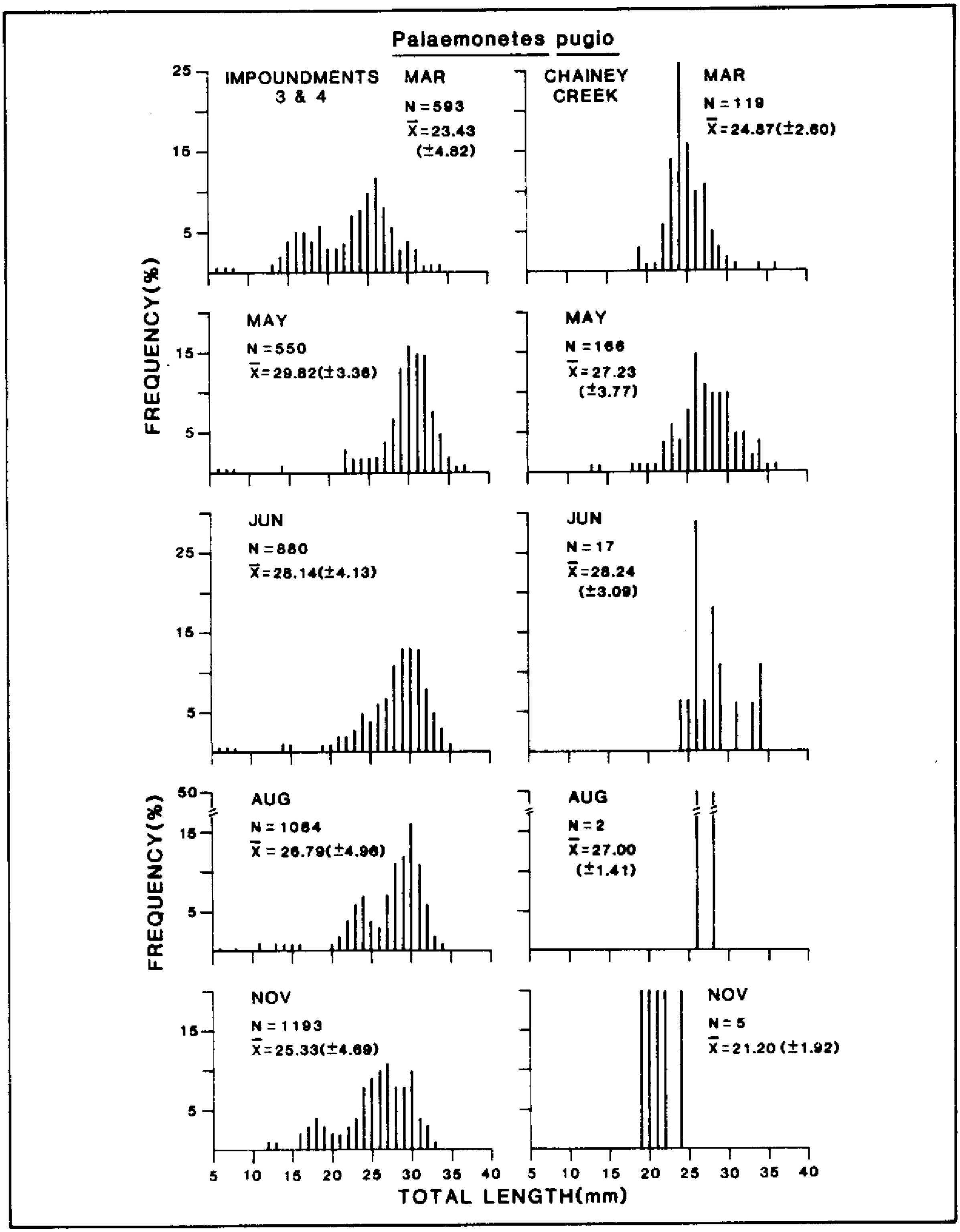


Figure 13.26 Length frequency (as % of subsample size N), mean (x) total length and standard deviation of the population of P. pugio from impoundments 3 and 4 and Chainey Creek, 1983.

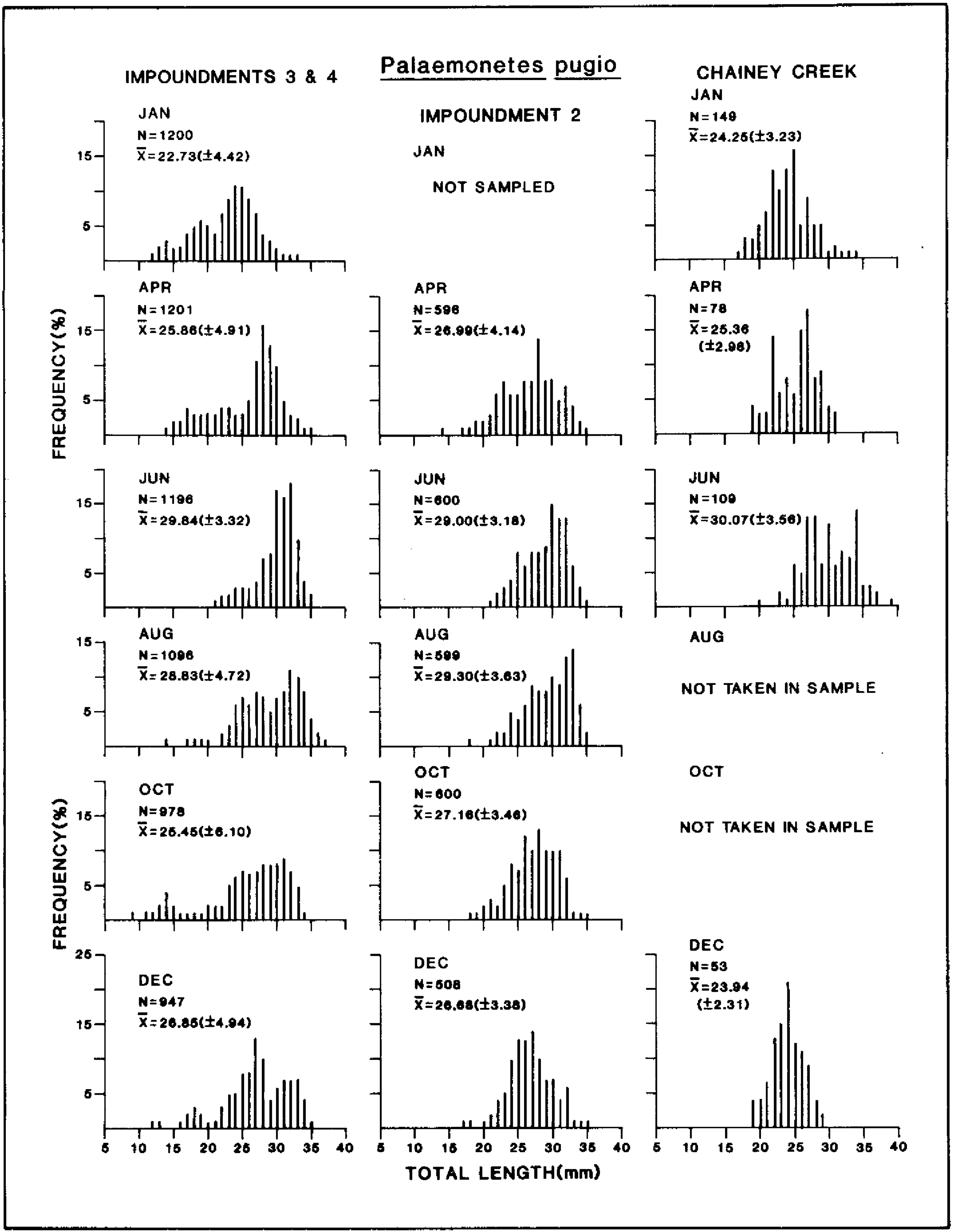


Figure 13.27 Length frequency (as % of subsample size N), mean (x) total length and standard deviation of the population of P. pugio from impoundments 3 and 4, impoundment 2, and Chainey Creek, 1984.

displayed size bimodality similar to that found for P. pugio, in which size separation by sex and recruitment were obvious. In Chainey Creek the population of P. vulgaris had a wide size distribution in March 1983 ($\bar{x}$ = 25.3 ± 4.01 SD, N = 181). By June, however, there was a bimodal distribution (23 mm and 27 mm) indicating size differences between males and females as well as recruitment. In August recruitment was more noticeable, with an increase in smaller-sized individuals ($\bar{x}$ = 23.38 ± 3.18, N = 123). By November 1983 recruitment had ceased, and the population consisted of previous recruits from spring and summer. Similar patterns were observed in 1984, with recruitment beginning in April and peaking in June. Recruitment had slowed by August and remained so through December 1984. A bimodal distribution occurred in October and December, probably indicative of sexual size differences.

Our data are consistent with published studies on the life history of P. pugio and P. vulgaris in the Carolinas. Both species overwinter and spawn in the spring (Fig. 13.28), with females becoming gravid in late March or early April (Knowlton and Williams, 1970; Welsh, 1975; Alon and Stancyk, 1982; Williams, 1984). Spawning takes place from late March to late September or early October (Knowlton and Williams, 1970; Alon and Stancyk, 1982), with larvae appearing in May (Knowlton and Williams, 1970; Williams, 1984). Larval and postlarval Palaemonetes spp. measuring 2 to 6 mm were collected only from the impoundments by the 1-mm seine, with greatest abundance occurring in August 1984 when 156,650 and 5211 individuals were taken in impoundments 3 and 4, respectively. A much smaller number (2608 individuals) was taken from impoundment 3 in October. Although larvae were present in the creek (E. Olmi, MRRI, pers. comm.), none was collected in trawl samples because of the comparatively large mesh size. Nevertheless, these results differ from those of Alon and Stancyk (1982), who collected no immediate postlarvae (6 to 7 mm TL) in nearby Minim Creek and suggested, in agreement with Sikora (1977), that immediate postlarvae do not join the population directly after metamorphosis. We surmise that postlarval abundance is high in impoundments because of limited emigration. In addition, Alon and Stancyk (1982) may have failed to collect immediate postlarvae because they sampled along the banks of Minim Creek and did not sample within the salt

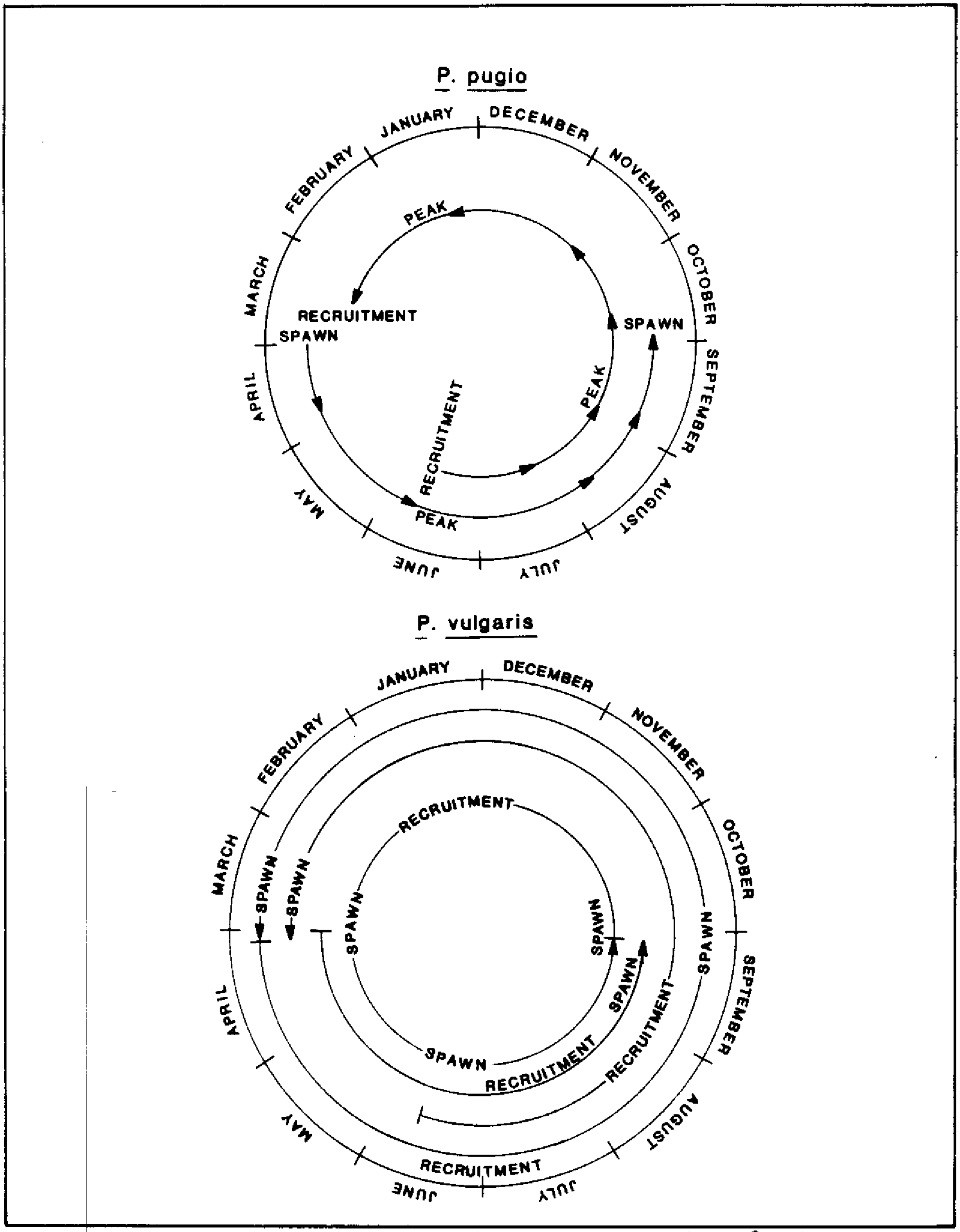


Figure 13.28 Generalized spawning and recruitment cycles of Palaemonetes pugio and P. vulgaris in the Carolinas (taken from Knowlton and Williams, 1970; Alon and Stancyk, 1982; Williams, 1984).

marsh which is the preferred habitat of P. pugio (Zimmerman and Minello, 1984).

Recruitment into the adult population takes place as metamorphosed juveniles about 25 to 47 days after hatching (Little, 1968). Summer-spawned females may reach maturity and spawn 3.5 to 4.8 months after hatching. A portion of the earliest-spawned generation in spring may also spawn by late summer or fall (Alon and Stancyk, 1982; Knowlton and Williams, 1970). Eggs can be redeposited one to two days after hatching of the last brood (Knowlton and Williams, 1970), so a winter-recruited female spawning in early spring may spawn several times during the summer.

Both P. pugio and P. vulgaris generally have a life span of 1 year (Knowlton and Williams, 1970; Welsh, 1975; Alon and Stancyk, 1982). Spring-spawned individuals may die after the summer spawning season while those individuals spawned in summer may die after spawning the following spring. A small portion of the population spawned in summer may live through a second winter (Welsh 1975). Predation, however, is thought to have a major effect on populations. Length-frequency data indicate that reduced numbers of larger individuals, especially gravid females, occur in late summer and fall. Alon and Stancyk (1982) collected few large grass shrimp during summer and noted that the population in habitats with abundant predatory fish may be continuously cropped before individuals reach maximum size of 50 mm. The importance of Palaemonetes spp. as food items for fishes such as Elops saurus, Fundulus heteroclitus, Paralichthys lethostigma, and Bairdiella chrysura (Chapter 14) suggests that predation on these species is substantial in the impoundments.

2. Penaeus spp. All three species of commercially important shrimps, P. aztecus, P. setiferus, and P. duorarum, were seasonal inhabitants at the study sites (Fig. 13.21). P. aztecus was first collected from the impoundments in April but reached maximum abundance in June at most sites. Brown shrimp were also abundant in May 1983 in Chainey Creek and impoundment 3. Postlarval brown shrimp have been reported from South Carolina estuaries as early as January, with maximum numbers in February and March (Bearden, 1961). In the study area, however, recruitment of subadult brown shrimp was first observed in plankton samples in early May 1983, with postlarval density highest during that month. Although

postlarvae may have immigrated to estuaries in late winter, ingress to the study area was delayed and coincided with increased salinity at the study site.

Lindner and Anderson (1956) reported that spawning of *P. setiferus* occurs from May through September in South Carolina waters, with immigration occurring from late spring through September (Bearden, 1961). Postlarvae of white shrimp were first collected from plankton samples in June in the study area, followed by a sharp peak in abundance in July. Pink shrimp, which were captured only occasionally during previous surveys of South Carolina estuaries (Bishop and Shealy, 1977) and were not as abundant as *P. aztecus* during the present study, were the most-numerous postlarvae collected. Postlarval *P. duorarum* were first collected in the study area in May, increased in abundance in August, and peaked in October. Few juveniles, however, were collected during the recruitment study, suggesting that they had either emigrated to deeper, saltier areas of the estuary or were not vulnerable to the sampling gear because of burrowing behavior (Williams, 1984).

Length-frequency distributions (not shown) indicated that similar-sized individuals initially occurred in impoundments and Chainey Creek and that shrimp grew rapidly within the study area. In May 1983 sizes of brown shrimp collected by seine and trawl were similar, with a modal peak at 4 cm. By June 1983 the mean size of brown shrimp had doubled (creek $\bar{x} = 8.3$; impoundment $\bar{x} = 9.6$). During 1984 a modal group of smaller individuals (4 cm) was evident only in the samples from Chainey Creek in June, where the mean size of brown shrimp was less ($\sim$6 cm) than in the impoundments (8 to 9 cm). Although sample sizes were low, larger shrimp (>10 cm) were present at all sites in August.

P. setiferus and *P. duorarum* differed little in size between impoundment and creek sites in August, showing similar trends as *P. aztecus*. In November 1983, however, mean size of white shrimp was greater in the impoundments ($\bar{x} = 12.7$ cm) than in the creek ($\bar{x} = 8.9$ cm). Too few white shrimp were caught in 1984 to meaningfully assess the length-frequency distribution in the study area. Larger individual pink shrimp were also present in impoundments in October ($\sim$6 cm) and December (7 to 10 cm) 1984.

The larger size of penaeid shrimp found in the impoundments may reflect the restricted access of individuals at those sites to emigration. Brown and white shrimp both undergo rapid growth during summer. Emigration of larger individuals during late summer and early fall account for smaller increases in the mean length of individuals in South Carolina estuarine systems sampled by Bishop and Shealy (1977). Pink shrimp also emigrate from nursery grounds as they increase in size and return to sea on reaching maturity (Williams, 1984). Our data suggest that larger individuals in the impoundments were prevented from emigrating while those in the creek had moved to deeper more saline waters, leaving behind mostly juveniles.

Few significant differences were found in the ratio of male to female shrimp for either species of Penaeus. Furthermore, no trends were apparent for sex ratios either by site or month. Previous investigations by Bishop and Shealy (1977) of South Carolina estuaries found more females than males were caught for each species, but no consistent trends were noted on a monthly basis. The dominance of female white shrimp has been noted by Pullen and Trent (1969) for Galveston Bay, Texas and by Harris (1974) for creeks and sounds in Georgia. Perez-Farfante (1969), however, observed considerable variation of sex ratios for this species. Brown shrimp in inshore waters have been reported by Joyce (1965) to have a M:F ratio of 0.81:1.00.

3. Callinectes sapidus. Blue crab were caught at all sites during every sampling period; however, abundance and biomass were greatest at impoundment and creek sites sampled in March 1983 and January and December 1984 (Fig. 13.29). Fewest crabs were caught during the summer months, when catches were reported by Wenner et al. (1982) to be lowest in the North Santee River.

The abundance of blue crab was apparently related to recruitment of juveniles into the study area in winter. Most individuals collected from Chainey Creek in March 1983 and January, April, and December 1984 were less than 30 mm. Size frequency of blue crab in impoundments 3 and 4 showed a higher percentage of very small crabs (<50 mm) occurred from March through May 1983 and April and August 1984. Similar-sized crabs were dominant in impoundment 2 in April 1984 and constituted a modal group (3 cm) in November 1984. Few commercial-sized (>127 mm) crabs were caught

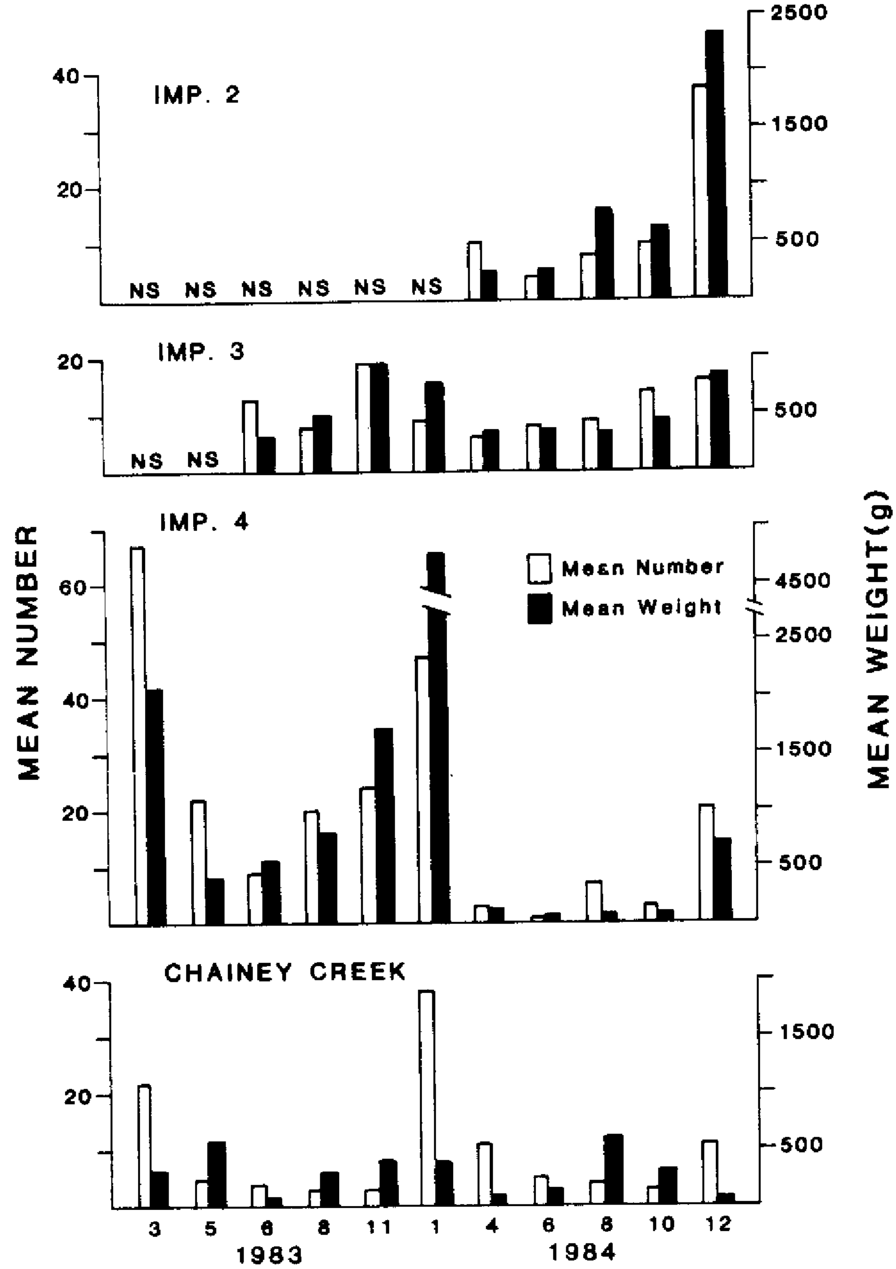


Figure 13.29 Mean number and mean weight of *Callinectes sapidus* from impoundments and Chainey Creek.

at any site; however, there was a tendency for mean size of individuals to be greatest in late summer and fall.

These data are similar to those reported elsewhere on seasonal abundance of juvenile blue crab (Weinstein, 1979; Dudley and Judy, 1973). In impoundments 3 and 4 during January 1984, few juveniles <60 mm were collected, while a high percentage of those from Chainey Creek during the same sampling period were <30 mm. This suggests that cold temperatures during January 1984 could have caused mortality of juveniles or effected their burying into mud, thereby avoiding capture.

Sex ratios of _C. sapidus_ collected by trawl and seine indicated greater abundance of male crabs during most sampling periods (Fig. 13.30); however, significant deviations from an expected 1:1 ratio were infrequent in Chainey Creek and occurred intermittently in impoundments 3 and 4 from April through October 1984. Sex ratios of adult _C. sapidus_ differ spatially and temporally in estuarine systems with respect to peak occurrence of mating and spawning migration of females to high salinity water (Milliken and Williams, 1984). Tagatz (1968) found males dominate the lower-salinity areas located farther upriver than 48 km from the mouth of the St. Johns River, Florida. Similarly, Eldridge and Waltz (1977) found that crab-pot catches in lower-salinity waters of southern South Carolina estuaries contain 72% males. In creeks of South Carolina trawled by Lunz (1951), male blue crab are overwhelmingly dominant. Palmer (1974), however, found sex ratios of blue crab to be more even in creeks than in sounds and outside waters of Georgia. He attributed differences in sex ratios between his study and Lunz's to selectivity of the trawl. Lunz (1951) collected mainly large crabs, while Palmer (1974) collected individuals encompassing a wide size range. Our results suggest that for much of the year equivalent numbers of males and females exist in the study area. Significant deviations from unity may occur during summer and fall as a result of migrational movement of females to deeper, more-saline waters.

Examination of maturity stages for female blue crab revealed that few mature crabs were collected in the study area (Table 13.12). Fewest mature female crabs were collected in the creek, where sample sizes were too low to evaluate any temporal trends. Within sampled impoundments, however, the greatest percentage of mature female crabs occurred in late

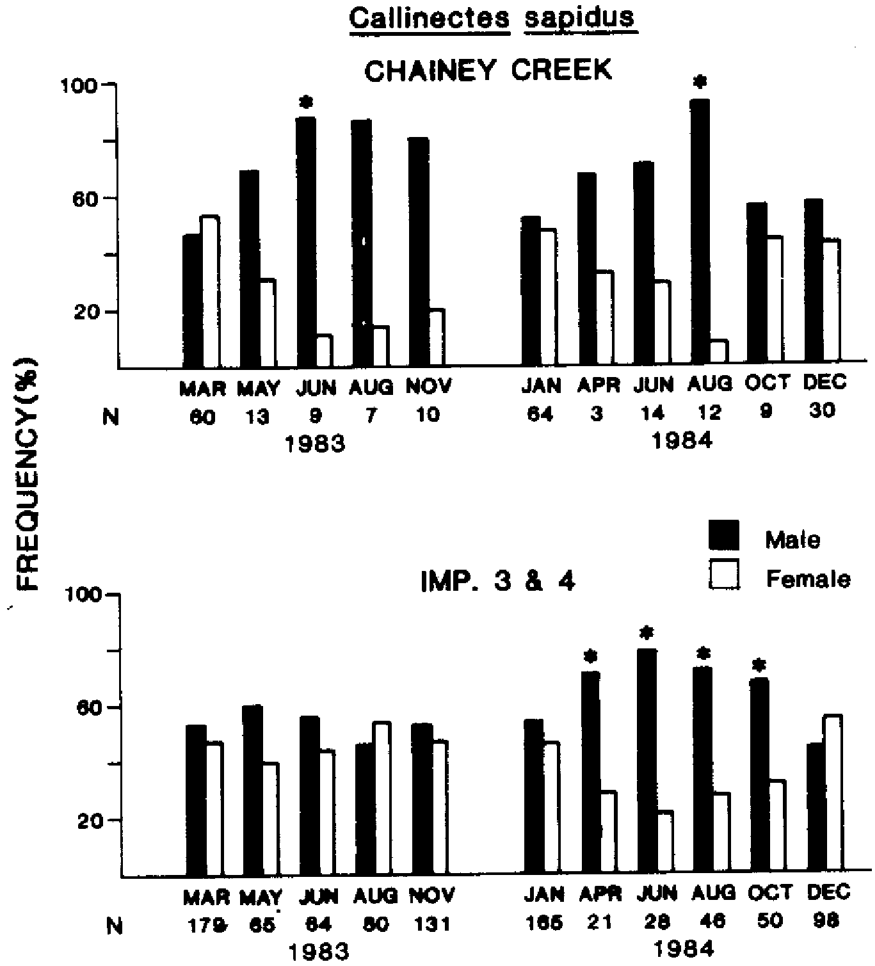


Figure 13.30 Temporal changes in ratio (expressed as % of subsample N) of male and female *C. sapidus* at sites sampled by seine and trawl. Statistical significance of ratios, as determined by Chi-square analysis, is indicated by * (P .05).

Table 13.12 Percentage of immature and mature *Callinectes sapidus* collected at study sites by seine and trawl.

	IMPOUNDMENT 2			IMPOUNDMENTS 3 AND 4			CHAINEY CREEK		
	N	Immature	Mature	N	Immature	Mature	N	Immature	Mature
1983									
March				84	100	0	32	100	0
May				26	100	0	4	75	25
June				28	93	7	1	100	0
August				43	100	0	1	100	0
November				62	76	24	2	50	50
1984									
January				76	55	45	13	97	3
April	13	100	0	6	100	0	1	100	0
June	2	100	0	6	100	0	4	75	25
August	9	100	0	13	100	0	1	100	0
October	13	92	8	16	100	0	4	75	25
December	44	86	14	54	85	15	13	100	0

fall and winter. In months when few mature females were collected in Chainey Creek, percentages were highest within impoundments. Our results suggest that mature female blue crab are retained within the impoundments and are thereby prevented from migrating to high-salinity water to spawn. From what is known concerning distribution and movement of female crabs in South Carolina waters, it appears that juvenile females that cohabit lower-salinity areas with males undergo their terminal molt mainly in August and September and then migrate to higher-salinity waters (Eldridge and Waltz, 1977). Ovigerous females, which are found predominantly in nearshore oceanic waters from May through August, were not collected by seine or trawl during this study.

Crab-Pot and Cast-Net Collections

Physical Variables. Many physical characteristics of the study area are discussed in Chapters 3, 5, and 10. Temperature and salinity measured concurrently with crab-pot and cast-net collections differed little between impoundment and creek study sites (Fig. 13.31 and Appendix 13.10). Water temperature varied predictably with season, being highest in July and August 1983 and June 1984 and lowest during November, which was the last sampling period each year. Salinity was lowest during spring, increasing abruptly from a low in April 1983 to 24 ppt in May. For the remainder of 1983 sampling, mean salinity did not go below 20 ppt in the impoundments or 21 ppt in the creek. A similar pattern occurred in 1984; however salinity remained <2 ppt through May and then abruptly increased in June to 24 ppt.

Species Composition and Catch per Effort. 1. *Crab Pots.* A total of 2921 blue crab, *Callinectes sapidus*, weighing 474.554 kg were collected by crab pots during the study. The number of crabs collected per trap fluctuated temporally among study sites (Fig. 13.32). Catches in the impoundments generally increased from spring to a high in summer. In 1984, however, the highest catch occurred in November. A similar trend of increased catches during summer was also noted at creek sites. In 1983 the number of crabs per pot was highest in May, decreased markedly in June, and then increased from July through September. Catches in 1984 were essentially trimodal, with early-spring, summer, and late-fall peaks. The Wilcoxon 2-sample test indicated no significant difference in

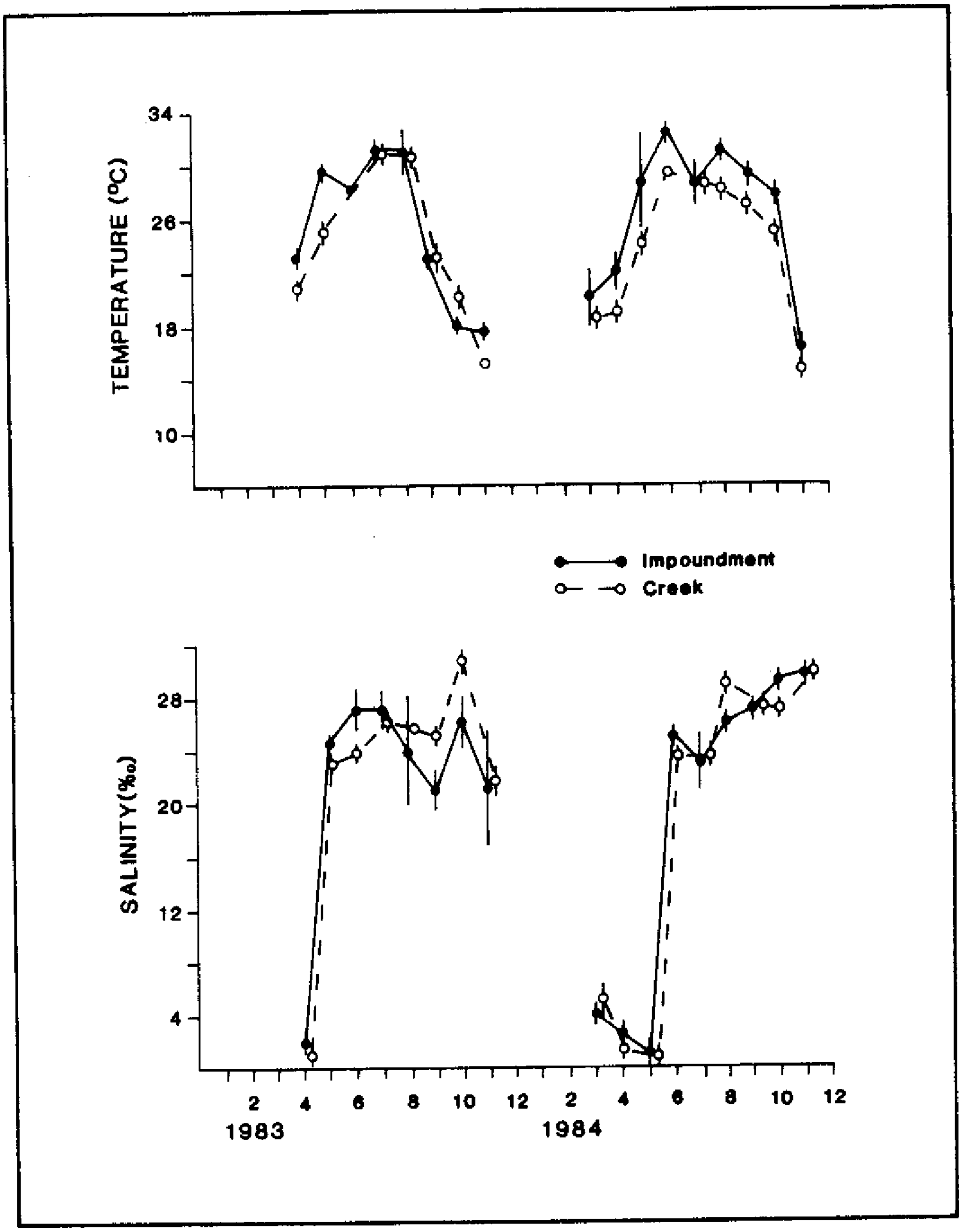


Figure 13.31 Variations in mean temperature and salinity at three impoundment and two creek sites sampled by crab pot and cast net. Vertical bars indicate standard deviation.

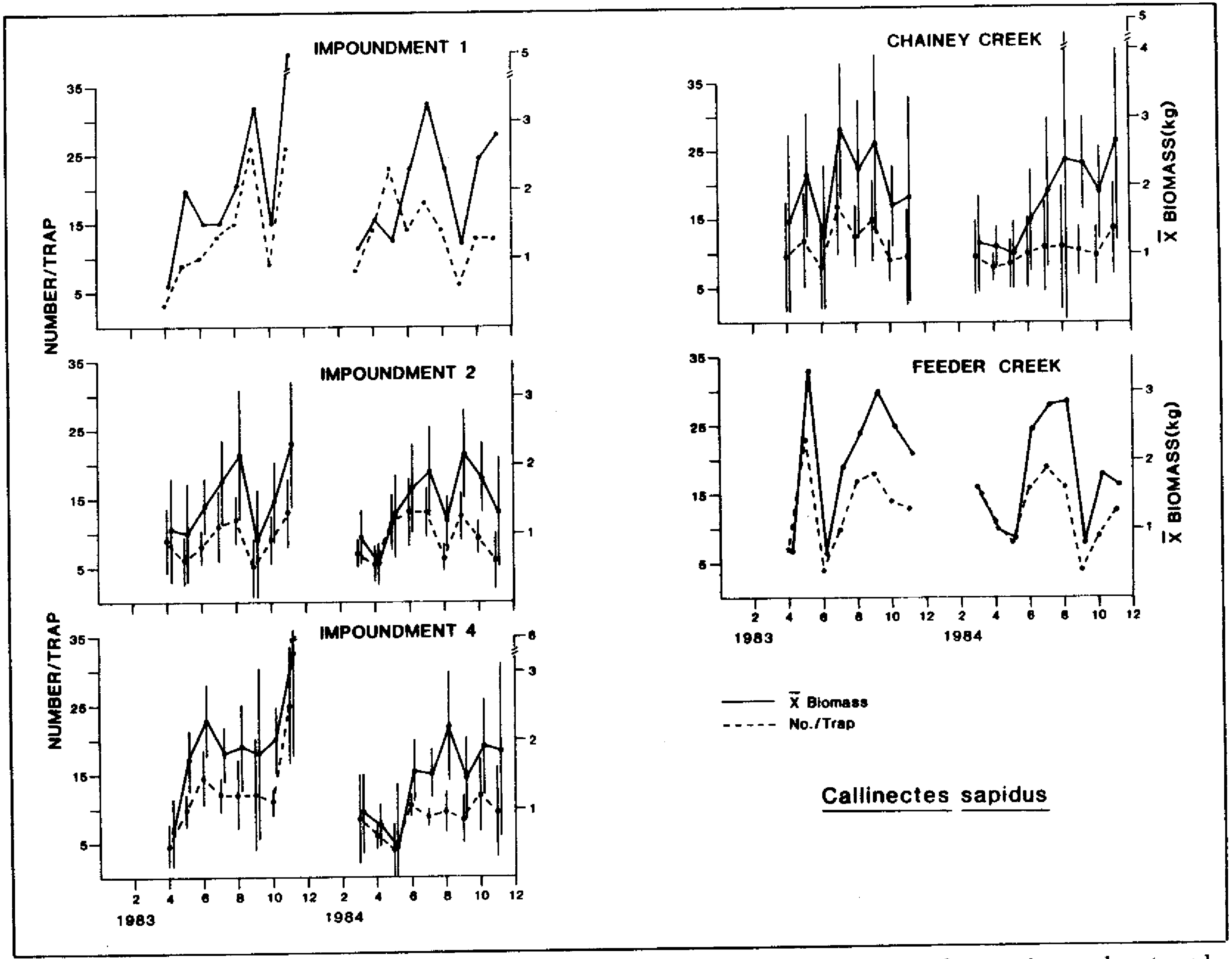


Figure 13.32 Temporal variation in number and biomass per trap of C. sapidus at impoundment and creek sites.

mean number of crabs collected over the study period between impoundment sites and creek sites for either 1983 ($P > 0.6$) or 1984 ($P > 0.5$).

The increased abundance of crab catches in the commercial pot fishery of South Carolina during summer and fall has been documented by Eldridge and Waltz (1977). They noted that crab catches are lower during the months of December through March, because cold weather initiates migrational movement and behavioral responses that lessen availability of crabs to the fishery. Catches generally increase from May to October, with peak catches occurring from July to October. Tagatz (1965) noted similar trends in catch and effort for the St. Johns River, Florida, where catches rise from a low in January to March to a peak in August.

Width-frequency distributions of blue crab collected by pots indicated that monthly mean sizes were generally >120 mm at sampling sites (Figs. 13.33 to 13.35). In Chainey Creek modal groups ranged from 130 to 150 mm, indicating that most of the crabs were above the minimum legal size of 5 in. (127 mm). No marked change in size composition occurred on a monthly basis, with the exception that modal groups of crabs measuring 100 mm were collected in June 1983 and May 1984 (Fig. 13.34). Crabs from sampled impoundments showed a similar general trend of smaller-sized individuals in spring and modal groups at larger sizes in summer (Figs. 13.34 and 13.35). Mean sizes of crabs from impoundments 2 and 4 were smallest in March and April. Crabs generally were larger for the period May to November, with the greatest percentage of individuals being >120 mm. The largest crabs from impoundment sites were collected in October and November, however, when modal groups of 150 to 160 mm occurred.

Male C. sapidus made up the majority of the catch from pots at study sites, constituting 76% of the blue crabs collected from impoundments and 93% of the catch from creek sites. In Chainey Creek significantly more male than female crabs were collected monthly throughout the two-year study period. Males also consistently outnumbered females in samples from the small feeder creek. In the impoundments male crabs generally dominated, although significant deviations from a 1:1 sex ratio were not observed every month. The dominance of males in the commercial pot fishery of South Carolina has been documented by Eldridge and Waltz (1977). Tagatz (1965) also noted that males dominated in the upper St. Johns River in Florida.

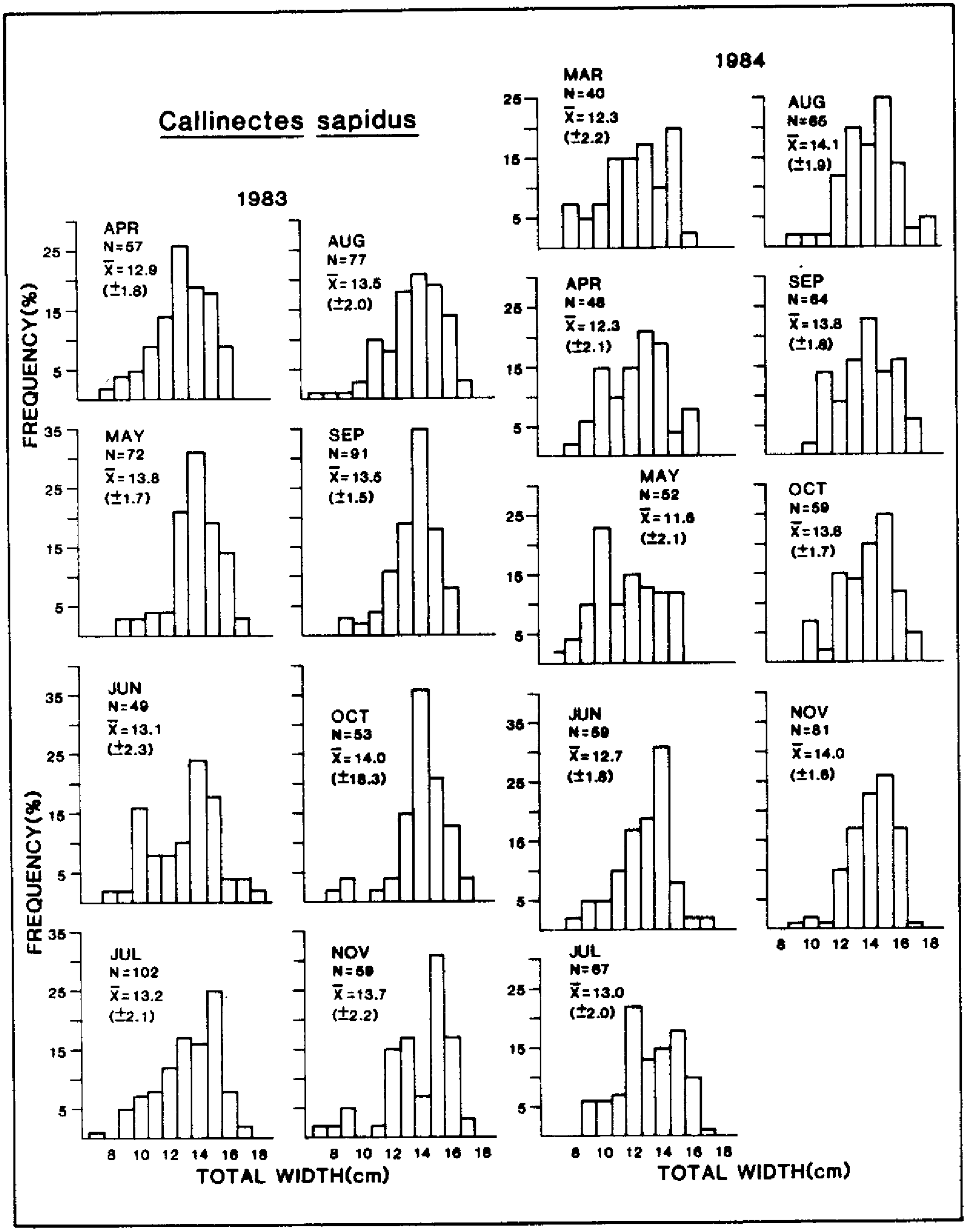


Figure 13.33 Total width frequency (as % of sample size N), mean (x) total width and standard deviation of the population of *C. sapidus* taken with crab pots from Chainey Creek in 1983 and 1984.

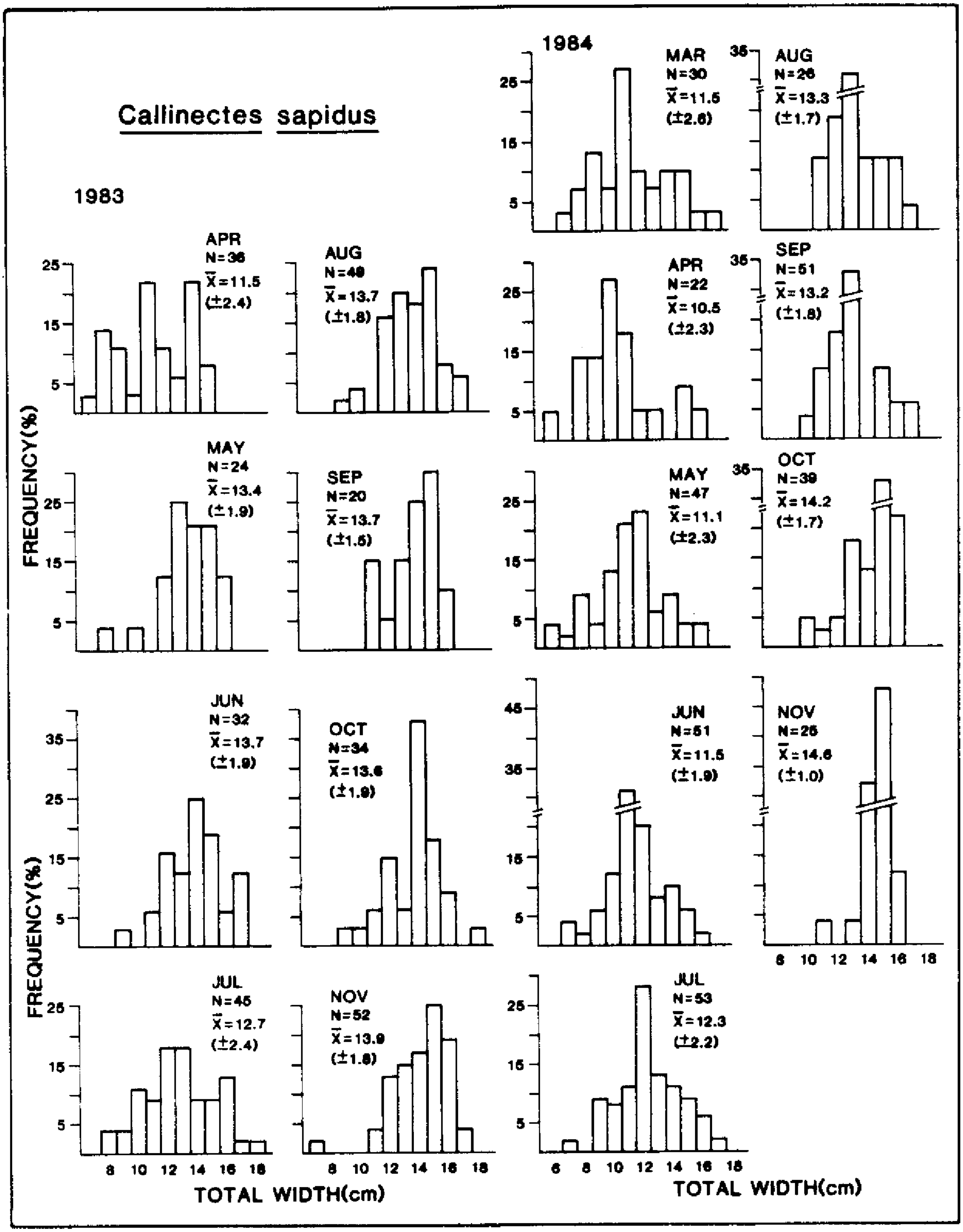


Figure 13.34 Total width frequency (as % of sample size N), mean (x) total width and standard deviation of the population of C. sapidus taken with crab pots from impoundment 2 in 1983 and 1984.

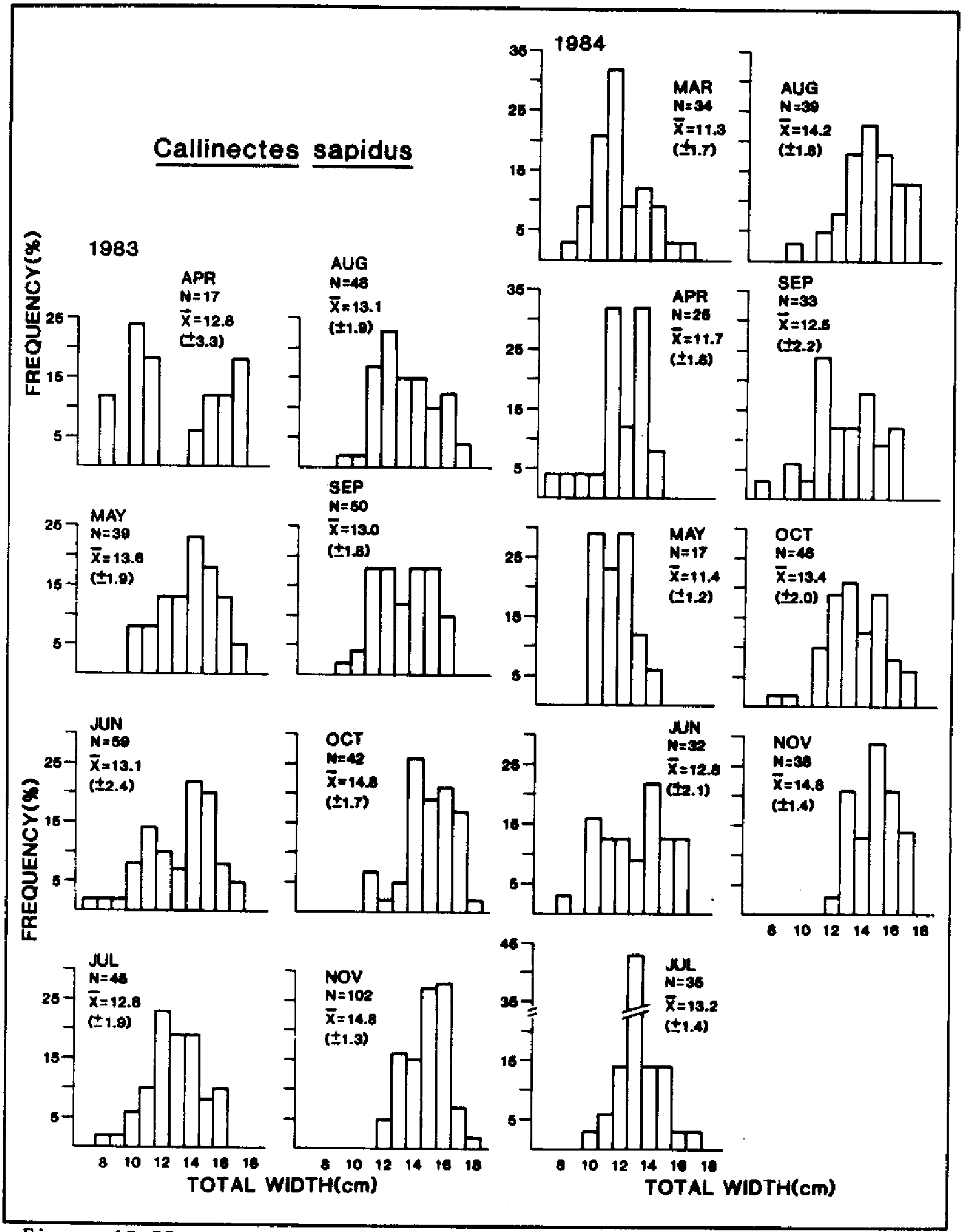


Figure 13.35 Total width frequency (as % of sample size N), mean (x) total width and standard deviation of the population of *C. sapidus* taken with crab pots from impoundment 4 in 1983 and 1984.

Of the female crabs collected by pots, 58% were immature; however, more-mature crabs were collected in impoundments than at creek sites during the study (Table 13.13). In addition to spatial differences, the percentage of mature females changed seasonally, with increased numbers collected from impoundments in October and November. Mature female crabs collected in fall were generally larger than males and were primarily responsible for the skewed size-frequency distributions observed in October and November at impoundment sites. Mature female crabs inhabiting impoundments were probably prevented from emigrating to higher-salinity estuarine or coastal areas, which occurs as water temperature decreases in fall (Eldridge and Waltz, 1977).

Only eight ovigerous female C. sapidus were collected during the study. These individuals were collected in Chainey Creek and the small feeder creek in July, when salinity was favorable for their occurrence. The majority of ovigerous female blue crab occur in late May and early June in nearshore waters or bays and sounds of South Carolina (Eldridge and Waltz, 1977).

Of the 915 crabs tagged and released during the study, only 20 were recaptured. The number of recaptures was too low to permit statistical assessment of growth rates or movement; however, two specimens tagged and recaptured did show an increase in carapace width of ~20 %. Movement was observed for four specimens that were captured in Chainey Creek and recaptured in an impoundment. Without further study, it is inconclusive as to whether the low number of tag returns in this tudy reflected that a large population of blue crabs exist in the study area or that tagging increased mortality of crabs directly or made them more susceptible to predation.

2. Cast Nets. Six species were collected by cast net during the study, but only three, P. setiferus, P. aztecus, and C. sapidus, were important in terms of total number and biomass (Table 13.14). These species accounted for 97.8% of the total number of decapod crustaceans taken with this gear. Only one species, Callinectes ornatus, was collected solely from the impoundments, and the mud crabs, Eurypanopeus depressus and Neopanope sayi, were only collected from Chainey Creek and the feeder creek (site SC).

Table 13.13

Percentage of immature and mature female *Callinectes sapidus* collected at creek and impoundment sites.

	CREEK			IMPOUNDMENT		
	N	Immature	Mature	N	Immature	Mature
1983						
April	7	86	14	18	83	17
May	8	100	0	4	75	25
June	13	54	46	24	21	79
July	2	100	0	11	82	18
August	6	100	0	23	83	17
September	4	100	0	45	73	27
October	3	33	67	29	14	86
November	5	40	60	65	9	91
1984						
March	5	100	0	6	100	0
April	7	100	0	19	95	5
May	6	100	0	35	100	0
June	4	75	25	13	54	46
July	2	50	50	7	57	43
August	3	100	0	10	100	0
September	9	67	33	18	89	11
October	2	50	50	33	27	73
November	4	100	0	22	9	91

The penaeid shrimps, *P. setiferus* and *P. aztecus*, were highly seasonal in their occurrence. Catches of white shrimp were limited to summer and fall, with greatest catch per unit effort (CPUE) occurring from August through September 1983 (Table 13.15). Few white shrimp were caught at any site in 1984. Individuals taken from impoundments during late summer and fall were consistently larger than those collected from the creek, suggesting that larger shrimp had emigrated from the creeks but were retained in the impoundments.

Table 13.14

Total number and weight of decapod crustaceans collected by cast net.

	NUMBER		WEIGHT	
Species	Total	%	Total	%
Penaeus setiferus	376	61.2	4.423	47.1
Penaeus aztecus	146	23.8	1.690	17.9
Callinectes sapidus	79	12.9	3.256	34.6
Eurypanopeus depressus	8	1.3	--	--
Penaeus duorarum	3	0.5	0.018	0.2
Callinectes ornatus	1	0.2	0.009	0.1
Neopanope sayi	1	0.2	--	--
TOTAL	614		9.396	

Brown shrimp were much less abundant and more limited in their occurrence than white shrimp, being consistently collected by cast net only in June and July. Too few individuals were collected to assess comparisons between sites; however, brown shrimp from impoundments were consistently larger than those taken from creeks for the same months.

Blue crab were collected during every sampling period in impoundment 2 except in September; however catches were very low, with highest CPUE of 2.8 (s = 2.2) in November 1983. In Chainey Creek, blue crab were collected by cast net from April through June 1983 and in June and July 1984. Sex ratio of blue crab was not significantly different in

Table 13.15 Mean catch, mean length (mm), and mean weight (g) per site of *Penaeus setiferus* from cast-net collections.

Month	CC (N = 6)			IMP 2 (N = 4)			IMP 4 (N = 4)			IMP 0 (N = 4)			SC (N = 1)		
	$\bar{x}$ No.	$\bar{x}$ Length (mm)	$\bar{x}$ Weight (g)	$\bar{x}$ No.	$\bar{x}$ Length (mm)	$\bar{x}$ Weight (g)	$\bar{x}$ No.	$\bar{x}$ Length (mm)	$\bar{x}$ Weight (g)	$\bar{x}$ No.	$\bar{x}$ Length (mm)	$\bar{x}$ Weight (g)	$\bar{x}$ No.	$\bar{x}$ Length (mm)	$\bar{x}$ Weight (g)
1983															
April	0	--	--	0	--	--	0	--	--	0	--	--	0	--	--
May	0	--	--	0	--	--	0	--	--	0	--	--	0	--	--
June	0	--	--	0	--	--	0	--	--	0	--	--	0	--	--
July	2.00	76	6	0.25	69	1	0	--	--	0	--	--	0	--	--
August	7.17	86	36	7.50	122	99	7.50	122	99	0	--	--	2	70	4
September	7.50	98	57	4.00	120	51	1.50	113	17	0	--	--	1	96	7
October	3.50	1.06	31	20.50	128	337	3.75	123	54	3	121	39	0	--	--
November	0.50	62	1	3.75	129	62	3.00	135	58	0	--	--	0	--	--
1984															
March	0	--	--	0	--	--	0	--	--	0	--	--	0	--	--
April	0	--	--	0	--	--	0	--	--	0	--	--	0	--	--
May	0	--	--	0	--	--	0	--	--	0	--	--	0	--	--
June	0	--	--	0	--	--	0	--	--	0	--	--	0	--	--
July	1.33	103	9	0	--	--	1.00	106	10	0	--	--	0	--	--
August	0	--	--	0.25	69	1	0.25	120	3	0	--	--	0	--	--
September	1.67	109	15	0.25	124	3	1.00	136	21	3	146	73	0	--	--
October	0	--	--	0	--	--	1.25	130	22	1	133	11	0	--	--
November	0	--	--	0.25	139	5	0	--	--	0	--	--	--	--	--

collections from the creek, whereas significantly more (64%) of the catch from the impoundments were males ($X^2 = 4.8$, $P < 0.5$). Of the females collected, only three were mature, and these were all collected in October from the impoundments.

CONCLUSIONS

The composition and number of species collected by seine and trawl was similar between the creek and impoundments. The most-abundant species (Palaemonetes pugio, P. vulgaris, Penaeus aztecus, P. setiferus, P. duorarum, Callinectes sapidus) were essentially the same between the major habitats sampled.

The temporal patterns in community structure observed during the two-year study were influenced by hydrographic conditions within the study area and by the life history of individual species. Increased species richness and total number of decapod species in impoundments and Chainey Creek occurred in summer and early fall, largely because of ingress of stenohaline marine species into the study area during periods of high salinity. Abundance and biomass, however, was lowest in summer and early fall, coinciding with high temperatures, high salinity, and low dissolved oxygen in the impoundments and Chainey Creek. These conditions may have stressed spring recruits such as penaeid shrimps and blue crab, which are sensitive to low dissolved oxygen. Grass shrimps (Palaemonetes sp.), which are relatively tolerant of low dissolved oxygen, were probably not stressed by environmental conditions at the study sites but may have been heavily cropped by predatory fishes during summer months.

Results suggest that blue crab and Penaeus sp. inhabiting impoundments had restricted access to the creek during periods of emigration. Larger brown and white shrimp were collected in the impoundments during fall, whereas juveniles dominated creek samples for the same period. Greater abundance of mature female blue crab within impoundments during months when spawning migrations to high-salinity waters occur suggested retention of crabs within impoundments.

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Chapter 14

ICHTHYOFAUNA

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INTRODUCTION

Many of the estuarine systems of coastal South Carolina have the remnants of a once-thriving industry that modified virgin marsh and swamp habitat to a system of dikes, ditches, and water-control structures for rice cultivation. Increased labor costs and other factors caused the demise of this industry after the Civil War (see Miglarese and Sandifer, 1982 for an historical review). These modified marsh habitats, generally referred to as impoundments, presently are the focus of controversy in coastal South Carolina. Although many impoundments fell into disrepair and reverted back to marsh habitat, others have been maintained as feeding and overwintering areas for migratory waterfowl. In addition to the utilization of these structures for waterfowl habitat, some have emphasized their possible value in the aquaculture of commercially important species such as penaeid shrimp, *Penaeus* spp., and blue crabs, *Callinectes sapidus* (Dean, 1975).

Little information is available concerning processes that determine the species composition, relative abundance, community structure, and trophic relationships of fishes inhabiting saltwater impoundments (Miglarese and Sandifer, 1982: impoundments with salinities greater than 0.5 ppt). Because impoundments are flooded by diverting water through control devices from tidal creeks, intuitively it is obvious that the faunal composition of the fish community in tidal creeks at the time of flooding is a significant factor in determining the species composition and relative abundance of fishes inside these structures. Shallow tidal creeks in estuaries along the southern Atlantic Coast are considered critical areas for the early developmental stages of numerous species of fishes (Weinstein, 1979). Although larval and juvenile fishes are found in this habitat throughout the year, maximum abundance of early-life-history stages of fishes occurs in winter and spring. Taxa recruited to the shallow-water marsh habitat during this period emigrate from these areas as they grow or as the water cools in early fall (Herke, 1971; Adams, 1976; Weinstein, 1979; Bozeman and Dean, 1980; Weinstein et al., 1980; Weinstein and Brooks, 1983).

Available information dealing with the fish community in South Carolina saltwater impoundments is limited to checklists, preliminary biomass estimates, and brief trophic analyses. Based on the work of C.M. Bearden in small saltwater impoundments at the Bears Bluff Laboratory on Wadmalaw Island, South Carolina, Miglarese and Sandifer (1982) present a list of 60 species of fishes in 33 families that occur in these structures. Biomass estimates of fishes in these 0.6 ha ponds range from 92.6 to 217.6 kg/ha (Lunz, 1951). Seasonal changes in the abundance and community structure of fishes in saltwater impoundments managed for waterfowl are unknown. Impoundments alter the hydrographic and physiographic properties of natural salt-marsh habitat (Copeland, 1974) and are rigorous habitats. Water circulation diminishes; sedimentation increases; temperature, salinity, and dissolved oxygen (DO) may reach more-extreme levels than in natural, estuarine waters. Mass mortalities of fishes in impoundments, because of low DO concentrations or low temperatures, are not uncommon (Miglarese and Sandifer, 1982).

Numerous accounts of the food habits of fishes known to occur in South Carolina saltwater impoundments are in the literature. All accounts, however, deal with these species in open estuarine systems, with the exceptions of brief descriptions of the diets of ladyfish, Elops saurus, and Atlantic croaker, Micropogonias undulatus, from South Carolina impoundments (Burns, 1975). Thus the impacts of impoundments on the diet of fishes recruited to these structures are unknown.

Given the lack of detailed knowledge of the ichthyofauna of saltwater impoundments in coastal South Carolina, we initiated this study to achieve the following objectives: (1) describe the seasonal species composition and relative abundance of larval fishes in a tidal creek adjacent to a series of experimental impoundments; (2) determine recruitment patterns of larval and juvenile fishes from the creek system into the impoundments; (3) describe the seasonal species composition and relative abundance of fishes in the experimental impoundments relative to that from the adjacent tidal creek; and (4) document the trophic relations of dominant fishes in experimental impoundments and compare these with dietary information from open estuarine systems.

METHODS

Ichthyoplankton

Field Sampling and Laboratory Analysis. Weekly ichthyoplankton samples, hereafter referred to as extensive samples, were taken in Chainey Creek and at the water-control structures (trunks) of the impoundments (Figure 14.1) in cooperation with the planktonic crustacean study (see Chapter 13) from January 1983 to January 1984. At the Chainey Creek site, simultaneous 20-min surface and near-bottom samples were taken with 0.5-m diameter, 500-μm mesh nitex nets suspended from an anchored jon boat during maximum current at night flood tide. The volume of creek water filtered by the nets was measured with calibrated General Oceanics flowmeters (General Oceanics, Inc. 1295 Northwest 163rd Street, Miami, FL 33169). No estimate of net blockage and backwash was made.

On the same date and when the management of the water levels inside the impoundments permitted passage of creek water through the water-control structure into impoundment 2 during flood tide, we collected larvae and juveniles recruited to the pond by sampling for 20 min with a 500-μm mesh, nitex plankton net at night. The net was attached to a 0.8 m x 0.3 m high frame that was set in the trunk so that all water entering the impoundment was filtered (See Fig. 14.2). The volume of water strained was determined from the depth of the water flowing over the inside sill of the trunk. Velocity was measured with a modified General Oceanics flowmeter from late March to June 1983 and with a Montedoro flow

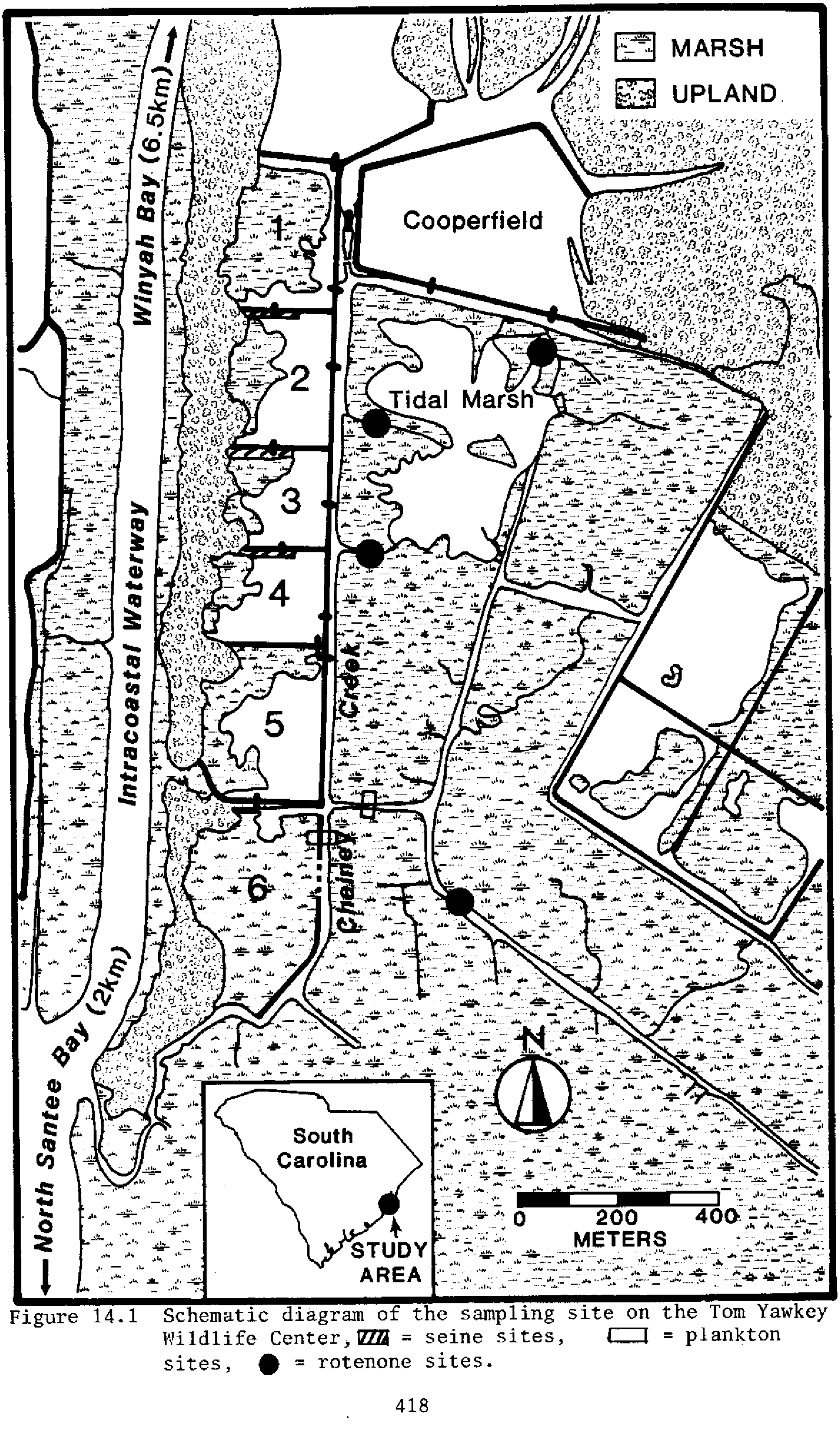

Figure 14.1 Schematic diagram of the sampling site on the Tom Yawkey Wildlife Center, ▨ = seine sites, ☐ = plankton sites, ● = rotenone sites.

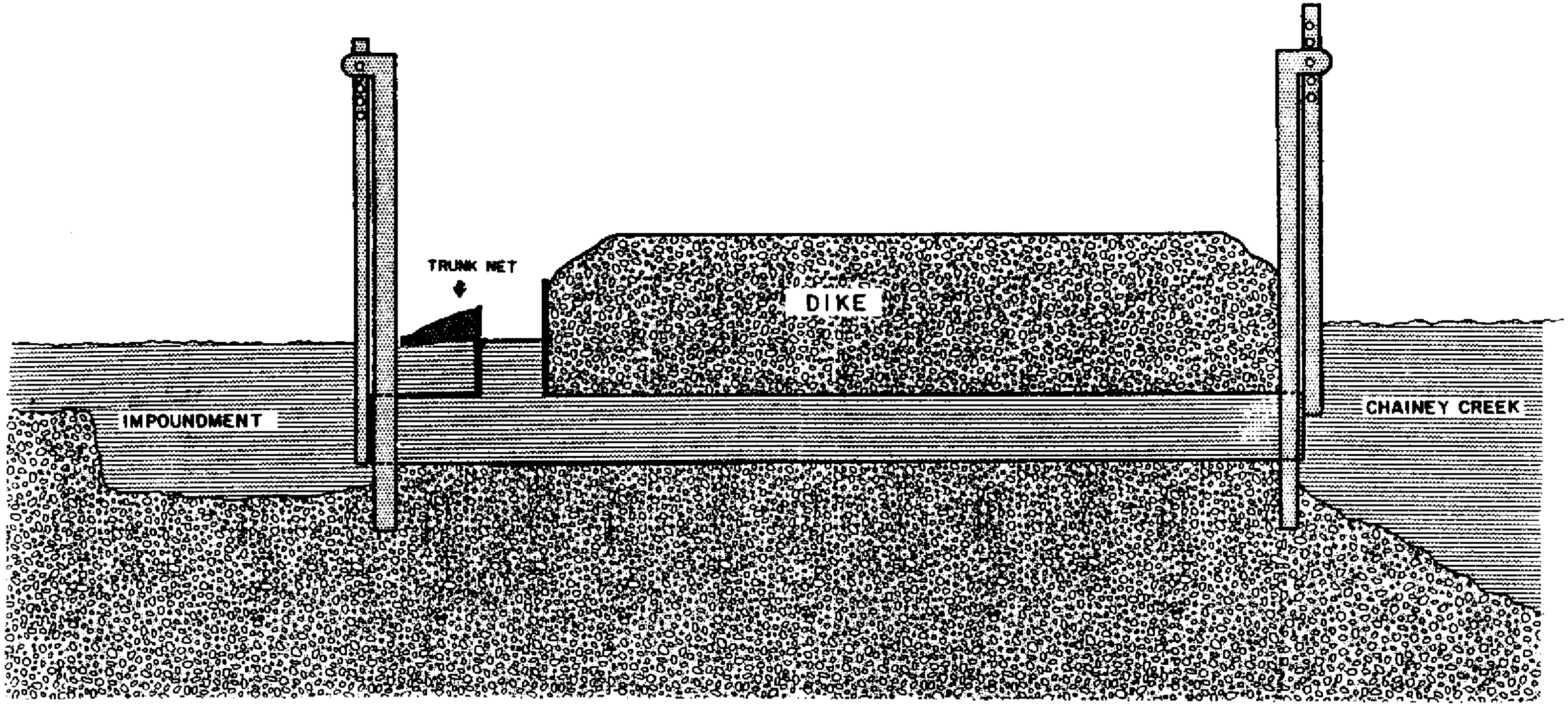

Figure 14.2 Diagrammatic cross-section of a trunk with the trunk plankton net set.

velocity meter (Montedoro-Whitney Corp., 2741-E McMillan Road, P.O. Box 1401, St. Luis Obispa, CA 93406) thereafter.

In addition to these weekly extensive samples, we made monthly intensive collections to determine if tidal and diel changes occurred in the ichthyoplankton community. Twenty-minute collections were made during early, middle, and late flood and ebb tides over 25 consecutive hours thus sampling a complete tidal cycle during both day and night. Nets (500-μm mesh) were fished in Chainey Creek (0.5-m diameter net: surface and near bottom), in a feeder creek that connected the high marsh with Chainey Creek (0.5-m diameter net: near bottom), and at the trunks of impoundments 2, 3, and 4 (0.8 x 0.3 m frame net). Theoretically, this intensive sampling scheme would have resulted in 72 plankton collections, but water-management practices eliminated tidal exchange between the impoundments and the creek during some periods, thereby eliminating those samples. From February to December 1984 we sampled Chainey Creek and at the trunk of impoundment 2 during the maximum current of flood tide at night on the new and full moons of each month. This reduction in effort was not based on any statistical analysis of the first year's data, but on the fact that a cutback was necessary to complete the analysis of the samples in a timely fashion.

Following each collection, weather conditions (air temperature, wind velocity and direction, cloud cover, precipitation), tidal stage, and water temperature were recorded. Water samples were taken for laboratory determination of salinity with an induction salinometer. Plankton was preserved in 10% formalin in the field; in the laboratory, fishes were removed, identified to the lowest possible taxon, and counted. During the first year (January 1983 to January 1984), either all the individuals in a sample were measured to the nearest millimeter standard length (SL), or for very abundant species, 50 individuals were removed from the well-mixed sample and measured. During the second year, we only determined minimum and maximum standard lengths of individual taxa within a sample. Numerical catch rates of larval fishes in creek samples were converted to densities (number/100 m^3); however, this was not possible for all collections at the water-control structures, because water velocity-measurements were considered reliable only after June 1983, when the electronic flowmeter was used. To facilitate taxonomic identification some fish larvae were cleared and stained following the procedure described by Dingerkus and Uhler (1977) as modified by Fritzsche and Johnson (1979) and Pottoff (1984).

Data Analysis. Data from samples taken at each of the creek sites [Chainey Creek surface (years I and II); Chainey Creek bottom (years I and II); marsh feeder creek (year I)] were pooled by month by station. Samples taken at the water-control structure of impoundment 2 during year II were pooled by month, whereas those taken at the water control structures of impoundments 2, 3, and 4 during year I were pooled by tidal stage (ebb or flood) by month.

Species richness and the degree of community dominance were calculated on the pooled data using the following formulas:

Species richness = $S - 1/\ln N$ (Margalef, 1968)

where S = number of species
N = number of individuals.

Community dominance index = $\frac{(x_1 + x_2) \times 100}{x}$ (McNaughton, 1968)

where x_1 = abundance of most abundant species
x_2 = abundance of second most abundant species
x = total abundance for all species.

Normal and inverse cluster analyses (Clifford and Stephenson, 1975) were used to analyze the pooled ichthyoplankton data collected only with the 0.5-m diameter nets. Prior to the analyses, data were reduced by elimination of species that had only a single occurrence and specimens identified only to family or genus. In addition, those collections made at the water-control structures (impoundment samples) were not included in these analyses, because the temporal effects were compounded by the water-management strategy. We used the Jaccard similarity coefficient for presence-absence data (Clifford and Stephenson, 1975) because a quantitative similarity coefficient was inappropriate, due to the variability in the amount of water strained between samples and the unequal numbers of samples in different months and years. The sorting strategy was flexible, with $\beta = -.25$ (Clifford and Stephenson, 1975).

Subsequent to cluster analysis, nodal analysis (Williams and Lambert, 1961; Lambert and Williams, 1962) was used to describe each season (winter: January to March; spring: April to June; summer: July to September; fall: October to December) in terms of characteristic species groups produced by inverse cluster analysis. Constancy and fidelity were used to determine how consistently species groups were collected during each season and the extent to which species groups were restricted to a season. A constancy value of 1 indicates that species occurred in all collections during a season, whereas 0 results when none of the species occurred in the collections. Fidelity values greater than 2 suggest preference of species for a season, whereas values less than 1 suggest that larval and juvenile fishes of a particular species group were not recruited into the marsh areas of the sampling site during a particular season.

Juvenile And Adult Fishes

Field Sampling. 1. Impoundment Seine Collections. Approximately every other month from March 1983 to December 1984 we sampled three seine sites in the perimeter ditch of each of the study impoundments. Random sampling was not possible because of the presence of "hangs" and the physiography (i.e., lack of a good landing site for the seine net) of the impoundments. The sites were 30.5 m long and, approximately 6.1 m wide, and the water depth, which varied according to the water-management cycle, ranged from 0.5 to 1.75 m. The day before sampling, the sides of the site were blocked with 2.0-m deep, 0.8-mm bar mesh blocknets that were heavily weighted with chain on the leadline. Immediately prior to sampling, additional 0.8-mm bar mesh block nets were set across the perimeter ditch to partition the site into three equal areas (186 m^2). There was a delay of from 11 to 15 hr between placing the block nets along the sides to setting those across the perimeter ditch to seal off the site. We felt that this period was necessary to minimize the effects of our activities. Our preliminary sampling demonstrated that seine collections made without block nets in the perimeter ditches of impoundments underestimated the biomass and diversity of fishes and decapod crustaceans. In addition, more-motile species avoided the sampling gear in the absence of blocknets, and descriptions of the fish community based on these data were misleading.

After closure of the sites, we made three pulls of a 9.1-m long, 1.8-m deep, 6.4-mm bar mesh bag seine. This was followed by a single haul of a 9.1-m long, 1.8-m deep, 0.8-mm bar mesh bag seine. Both nets had many end bottom lines attached to the lead line to prevent them from digging into the muddy bottom of the perimeter ditch. Contents of each seine haul were washed in a 1-mm screen and preserved immediately in 15% formalin.

2. Cast-Net Collections. A 1.5-m radius, 0.95-cm bar mesh (1.9-cm stretch mesh), monofilament cast net was used to sample fishes in both Chainey Creek and the impoundments. Fifteen throws were made randomly down the axis of the creek, and three throws, made at each of the outside trunks of the five experimental impoundments, were pooled together for a single sample. Inside the impoundments (unit 4: March 1983 to December 1984; unit 3: June 1983 to December 1984; unit 2: April to December 1984), 15 throws were made randomly both in the perimeter ditch and on the flats (when water depth permitted), and an additional sample of the composite catch from 15 throws was taken near the impoundment side of the trunk.

3. Gill-Net Collections. At randomly selected locations in Chainey Creek, 3-hr sets of two gill nets of differing mesh sizes were made during daylight hours during either maximum flood or ebb tide. Characteristics of the nets were: (1) small mesh: 2.4 m deep, 15.2 m long, 1.27-cm bar mesh (2.54-cm stretch mesh) floating monofilament gill net; (2) large mesh: 2.4 m deep, 15.2 m long, 3.81-cm bar mesh (7.62-cm stretch mesh) floating monofilament gill net. The nets were set perpendicularly across the creek from bank to bank, and three 0.45-kg weights were attached to the leadline so that the net hung properly in the brisk current. The nets were cleared of fishes and debris every hour during each sampling period.

4. Otter-Trawl Collections. A 1-km length of Chainey Creek adjacent to the experimental impoundments was divided into 100-m lengths. Three lengths were randomly selected and sampled during late ebb or early flood tide by towing a 0.6-cm bar mesh (1.25-cm stretch mesh) flat trawl net a distance of 100 m against the tidal current. The trawl net had a 3.4-m headrope, 4.5-m footrope, and 0.8-m leglines attached to 33x63 cm wooden

chain doors. These were towed behind a jon boat with 12.2-m long bridles. A tickler chain was attached to the heel of each door and adjusted to stir up the bottom 0.3 m in front of the foot rope.

5. Rotenone Collections. Beginning in August 1983, we sampled the ichthyofauna of the relatively small subtidal creeks that drained into Chainey Creek from the high marsh with rotenone. Prior to sampling, which occurred during late ebb tide, one (August 1983) or three (all months thereafter) 30.5-m-long sites were closed in with 2.0-m deep, 0.8-mm bar mesh blocknets that were heavily weighted with chain on the leadline. The sites were approximately 4 to 5 m wide, with maximum water depths from 0.7 to 1.2 m. The substrates were mainly mud, with patches of oyster shells and, in some places, stumps. After the sites were completely enclosed, sufficient rotenone was added to ensure a good kill. At the downstream end of the sites, potassium permanganate was mixed with water, leaving the sites to oxidize the rotenone, thereby minimizing the impacts of the ichthyocide on areas below the sampling sites. Stressed individuals were captured with dipnets as they surfaced, and fishes were picked off the bank during the collecting period. After no more fishes were observed surfacing and a final examination of the bank was made, the downstream blocknet was carefully raised to as not to lose those individuals that were washed into the net by the tide. We made no attempt to estimate rotenone efficiency.

Immediately after each sampling event, the catch was preserved in 15% formalin. After a 1-week fixation period, the samples were washed in tap water and transferred to 50% isopropyl alcohol. Fishes were sorted to species, counted, blotted dry, and weighed to the nearest gram. Either all individuals of a given species in a collection or a random sample of 100 specimens was measured to the nearest mm total length (TL) and standard length (SL) for all species. We also measured fork length (FL) where appropriate.

Data Analysis. Species richness was calculated and cluster analyses performed on the pooled data sets for each of the three main gear types. The data set for seine nets was generated by pooling all collections made with this gear in a given experimental impoundment during a sampling trip. Fishes taken with the trawl net and rotenone were pooled by month for each gear type. Prior to normal and inverse cluster analyses, data were edited to remove species that occurred in two or fewer of the pooled monthly collections. The Bray-Curtis similarity measure was used on the $\log_{10}$-transformed species abundance scores. The sorting strategy was flexible, with $\beta = -.25$. Nodal analysis was used to examine the co-occurrence of species and site groups based on patterns of constancy and fidelity.

To compare the similarity in the ichthyofauna of the open-marsh system and the experimental impoundments, we produced faunal checklists of fishes taken with all gear types in each impoundment and the open-marsh habitat for each sampling month. After the removal of species that occurred in two or fewer of the lists, we subjected the data to cluster analysis (normal and inverse) using the Jaccard coefficient for presence-absence data (Boesch, 1977). These results were examined by nodal analysis as previously described.

Food Habits. In the laboratory, stomachs were removed from fishes utilized in the trophic analysis and placed in 50% isopropyl alcohol. Each stomach was examined for food items; when present, they were sorted to the lowest possible taxonomic level and counted. Parts (e.g., a pair of eyes or a single abdomen) were counted as one animal. Plant material and unidentifiable remains were counted as one item. Volume displacement of food items was measured with a graduated cylinder; in the case of small species, volume was estimated using a 1-mm^2 grid (Windell, 1971).

The relative contributions of individual prey species were compared using frequency of occurrence (F), numerical dominance (N), volume displacement (V), and the index of relative importance (IRI) ($\text{IRI} = [N + V]F$) (Sedberry, 1980; Pinkas et al., 1971).

Comparisons of the similarity in the diets among fishes were made by cluster analysis where the total contents of each species of predator was treated as a collection (Bortone et al., 1981; Sedberry, 1980). We used the Bray-Curtis coefficient as described by Sedberry (1980), after standardizing the collections by percentage of numerical abundance because sample sizes were unequal. The sorting strategy was flexible, with $\beta = -.25$.

RESULTS

Water Management and Hydrography

Plots of the mean monthly depth of water on the beds of the study impoundments showed the effects of the water management strategy (Fig. 14.3). In 1983 the beds were allowed to go dry in April and were reflooded in May, when tidal exchange was permitted. The water level was raised gradually during the summer by the addition of flash boards at the trunks (Fig. 14.2) until maximum water depth was achieved in late summer or early fall. Water levels gradually decreased throughout the fall and winter, until the beds were once again allowed to dry out (March to May in impoundment 4; May in impoundment 3). These impoundments were reflooded in May 1984, and the water level was gradually increased again. Impoundment 2 was drawn down during January and February 1983, and the water level was increased through the summer. The water level was lowered during fall, and the trunk was set to act as a weir with constant tidal exchange for the remainder of 1984.

Salinity was lowest during winter and early spring and rapidly increased in May of both years (Fig. 14.4). Values remained relatively constant through the summer until the winter decline. Salinities inside the impoundments followed the same trends as those from Chainey Creek; however, the minimum values seen in April 1984 were higher in the impoundments than in the creek.

The range of air temperatures at the study site was 38°C (-5°C to 33°C) (Fig. 14.5). Observed mean water temperatures were highest during June 1984, whereas minma occurred in January (Fig. 14.4). Water temperatures inside the impoundments followed a similar trend to those in Chainey Creek. Because the impoundments were very shallow and lacked the thermal buffering capacity of large bodies of water, they were much more susceptible to extreme temperatures caused by atmospheric conditions. Several times during the winter of 1983 skim ice was observed in the impoundments.

During the summer of 1983 both impoundments 3 and 4 showed marked reductions in DO concentrations for dawn or early-morning samples. Although less dramatic, a similar decline was seen in 1984 (Fig. 14.6).

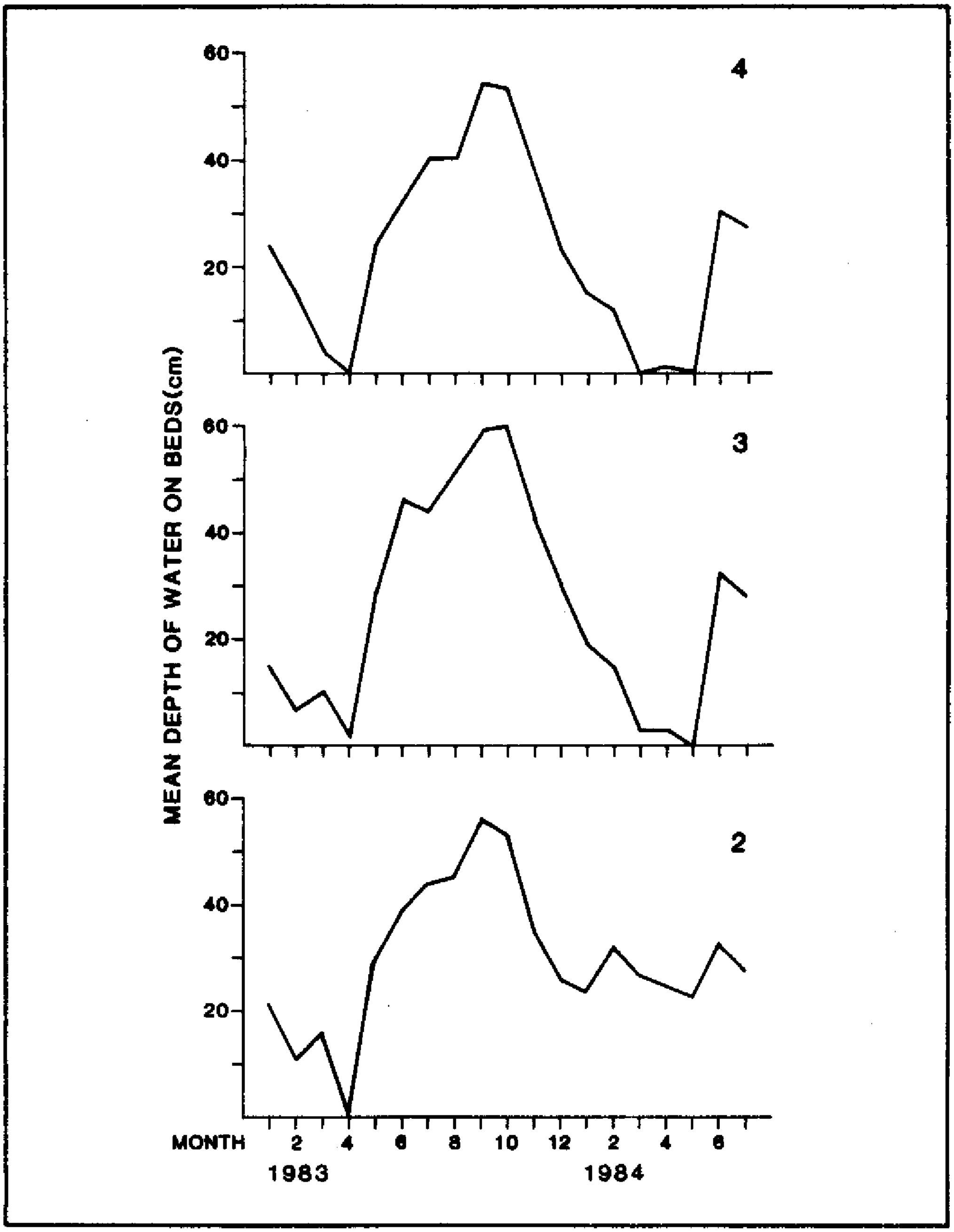

Figure 14.3 Monthly mean water depth on the flats of study impoundments 2, 3 and 4.

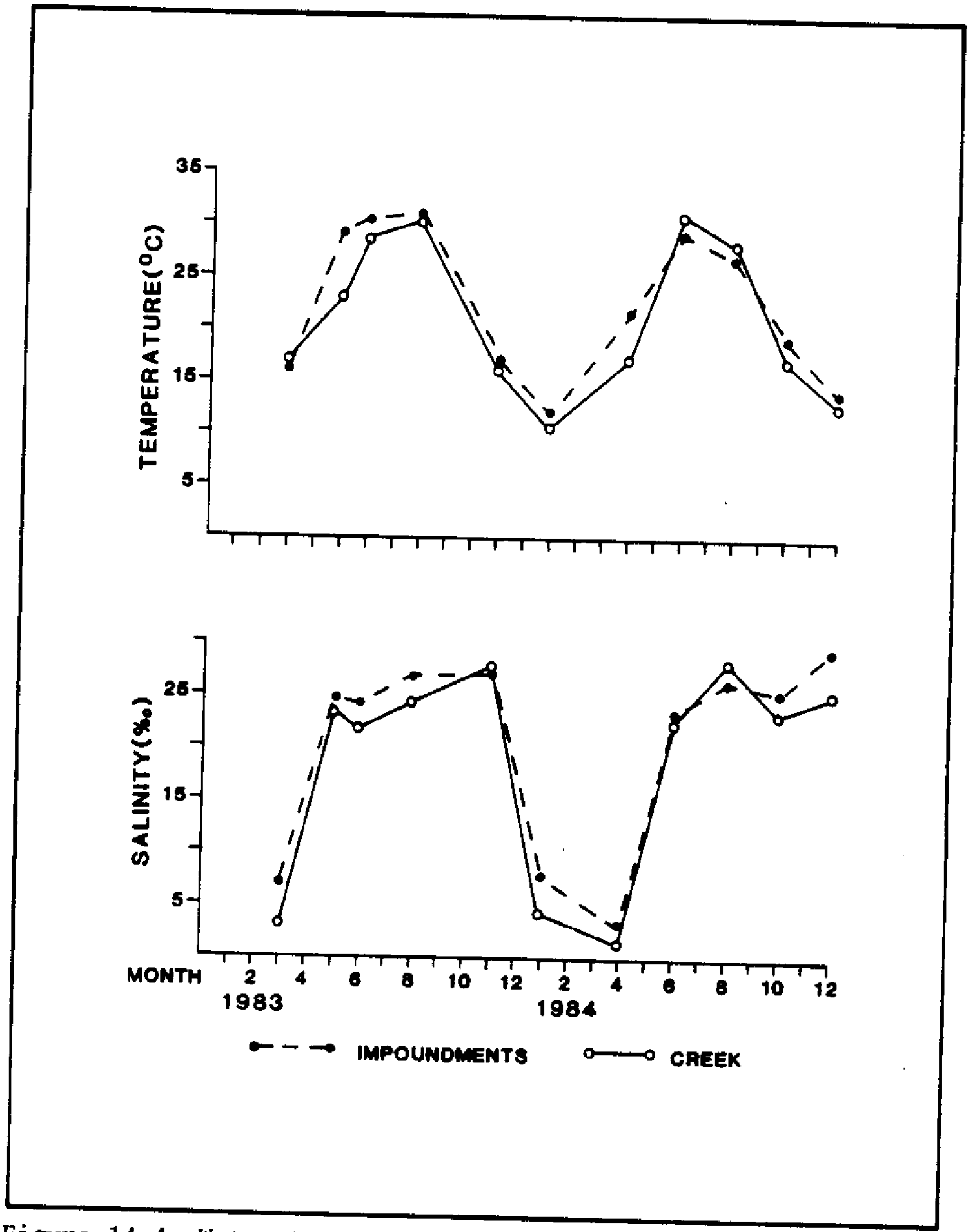

Figure 14.4 Water temperature and salinity values for the study impoundments and Chainey Creek during fish sampling.

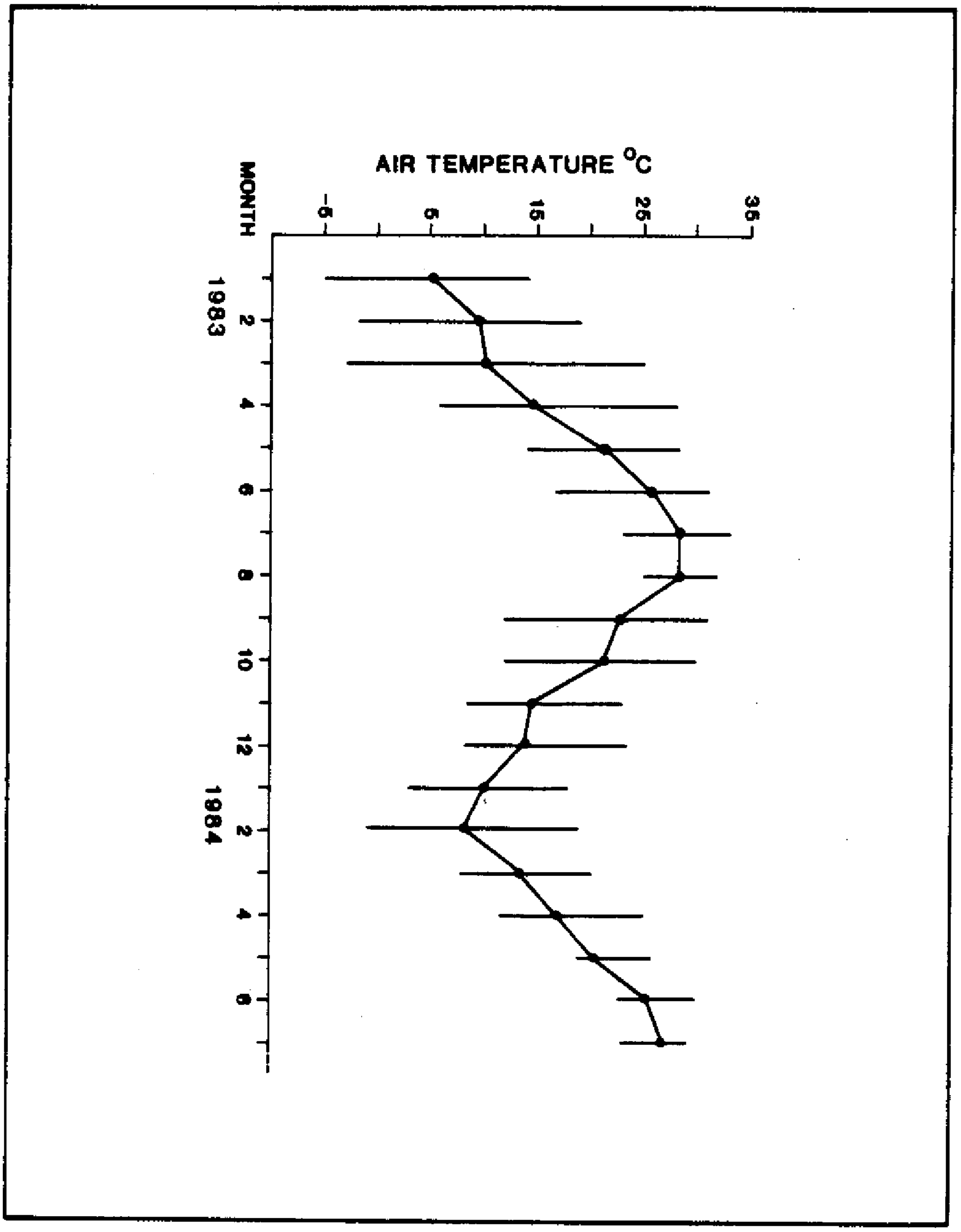

Figure 14.5 Monthly mean air temperatures (dots) and ranges (vertical bars) for the Cat Island study site.

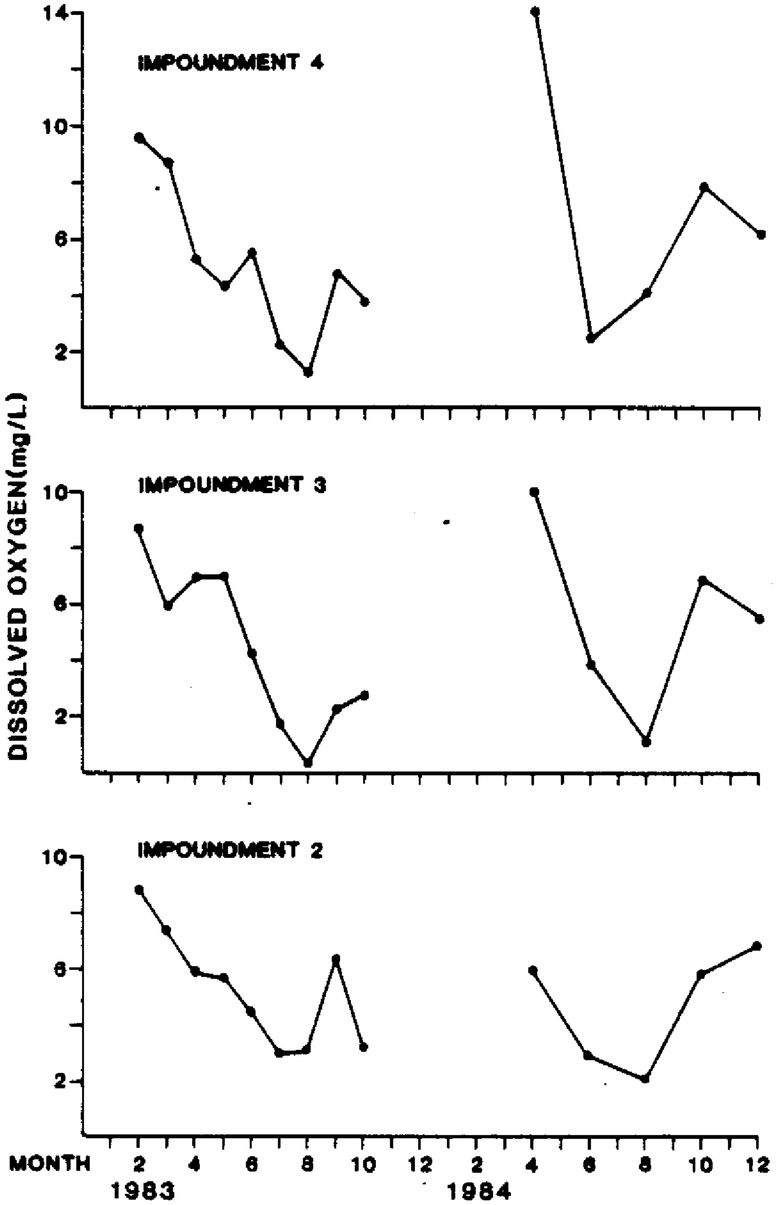

Figure 14.6 Early morning dissolved oxygen concentrations in the study impoundments.

Ichthyoplankton

From January 1983 to December 1984 we collected 747 ichthyoplankton samples, of which 623 had fishes (Table 14.1). With the exception of collections made during early and mid-ebb tide, volumes filtered were consistently higher in the marsh feeder creek than in Chainey Creek (Fig. 14.7). Maximum rates occurred during early ebb tide at all stations, and the mean volume filtered for creek stations ranged from 35 to 85 m^3. When the management strategy allowed water exchange between the impoundments and the tidal creek, mean volume filtered (mid-March 1983 to December 1984) across the water-control structures ranged from 10 to 55 m^3.

Species Composition. A total of 53,222 larval and juvenile fishes, representing 83 taxa, 60 species, and 29 families, was collected during the study (Appendix Table 14.1). Eight species accounted for 88.9% of the total number of fishes taken during the study (Table 14.2). Spot, Leiostomus xanthurus, was the most-numerous species, comprising 55.33% of the total catch. It dominated the catches regardless of sampling site and was the second most frequently occurring taxon (Table 14.3). We found spot from January through July during 1983 (Appendix Table 14.2) and from January through June 1984 (Appendix Table 14.3) in salinities of 3.0 to 27.8 ppt and temperatures of 4.1 to 30.5°C. The peak abundance of spot was in February 1983, when 16,633 individuals with an average size of 16.5 mm SL were collected. Data from the intensive samples (25-hr stations) showed that spot were most abundant in night collections made during ebb tide (Fig. 14.8). Nets fished during ebb tide in the small feeder creek that drained the high marsh caught the most spot. The intensive collections at the water-control structures of impoundment 2 indicated that spot move freely through the trunks during both ebb and flood tides; however, more individuals were taken during flood tides (Table 14.4).

Atlantic croaker, Micropogonias undulatus, was the most frequently occurring species (Table 14.3) and the second most numerous taxon (Table 14.2). Atlantic croaker was absent only in those collections from July through September 1983 and May through August 1984 (Appendix Tables 14.2 and 14.3). This species was taken in salinities from 0 to 31.9 ppt and temperatures from 3.8 to 28.1°C and ranged in size from 4 to 59 mm SL;

Table 14.1

Total number of samples, those with fishes, and number of taxa, species and individuals in plankton collections by year and station. Year I = January 1983-January 1984; Year II = February 1984-December 1984; CCS = Chainey Creek Surface; CCB = Chainey Creek Bottom; MFC = marsh feeder creek; IMP = impoundment.

Year	Station	Total Samples	Samples with Fishes	Number of Taxa	Number of Species	Number of Individuals
I	CCS	176	147	60	47	14,819
I	CCB	177	150	55	44	11,198
I	MFC	139	125	52	39	13,293
I	IMP-2	119	93	55	42	5,042
I	IMP-3	29	17	14	14	97
I	IMP-4	45	36	40	30	2,732
II	CCS	22	19	30	24	1,415
II	CCB	22	20	27	25	1,062
II	IMP-2	18	16	33	28	3,566

Table 14.2

Ranking by numerical abundance of larval and juvenile fishes taken in all plankton collections from January 1983 to December 1984.

Taxa	Number of Individuals	Percentage of Total Catch	Cumulative Percent
Leiostomus xanthurus	29,452	55.33	
Micropogonias undulatus	4,154	7.80	63.13
Mugil cephalus	3,098	5.82	68.95
Lagodon rhomboides	2,915	5.48	74.43
Anchoa mitchilli	2,503	4.70	79.13
Gobiosoma bosci	1,854	3.48	82.16
Brevoortia tyrannus	1,701	3.20	85.81
Elops saurus	1,648	3.10	88.91
Cynoscion regalis	695	1.31	90.22
Menidia beryllina	675	1.27	91.49
Engraulidae	639	1.20	92.69
Gobionellus boleosoma	406	0.76	93.45
Bairdiella chrysoura	363	0.68	94.13
Symphurus plagiusa	260	0.49	94.62
Fundulus heteroclitus	246	0.46	95.08
Microgobius thalassinus	235	0.44	95.52
Poecilia latipinna	188	0.35	95.87
Cyprinodon variegatus	176	0.33	96.20
Gerreidae Type I	166	0.31	96.51
Lucania parva	151	0.28	96.79
Gambusia affinis	147	0.28	97.07
Sciaenops ocellatus	141	0.26	97.33
Sciaenidae	131	0.25	97.58
Fundulus sp.	117	0.22	97.80
Myrophis punctatus	111	0.21	98.01
Paralichthys lethostigma	110	0.21	98.22
Paralichthys dentatus	102	0.19	98.41
Gobiidae	100	0.19	98.60
Atherinidae	72	0.14	98.74
Gobiosoma ginsburgi	60	0.11	98.85

Table 14.2 Continued

Taxa	Number of Individuals	Percentage of Total Catch	Cumulative Percent
Gobionellus hastatus	57	0.10	98.95
Menticirrhus sp.	51	0.10	99.05
Cynoscion nebulosus	46	0.09	99.14
Gobiosoma sp.	39	0.07	99.21
Gobionellus shufeldti	38	0.07	99.28
Pogonias cromis	34	0.06	99.34
Dormitator maculatus	34	0.06	99.40
Megalops atlanticus	31	0.06	99.46
Anguilla rostrata	26	0.05	99.51
Trinectes maculatus	26	0.05	99.56
Citharichthys spilopterus	25	0.05	99.61
Syngnathus scovelli	24	0.05	99.66
Gobiesox strumosus	21	0.04	99.70
Syngnathus louisianae	18	0.04	99.74
Menidia menidia	11	0.02	99.76
Stellifer lanceolatus	11	0.02	99.78
Syngnathus fuscus	9	0.02	99.80
Stephanolepis hispidus	7	0.01	99.81
Gerreidae Type 2	7	0.01	99.82
Gobionellus sp.	7	0.01	99.83
Anchoa hepsetus	6	0.01	99.84
Dorosoma petenense	6	0.01	99.85
Unidentifiable	6	0.01	99.86
Elopidae	5	0.01	99.87
Evorthodus lyricus	5	0.01	99.88
Paralichthys albigutta	4	0.01	99.89
Hypsoblennius sp.	4	0.01	99.90
Caranx hippos	3	0.01	99.91
Chaetodipterus faber	3	0.01	99.92
Mugil curema	3	0.01	99.93
Cyprinodontidae	3	0.01	99.94
Syngnathus sp.	3	0.01	99.95

Table 14.2 Continued

Taxa	Number of Individuals	Percentage of Total Catch	Cumulative Percent
Eleotridae	3	0.01	99.96
Lutjanus griseus	2	-	
Orthopristis chrysopterus	2	-	
Etropus crossotus	2	-	
Blenniidae	2	-	
Fundulus confluentus	2	-	
Sparidae	2	-	
Ictalurus catus	1	-	
Opsanus tau	1	-	
Archosargus probatocephalus	1	-	
Diplodus holbrooki	1	-	
Eleotris pisonis	1	-	
Prionotus carolinus	1	-	
Prionotus scitulus	1	-	
Prionotus tribulus	1	-	
Anguilliformes	1	-	
Sphoeroides sp.	1	-	
Mycteroperca microlepis	1	-	
Lepomis gulosus	1	-	
Prionotus sp.	1	-	
Symphurus civitatum	1	-	
	53,222		

Table 14.3
Ranking of taxa by frequency of occurrence in ichthyoplankton samples from January 1983 to December 1984.

Taxon	Count	Occurrence (%)
Micropogonias undulatus	237	31.73
Leiostomus xanthurus	184	24.63
Gobiosoma bosci	183	24.50
Gobionellus boleosoma	153	20.48
Anchoa mitchilli	152	20.36
Lagodon rhomboides	127	17.00
Engraulidae	113	15.13
Mugil cephalus	93	12.45
Menidia beryllina	79	10.58
Elops saurus	69	9.24
Cynoscion regalis	65	8.70
Symphurus plagiusa	62	8.29
Microgobius thalassinus	60	8.03
Gerreidae Type I	58	7.76
Bairdiella chrysoura	52	6.96
Gobiidae	47	6.29
Brevoortia tyrannus	46	6.16
Sciaenidae	44	5.89
Myrophis punctatus	43	5.76
Fundulus heteroclitus	43	5.76
eciaenops ocellatus	43	5.76
Paralichthys lethostigma	41	5.49
Gambusia affinis	40	5.35
Paralichthys dentatus	39	5.22
Cyprinodon variegatus	38	5.08

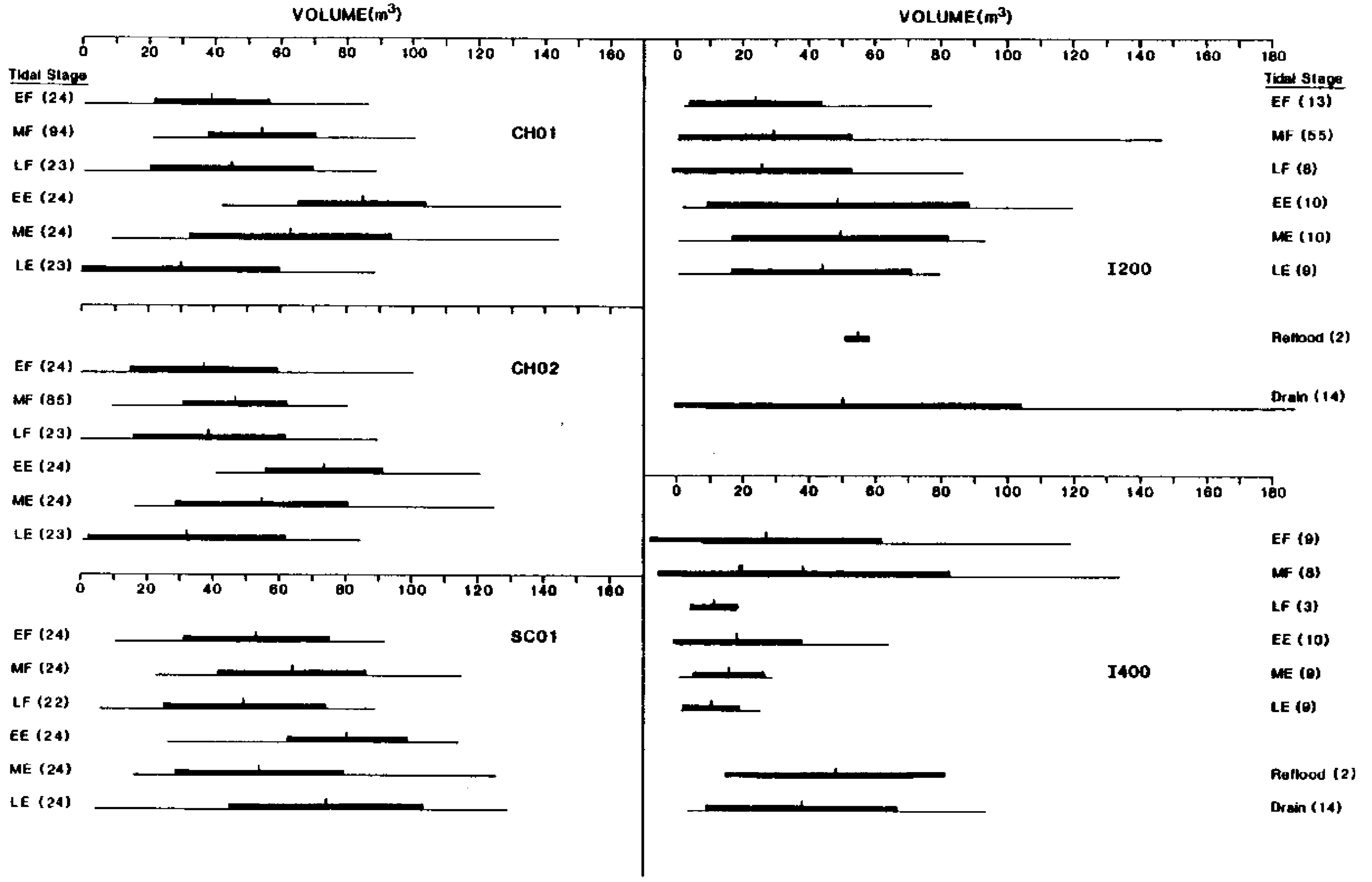

Figure 14.7 Volume of water filtered (m^3) for cbb (EE = early ebb; ME - mid-ebb; LE = late ebb) and flood (EF = early flood; MF = mid-flood; LF = late flood) tides at Chainey Creek surface (CH01), and bottom (CH02), marsh feeder creek (SC01), impoundment 2 (1200) and impoundment 4 (I400).

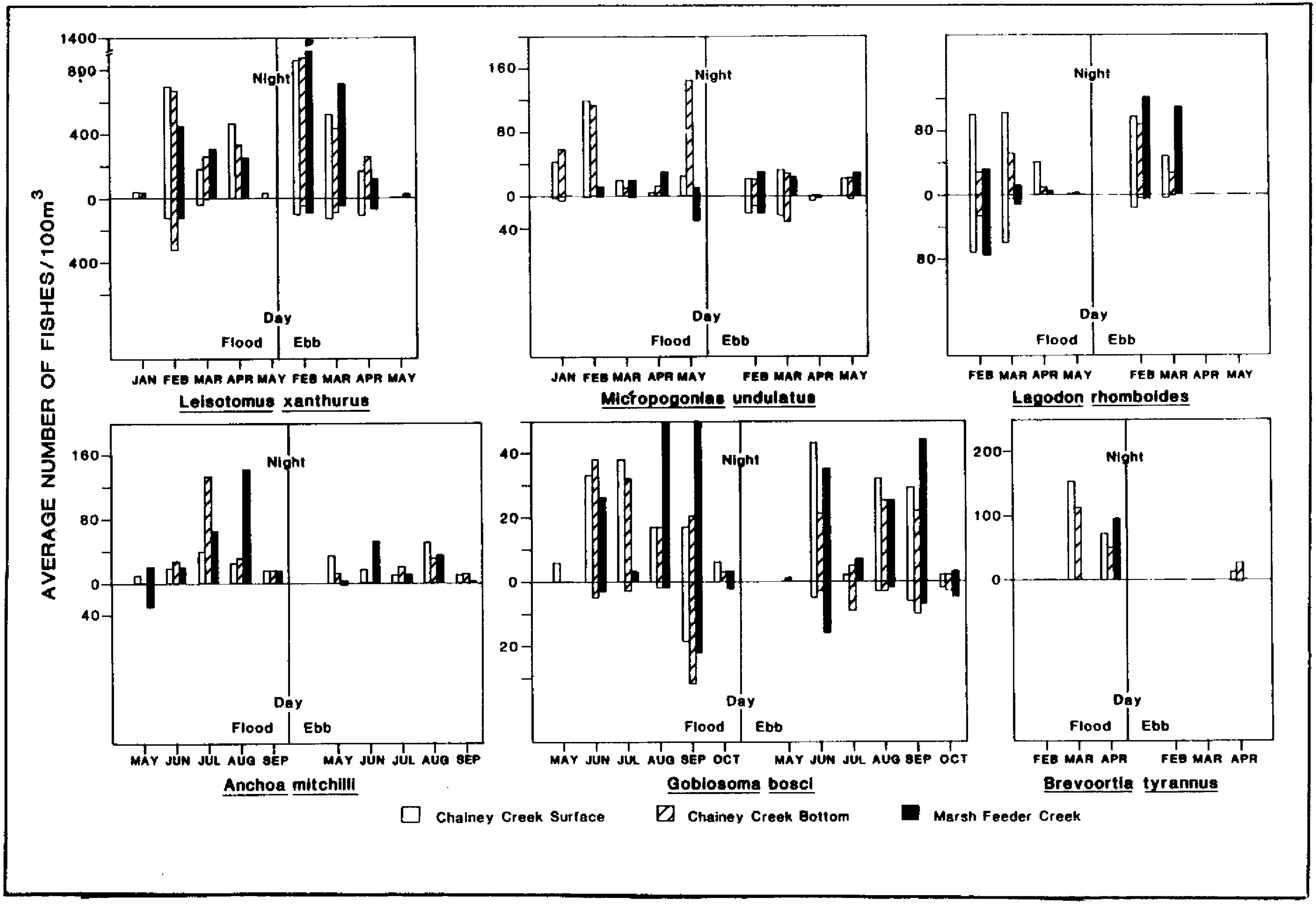

Figure 14.8 Surface-bottom, day-night, and tidal (ebb-flood) differences of the numerically dominant fishes taken in ichthyoplankton samples.

Table 14.4 Number of fishes collected on ebb and flood tides at all impoundment stations from January 1983 to January 1984 in order of decreasing abundance.

Species	Tide Stage	Jan'83	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan'84	Total
Elops saurus	Flood					834	13	15	2		1	2			867
	Ebb					617	30	2							649
Micropogonias undulatus	Flood	13	6	4		198	2				2	1	2	13	241
	Ebb		5			619	2								626
Anchoa mitchilli	Flood					246	150	110	93	4	1				573
	Ebb					132	20	124							276
Leiostomus xanthurus	Flood	139	358	196		89	14	1						3	790
	Ebb		10	5		23	2								40
Mugil cephalus	Flood		89	1		385	2	2					2	103	584
	Ebb		56	9		13									78
Menidia beryllina	Flood	2	12	20	1	208	140	8					2	22	416
	Ebb		7	128		22	2	12							164
Gobiosoma bosci	Flood						115	82	27	21	4		5		254
	Ebb			2	1		63	18			2	7			107
Lagodon rhomboides	Flood		159	30		6								5	190
	Ebb		45	6		5									56
Fundulus heteroclitus	Flood	1	2	6		25	2	2				1	82	42	153
	Ebb		18	10		29		2							59
Poecilia latipina	Flood	1				56	3	1					109	1	170
	Ebb			2		2		3			1	9		1	18

Table 14.4 Continued

Species	Tide Stage	Jan'83	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan'84	Total
Engraulidae	Flood					9	14	93	9	1	1				127
	Ebb					9	10	42							61
<u>Cynoscion regalis</u>	Flood					28	70	51	19	5					173
	Ebb					2	4	1							7
<u>Cyprinodon variegatus</u>	Flood	1	4			7		1					13	12	37
	Ebb		109	4		1	2	5							121
<u>Gambusia affinis</u>	Flood					4	4	1					82		91
	Ebb		10	12		2	1	9		4		5		3	46
<u>Lucania parva</u>	Flood			3		18		1		1			14		37
	Ebb		27	65		2		1				3		1	99
<u>Bairdella chrysoura</u>	Flood					8	38	35		6					87
	Ebb					3	4	7							14
Sciaenidae	Flood					15	8	4	2	1					40
	Ebb					19	2								21
<u>Myrophis punctatus</u>	Flood		4			36	1								43
	Ebb					17									17
<u>Fundulus</u> sp.	Flood					48	2	1						1	52
	Ebb					3									3
Atherinidae	Flood					13									13
	Ebb					1		43							44
<u>Gobionellus boleosoma</u>	Flood		1	1	1	1	1	4	16	2	2		2		31
	Ebb							18							18

Table 14.4 Continued

Species	Tide Stage	Jan'83	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan'84	Total
Gerreidae Type I	Flood					2	3	1	2	2	22				31
	Ebb														0
Menticirrhus sp.	Flood					4	25								29
	Ebb					1									13
Megalops atlanticus	Flood						3	15	3	1	4				26
	Ebb														0
Gobionellus hastatus	Flood					14	1								15
	Ebb					9		1							10
Gobiidae	Flood					1	10	7	2	1					21
	Ebb						2	1							3
Microgobius	Flood					1			6	3	3				13
thalassinus	Ebb						1								1
Pogonias cromus	Flood					10									10
	Ebb					3									3
Gobiosoma ginsburgi	Flood								2	4	3				9
	Ebb														0
Syngathus louisianae	Flood					5		1			1				7
	Ebb		1					1							2
Gobiesox strumosus	Flood						8								8
	Ebb														0
Synganthus scovelli	Flood					1		1		1					3
	Ebb					1	1				1	2			5

Table 14.4 Continued

Species	Tide Stage	Jan'83	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan'84	Total
Auguilla rostrata	Flood			1		1							1		3
	Ebb		1	3											4
Gobionellus shufeldti	Flood							4							4
	Ebb					2		1							3
Symphurus plagiusa	Flood							5			1	1			7
	Ebb														0
Dormitator maculatus	Flood					4	2								6
	Ebb														0
Menidia menidia	Flood					3								2	5
	Ebb			1											1
Syngnathus fuscus	Flood					1		1							2
	Ebb					2		1							3
Gerreidae Type II	Flood										6				6
	Ebb														0
Elopidae	Flood							5							5
	Ebb														0
Gobiosoma sp.	Flood					1	1		2						4
	Ebb														0
Trinectes maculatus	Flood						1	1							2
	Ebb					2									2
Paralichthys dentatus	Flood		1	2											3
	Ebb														0

Table 14.4 Continued

Species	Tides Stage	Jan'83	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan'84	Total
Mugil curema	Flood					2									2
	Ebb					1									1
Stephanolepis hispidus	Flood						1			1					2
	Ebb					1									0
Caranx hippos	Flood														0
	Ebb					2									2
Anchoa hepsetus	Flood						1								1
	Ebb				1										1
Cynoscion nebulosus	Flood							1							1
	Ebb							1							1
Fundulus confluentus	Flood							1							1
	Ebb		1												1
Gobionellus sp.	Flood														0
	Ebb					1									1
Sparidae	Flood														0
	Ebb					2									2
Syngnathus sp.	Flood						1								1
	Ebb							1							1
Chaetodipterus faber	Flood							1							1
	Ebb														0
Diplodus holbrooki	Flood														0
	Ebb					1									1

Table 14.4 Continued

Species	Tides Stage	Jan'83	Feb	Mar	Apr	May	June	Jul	Aug	Sep	Oct	Nov	Dec	Jan'84	Total
Ictalurus catus	Flood					1								1	2
	Ebb														0
Hypsoblennius sp.	Flood					1									1
	Ebb														0
Paralichthys lethostigma	Flood					1									1
	Ebb														0
TOTAL	Flood	157	628	265	2	2359	814	457	192	47	51	5	314	207	5497
	Ebb	0	290	247	2	1565	146	294	0	0	8	26	0	5	2587

however, most specimens were between 9 and 25 mm SL. Peaks in the abundance of Atlantic croaker occurred in February (1233 individuals, $\bar{x}$ SL = 14 mm) and May 1983 (1183 individuals; $\bar{x}$ SL = 16 mm). The Atlantic croaker was the second most abundant species taken in surface and bottom samples in Chainey Creek during 1983 and was a common but less-abundant species at other stations (Appendix Table 14.1). Most were collected on flood tides at night (Fig. 14.8), and few larvae or juveniles were taken during either daytime flood tides or ebb tides regardless of sampling time. In contrast to other species, more Atlantic croakers were collected emigrating on the ebb tide at the trunks of the impoundments than entering the units during flood tides (Table 14.4).

Striped mullet, *Mugil cephalus*, was the third most numerous and the eighth most frequently occurring species (Tables 14.2 and 14.3). Striped mullet was absent in collections made from August through November during the first year and from May through December in 1984 (Appendix Tables 14.2 and 14.3). Salinities and temperatures at the time of capture ranged from 0 to 25.6 ppt and 4.0 to 29.6°C. This species had a size range from 15 to 97 mm SL, but most individuals were between 20 to 28 mm SL. Largest catches during 1983 were in February (347 individuals; $\bar{x}$ SL = 22 mm) and May (398 individuals; $\bar{x}$ SL = 28 mm). Forty-two percent of the striped mullet from February and all those from May were taken in samples at the trunks of the impoundments (Appendix Table 14.1). We collected 2142 individuals (69% of the total catch of striped mullet) at the water-control structure of impoundment 2 and only five fish in creek samples during 1984. More striped mullet were taken during flood tide samples at the water-control structure than during ebb tide.

Pinfish, *Lagodon rhomboides*, ranked fourth in numerical abundance and was the sixth most frequently occurring species (Tables 14.2 and 14.3). During the first half of 1983, pinfish were present in the samples from January through May. Although they occurred in collections from November 1983 through May 1984, most individuals taken in April and May were juveniles (>15 mm SL). During the course of the two year ichthyoplankton study, pinfish ranged in size from 11 to 24 mm SL and were found in salinities of 0 to 14.7 ppt and temperatures of 5.4 to 19.6°C. The largest catch was in February 1983, and these fish averaged 14 mm SL. We collected this species at every station during both years, but it occurred more frequently in nets fished at the surface in Chainey Creek and in the marsh feeder creek (Appendix Table 14.1). During both day and night flood tides, pinfish were more abundant in surface rather than bottom collections (Fig. 14.8), and four individuals were taken during day ebb tide. More were collected at the water-control structures during flood tides than during ebb tide, when water flowed out of the impoundments (Table 14.4).

The bay anchovy, Anchoa mitchilli, was the fifth most abundant and fifth most frequently encountered species (Tables 14.2 and 14.3). Bay anchovies had a large size range (10 to 50 mm SL), and both larvae and juveniles were collected. Most bay anchovies in samples from June to November 1983 and May to October 1984 (salinity range: 2.0 to 31.9 ppt; temperature range: 4.0 to 33.0°C) were larvae, whereas juveniles dominated in February, March, May, and December 1983. We collected 639 engraulid larvae (<10 mm SL) that could not be identified to species, and we believed many of these, if not most, were A. mitchilli. Bay anchovies were taken at every sampling locale except at the water-control structure of impoundment 3. Few bay anchovies were collected during daytime, and most were in nets fished during night flood tides. Catches at the water-control structure of impoundments other than number 3 indicated a net ingress into the units (Table 14.4).

The naked goby, Gobiosoma bosci, ranked sixth in numerical abundance and was the third most frequently occurring species (Tables 14.2 and 14.3). Naked gobies were collected from March through December 1983 and May through October 1984 (salinity range: 1.2 to 31.9 ppt; temperature range: 4.0 to 33.0°C). In November and December 1983, only juvenile naked gobies were caught, and the greatest number were in the samples taken from June through September 1983. Fishes from this latter period averaged 8 mm SL, and the size range over the course of the whole study was 3 to 36 mm SL. Although this species was taken in both ebb and flood tides, more individuals were taken at night (Fig. 14.8). Samples at the water-control structures indicated a net influx of larval and juvenile G. bosci into the impoundments.

The Atlantic menhaden, Brevoortia tyrannus, was the seventh most numerous but only the seventeenth most frequently occurring taxon (Tables 14.2 and 14.3). This species caught from February through May in both years (salinity range: 0 to 29.7 ppt; temperature range: 7.7 to 28.6oC) and had a size range from 21 to 43 mm SL. Although Atlantic menhaden were taken at every station except at the water-control structure of impoundment 3, they were more numerous in collections made in Chainey Creek (Appendix Table 14.1). Atlantic menhaden were more abundant in samples made during night flood tides, and more individuals were in samples made during water movement into the impoundments than when water flowed out during ebb tide (Table 14.4).

The ladyfish, Elops saurus, was the eighth most numerous and the tenth most frequently occurring species (Tables 14.2 and 14.3). They ranged in size from 19 to 52 mm SL and were collected from May through December during 1983 and April through October during 1984 (salinity range: 1.5 to 31.7 ppt; temperature range: 5.4 to 29.0°C) (Appendix Tables 14.2 and 14.3). During May 1983, 40 stage III leptocephali, 23 juveniles, and 1419 stage II leptocephali were caught. The stage II leptocephali were taken in every month when ladyfish occurred in the collections. Most ladyfish were caught during sampling at the water-control structures (Appendix Table 14.1) and the greatest percentage of these occurred in flood tide samples (Table 14.4). During 1983 only 39 ladyfish were in creek samples, as opposed to 1516 at the water-control structures.

The Sciaenidae was the most-diverse and abundant family of fishes collected during the course of the study (eight genera, eight species). Because of damage to the specimens during collection or the loss of pigment after the clearing and staining process, 131 sciaenids could only be identified to the family level. In addition to L. xanthurus and M. undulatus, we collected Bairdiella chrysoura, Cynoscion nebulosus, C. regalis, Menticirrhus spp., Pogonias cromis, Sciaenops ocellatus and Stellifer lanceolatus (Table 14.2).

Other frequently occurring taxa included the darter goby, Gobionellus boleosoma (20.4% of the samples), the inland silverside, Menidia beryllina (8.3% of the samples), the green goby, Microgobius thalassinus (8.0% of the samples), Gerreidae Type I (7.8% of the samples), the speckled worm eel, Myrophis punctatus (5.8%), the mummichog, Fundulus heteroclitus (5.8%), the southern flounder, Paralichthys lethostigma (5.5%), the mosquitofish, Gambusia affinis (5.3%), the summer flounder, Paralichthys *dentatus* (5.2%), and the sheepshead minnow, *Cyprinodon variegatus* (5.1%). The remaining taxa occurred in less than 5% of the samples (Table 14.3).

During the first year, 49 species were common to creek and impoundment samples. Species unique to the creek were *Sciaenops ocellatus*, *Dorosoma petenense*, *Evorthodus lyricus*, *Paralichthys albigutta*, *Lutjanus griseus*, *Orthopristis chrysopterus*, *Etropus crossotus*, *Opsanus tau*, *Archosargus probatocephalus*, *Eleotris pisonis*, *Prionotus carolinus*, *P. scitulus*, and *P. tribulus*. These species constituted less than 0.32% of the total number of fishes collected during the first year.

The species composition and abundance of larvae and juveniles collected on flood flow into the impoundments at the water-control structures differed from the catches during flood tide into the marsh feeder creek. A total of 5275 individuals in 42 species were taken at impoundment stations, whereas 5124 individuals in 32 species were taken on flood tides in the marsh feeder creek (Appendix Table 14.1). Species found entering the impoundments but not the marsh feeder creek were *Poecilia latipinna*, *Megalops atlanticus*, *Gobiesox strumosus*, *Menidia menidia*, *Syngnathus fuscus*, *Mugil curema*, *Anchoa hepsetus*, *Fundulus confluentus*, *Diplodus holbrooki*, and *Ictalurus catus*. Species collected in the marsh feeder creek but not at the water-control structure during flood tides were *Sciaenops ocellatus*, *Citharichthys spilopterus*, *Stellifer lanceolatus*, and *Lutjanus griseus*.

Community Structure. Seasonal changes in ichthyoplankton abundance and diversity (total number of species, species richness) followed the same general trends at the three creek sampling sites (Fig. 14.9). The mean number of individuals per collection (catch per unit effort, which is an index of relative abundance) was highest during the winter months, when the transient species *L. xanthurus*, *M. undulatus*, and *L. rhomboides* were dominant. A second peak in abundance occurred during summer, when the larvae of the estuarine residents *G. bosci* and *A. mitchilli* were the dominant species. Diversity was highest during May of both years (Fig. 14.9); however, higher values occurred in 1983 than in 1984 because the sampling effort was greatly reduced in 1984. The dominance index peaked during late fall and winter of both years, when the community had large numbers of the three most-abundant estuarine transient species mentioned above.

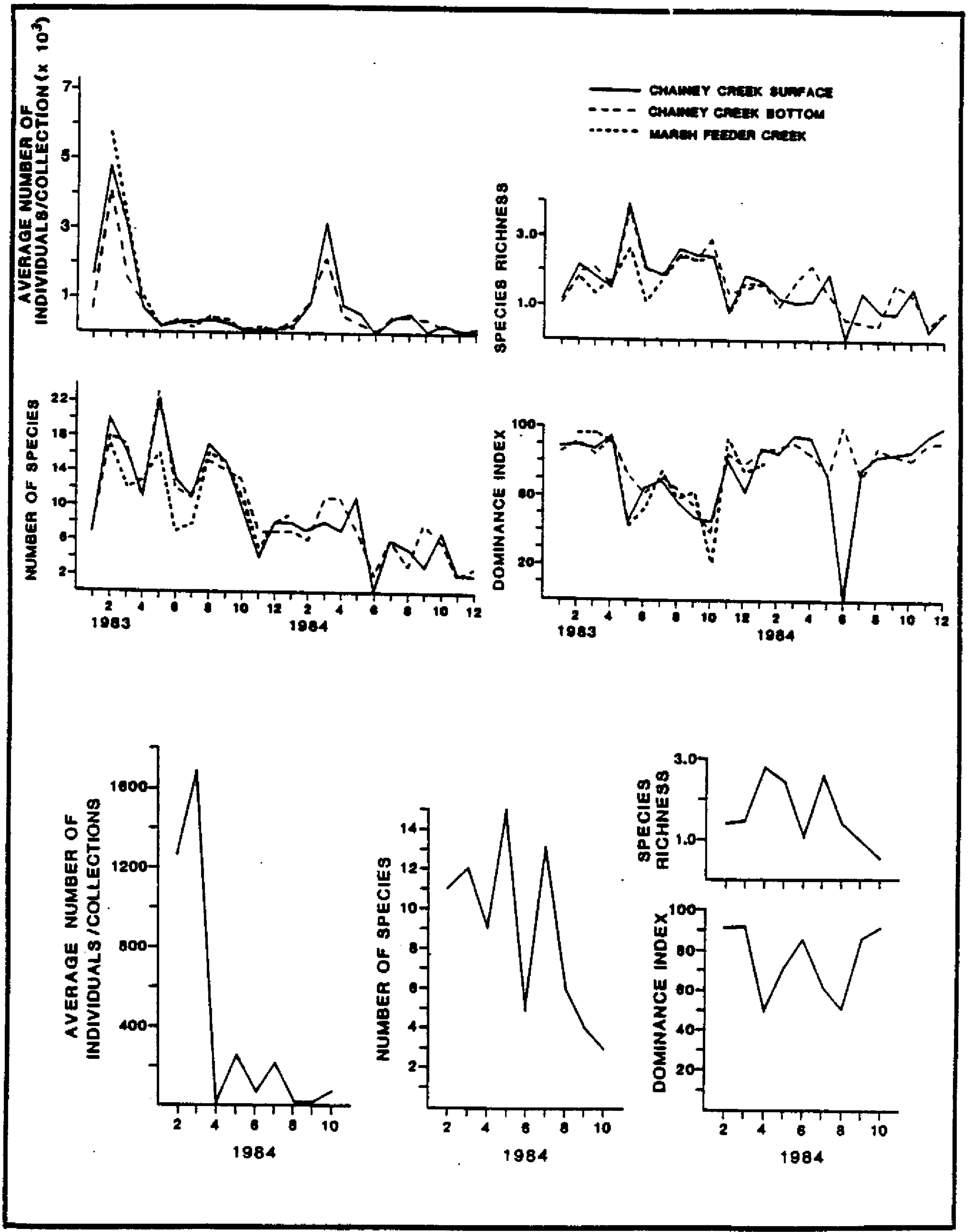

Figure 14.9 Average number of individuals per collection, total number of species, species richness and dominance for ichthyoplankton samples in the tidal creek (upper) and at the water control structures of impoundment 2 (lower). Data were pooled by month.

Ichthyoplankton samples collected at the water-control structures of the impoundments during 1983 had a maximum numerical mean catch per sample during May for both ebb and flood tides (Fig. 14.9). At this time, the outside gates of the water-control structures were open, thus permitting tidal movement of water into and out of the impoundments. In comparison, few individuals were collected at other times of the year. Flood tides during May had more species and the highest value for species richness, whereas more species were taken during ebb tides in June. Trends were obscured, however, by other peaks that occurred during periods that had few individuals. All measures of community diversity were temporally variable, with reduced number of individuals and species collected when water flow was restricted. Diversity values for collections at the trunk of impoundment 2 during 1984 were similar to those for creek stations, in that more species occurred in spring and summer (Fig. 14.9) when species richness was highest.

Cluster Analysis. Normal cluster analysis of the monthly pooled data from creek samples resulted in four seasonal groups (Fig. 14.10): winter early spring (group 1); late spring (group 2); summer early fall (group 3); late fall (group 4). Collections made during a particular month for both 1983 and 1984 were very similar and almost always were within the same group. As indicated by the hierarchical structure of the dendrogram, species composition of the collections making up each of the four groups was very dissimilar. Low similarity values showed that collections made during winter early spring (group 1) were very different from those made during any other time of 1983 and 1984.

Eight species groups (Table 14.5) were formed by inverse analysis, with the major division in the dendrogram being between those species that occurred in the winter months and those found at other times of the year (Fig. 14.11). Group A contained winter spawned transient species. Included in this group were the numerically dominant species *L. xanthurus*, *M. undulatus*, *L. rhomboides*, and *B. tyrannus*. Nodal analysis (Fig. 14.11) indicated that species in this group were most consistently collected in the winter but were not restricted to this season. Atlantic croaker showed a protracted period of recruitment to the creek habitat, with larvae and small juveniles present in collections from September through May. Atlantic menhaden were more frequently taken in March and April.

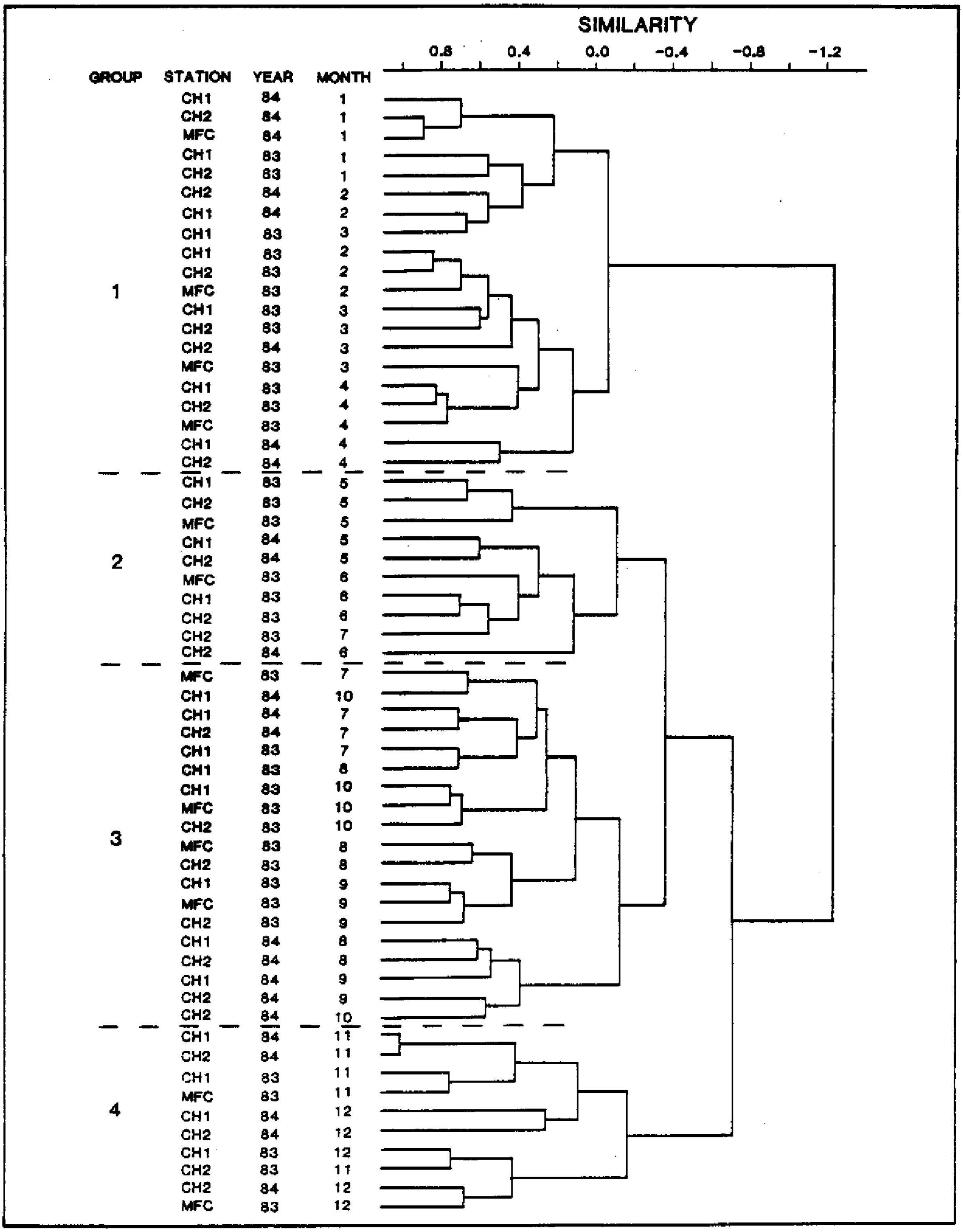

Figure 14.10 Station cluster (normal analysis) for creek ichthyoplankton stations (CH1 = Chainey Creek surface; CH2 = Chainey Creek bottom; MFC = marsh feeder creek) during 1983 and 1984. Jaccard similarity coefficient, flexible sorting with = 0.25. Data were pooled by month of collection.

Table 14.5

Species groups as defined by inverse cluster analysis for creek stations (Chainey Creek surface, Chainey Creek bottom, and marsh feeder creek) during 1983 and 1984.

Group A
- *Lagodon rhomboides*
- *Mugil cephalus*
- *Leiostomus xanthurus*
- *Paralichthys lethostigma*
- *Micropogonias undulatus*
- *Myrophis punctatus*
- *Brevoortia tyrannus*
- *Citharichthys spilopterus*
- *Paralichthys dentatus*

Group B
- *Paralichthys albigutta*
- *Dorosoma petenense*
- *Gambusia affinis*
- *Menidia beryllina*
- *Anguilla rostrata*
- *Cyprinodon variegatus*
- *Fundulus heteroclitus*

Group C
- *Dormitator maculatus*
- *Evorthodus lyricus*

Group D
- *Gobionellus hastatus*
- *Elops saurus*
- *Gobionellus shafeldti*
- *Lucania parva*
- *Trinectes maculatus*
- *Syngnathus louisianae*
- *Megalops atlanticus*

Group E
- *Chaetodipterus fabe*
- *Etropus crossotus*

Group F
- *Anchoa hepsetus*
- *Lutjanus griseus*
- *Orthopristis chrysopterus*
- *Pogonias cromis*
- *Gobiesox strumosus*
- *Syngnathus scovelli*
- *Bairdiella chrysoura*
- *Syngnathus fuscus*

Group G
- *Cynoscion regalis*
- *Gobiosoma bosci*
- *Anchoa mitchilli*
- *Gobionellus boleosoma*
- *Symphurus plagiusa*

Group H
- *Sciaenops ocellatus*
- *Gobiosoma ginsburgi*
- *Microgobius thalassinis*
- *Cynoscion nebulosus*
- *Stellifer lanceolatus*
- *Stephanolepis hispidus*

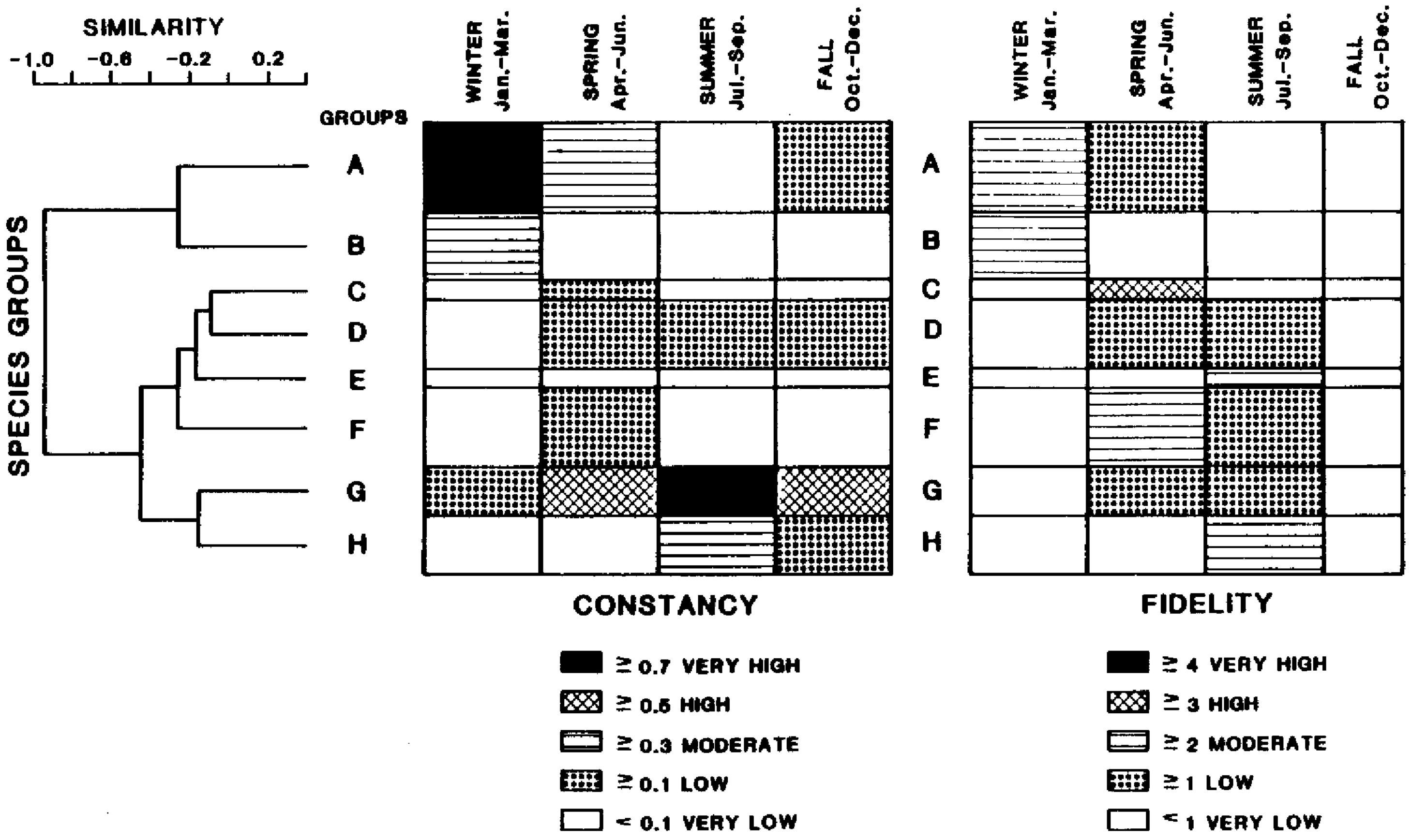

Figure 14.11 Nodal constancy and fidelity in a two-way table of species groups and season for 1983 and 1984 ichthyoplankton samples from Chainey Creek.

Spot were very abundant during the winter months, but significant numbers were collected in the spring as well.

The dendrogram indicated that species in group B had seasonal distribution patterns that were most similar to those of group A. Like group A, group B species were most-consistently collected during the winter and were moderately faithful to that season; however, in comparison to the species in group A, they had an overall low frequency of occurrence.

Species in group G were consistently collected in the spring, summer, and fall months, and because of their extended spawning period, they showed low fidelity to any season. Contained within the group were the numerically-dominant estuarine residents *A. mitchilli* and *G. bosci*, which were very abundant from June through September of both years. Species group H were most constant and faithful to the summer season and were members of the ichthyoplankton community from August through October.

Species in the remaining groups were collected infrequently. Although the two species in group C (*D. maculatus* and *E. lyricus*) had a relatively low frequency of occurrence in ichthyoplankton collections, they had a high fidelity value in spring and were not found in any other season. Species in group F were also uncommon, being almost exclusively taken during spring. Species in group D were sporadically taken in spring, summer, and fall collections.

Juvenile And Adult Fishes

Seine Collections. Seine hauls in the three experimental impoundments sampled during 1983 and 1984 caught 137,599 individuals in 52 species with a total weight of 294.2 kg. The mosquitofish, *Gambusia affinis*, was the most-numerous species, accounting for 42.1% of the total catch; because of its small size, however, it contributed only 2.7% of the total weight. The 10 most-numerous species of fishes comprised 93.4% and 77.1% of the number and weight, respectively, of fishes taken with seine nets (Table 14.6).

The mean number of species per site was highest in the spring for all impoundments (Table 14.7). There appeared to be a gradual decline in the mean number of species in the latter months of the year in all sites. Values of the catch per unit effort (CPUE) for weight were relatively

Table 14.6

Numbers and weights of fishes taken in seine hauls in the perimeter ditches of the experimental impoundments during 1983 and 1984.

Species	Number	Percentage of Catch	Weight (kg)	Percentage of Catch
Gambusia affinis	57,988	42.1	8.010	2.7
Menidia beryllina	14,058	10.2	7.454	2.5
Mugil cephalus	12,706	9.2	153.948	52.3
Leiostomus xanthurus	8,567	6.2	19.462	6.6
Fundulus heteroclitus	8,070	5.9	15.836	5.4
Lucania parva	7,842	5.7	1.807	0.6
Poecilia latipinna	5,590	4.1	4.095	1.4
Gobiosoma bosci	4,871	3.5	0.422	0.1
Micropogonias undulatus	4,509	3.3	13.645	4.6
Anchoa mitchilli	4,452	3.2	2.559	0.9
Cyprinodon variegatus	3,667	2.7	2.905	1.0
Elops saurus	1,758	1.3	13.388	4.5
Bairdiella chrysoura	961	0.7	11.141	3.8
Brevoortia tyrannus	942	0.7	15.801	5.4
Cynoscion regalis	421	0.3	1.695	0.6
Lagodon rhomboides	385	0.3	6.047	2.1
Fundulus confluentus	214	0.2	0.208	0.1
Megalops atlanticus	101	0.1	3.649	1.2
Gobionellus hastatus	63	--	0.334	0.1
Paralichthys lethostigma	63	--	2.940	1.0
Symphurus plagiusa	50	--	0.231	0.1
Dormitator maculatus	39	--	0.619	0.2
Microgobius thalassinus	35	--	0.022	--
Anguilla rostrata	30	--	2.435	0.8
Mugil curema	30	--	0.488	0.2
Cynoscion nebulosus	23	--	0.998	0.3

Table 14.6 Continued

Species	Number	Percentage of Catch	Weight (kg)	Percentage of Catch
Eucinostomus harengula	18	--	0.051	--
Morone americana	14	--	0.426	0.1
Gobionellus boleosoma	12	--	0.013	--
Anchoa hepsetus	11	--	0.011	--
Gobionellus shufeldti	10	--	0.012	--
Syngnathus scovelli	10	--	0.010	--
Evorthodus lyricus	9	--	0.018	--
Menidia menidia	9	--	0.011	--
Pogonias cromis	9	--	0.070	--
Diapterus auratus	8	--	0.027	--
Gobiosoma ginsburgi	7	--	0.003	--
Sciaenops ocellatus	6	--	0.126	--
Syngnathus louisianae	6	--	0.007	--
Trinectes maculatus	6	--	0.024	--
Citharichthys spilopterus	5	--	0.062	--
Engraulidae	3	--	0.001	--
Lepomis macrochirus	3	--	0.007	--
Opisthonema oglinum	3	--	0.011	--
Prionotus tribulus	3	--	0.005	--
Archosargus probatocephalus	2	--	0.002	--
Dorosoma petenense	2	--	0.006	--
Etropus crossotus	2	--	0.005	--
Fundulus luciae	2	--	0.001	--
Centropomus undecimalis	1	--	0.009	--
Lepomis gulosus	1	--	0.008	--
Morone saxatilus	1	--	0.071	--
Opsanus tau	1	--	0.107	--
	137,599		294.246	

Table 14.7 Summaries of seine collections by month and impoundment for 1983 and 1984. Total = total number of species, individuals, and weight (kg) in the pooled samples. Mean and standard deviations are calculated from the subsamples in a given impoundment. Species richness was calculated on the pooled data.

Year	Month	Impound	Species			Individuals			Weight			Species
			Total	$\bar{x}$	sd	Total	$\bar{x}$	sd	Total	$\bar{x}$	sd	Richness
1983	3	4	15	13	2	18,895	6,298	6,143	14.22	4.74	6.57	1.422
	5	4	26	18	3	8,112	2,704	919	13.38	4.46	1.89	2.777
	6	4	24	19	2	3,861	1,287	641	10.62	3.54	0.71	2.785
	6	3	28	20	2	4,313	1,438	224	13.63	4.54	0.90	3.226
	8	4	19	16	1	3,774	1,258	445	8.80	2.93	1.51	2.186
	8	3	14	10	1	2,889	963	437	3.63	1.21	1.18	1.631
	11	4	16	12	2	14,597	4,866	4,048	18.34	6.11	1.80	1.564
	11	3	15	13	2	13,226	4,409	676	12.24	4.80	1.61	1.475
1984	1	4	14	11	1	1,740	580	70	8.06	2.69	1.17	1.742
	1	3	12	11	1	6,515	2,172	416	45.07	15.02	8.65	1.253
	4	4	11	9	1	1,448	483	377	13.49	4.50	3.60	1.374
	4	3	12	10	1	3,951	1,317	871	18.92	6.31	3.10	1.338
	4	2	19	16	2	7,068	2,356	626	11.48	3.83	1.84	2.031
	6	4	20	15	2	3,046	1,015	441	6.28	2.09	0.44	2.369
	6	3	25	18	2	3,104	1,035	111	5.57	1.36	0.58	2.985
	6	2	26	21	1	3,516	1,172	184	10.43	3.48	0.98	3.062
	8	4	24	17	3	9,300	3,100	1,045	5.43	1.81	1.00	2.517
	8	3	17	13	3	2,266	755	171	5.10	1.70	0.96	2.071
	8	2	28	21	2	2,343	781	145	13.36	4.62	1.92	3.480
	10	4	27	20	3	13,048	4,349	4,792	8.61	2.87	0.76	2.744
	10	3	23	19	2	3,642	1,214	561	14.36	4.79	2.91	2.683
	10	2	26	19	2	2,065	688	166	18.57	6.19	3.41	3.275
	12	4	14	10	1	3,338	1,113	923	3.42	1.14	0.89	1.602
	12	3	12	11	1	425	142	34	2.61	0.87	0.04	1.318
	12	2	22	16	5	1,117	372	54	5.15	1.72	1.63	2.992

consistent from month to month and between impoundments, generally fluctuating from about 1 to 5 kg. The elevated value for January 1984 in impoundment 3 was caused by the collection of 2167 striped mullet, whose weight accounted for 96% of the mean value of 15.02 kg. The numerical CPUE was more variable in impoundments 3 and 4, with lower values in the late fall and winter. Impoundment 2 showed a gradual decline in numerical abundance with time (Table 14.7).

The annual cycle in species diversity had the highest values in the spring and summer; these declined to winter early spring minima and then increased. In impoundment 4 the number of species in the pooled seine collections was highest during May 1983. This was followed by a gradual decline, until the minimum value was seen in April 1984. The decline in the number of species was much more dramatic in impoundment 3. The 1983 maximum in June was followed by a reduction of greater than 50% in the total number of species in August 1983. This low value was relatively stable until the late spring of the following year (Table 14.7). Impoundment 2 generally had a greater total number of species with a maximum in August. Species richness was highest in June 1983 for impoundments 3 and 4, and it decreased in impoundment 3 during the summer of 1983. Generally, impoundment 2 had the highest species richness (Table 14.7).

Comparisons of the faunal assemblages of fishes in the pooled seine samples from March 1983 to December 1984 by cluster analysis resulted in two major divisions, each containing two site groups (Fig. 14.12). At first inspection, this grouping of collections appeared confusing; however, when water-management strategy, hydrography, and predation by birds were examined, the underlying rationale for this assemblage became apparent (see Discussion).

Inverse analysis resulted in eight species groups containing from three to eight species. The major division in the dendrogram was between the widely occurring species (groups A and B) and the remainder that, for the most part, were less abundant in all site groups. With the exception of _C. variegatus_ in April 1984 samples from impoundments 2 and 4 (Table 14.8), species of group A occurred in all site groups regardless of the season or impoundment. This resulted in very high constancy and low fidelity to all site groups (Fig. 14.13). Those fishes were the core

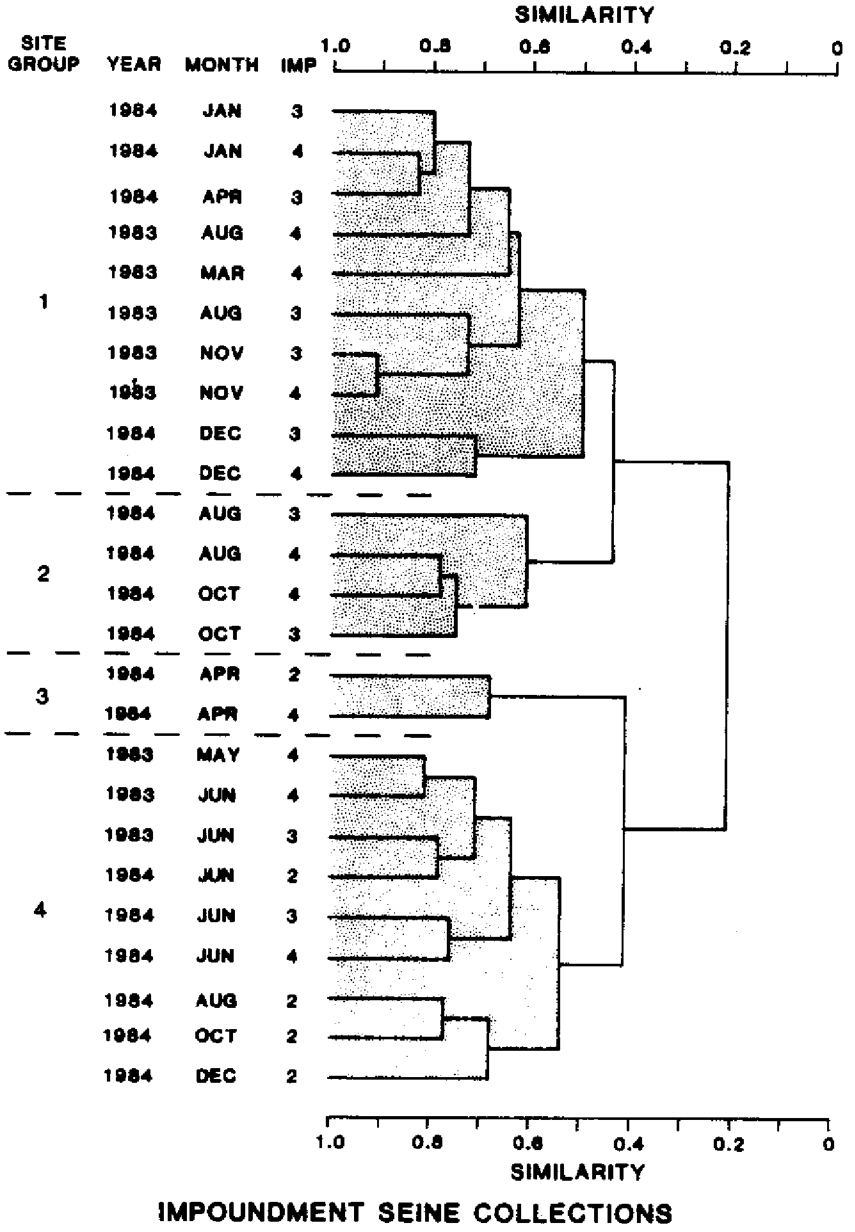

Figure 14.12 Normal cluster analysis of the seine collections inside the study impoundments; Bray-Curtis similarity coefficient, flexible sorting, β = 0.25.

Table 14.8 Two-way table (site groups across top; species groups down) showing the total number of individuals (n), and the mean (x) andstandard deviation (sd) of the number of each species taken in the seine samples that comprised the collections of a group as defined by the dendrogram. Sample sizes as follows: site group 1 = 30; site group 2 = 12; site group 3 = 6; site group 4 = 27. * = < 1.

Species Group	Species	Site Groups 1			2			3			4		
		n	$\bar{x}$	sd	n	$\bar{x}$	sd	n	$\bar{x}$	sd	n	$\bar{x}$	sd
A	Gambusia affinis	31,387	1046	1285	19888	1657	2486	260	43	49	6453	239	202
	Menidia beryllina	7,664	255	407	1965	164	139	263	44	28	4166	154	168
	Mugil cephalus	6,365	212	388	190	14	16	761	127	118	5390	200	251
	Gobiosoma bosci	685	23	46	2725	227	231	31	5	6	1430	53	69
	Cyprinodon variegatus	2,782	93	123	788	66	32	--	--	—	97	4	6
	Fundulus heteroclitus	6,503	217	694	1070	89	169	60	10	10	437	16	21
	Poecilia latipinna	4,465	149	421	600	50	64	1	*	*	524	19	34
	Lucania parva	7,537	251	478	16	1	2	123	20	14	166	6	8
B	Leiostomus xanthurus	1,142	38	76	33	3	4	5320	887	838	2072	77	91
	Micropogonias undulatus	394	13	20	90	8	17	1250	208	242	2775	103	134
	Brevoortia tyrannus	10	*	*	17	7	13	287	48	73	628	23	32
	Lagodon rhomboides	10	*	*	--	--	--	115	19	27	260	10	11
	Anchoa mitchilli	3	*	*	352	29	55	2	*	*	4095	152	160
	Bairdiella chrysoura	68	2	3	182	15	16	--	--	--	711	26	34
	Elops saurus	26	1	2	163	14	14	--	--	—	1569	58	77
C	Menidia menidia	1	*	*	--	--	--	--	--	--	8	*	*
	Trinectes maculatus	--	--	--	--	--	--	--	--	--	6	*	*
	Evorthodus lyricus	--	--	--	--	--	--	--	--	--	9	*	*
	Archsargus probatocephalus	--	--	--	--	—	--	--	--	--	2	*	*
	Pogonias cromis	1	*	*	--	--	--	--	--	--	8	*	*
	Morone americana	--	--	--	4	*	*	--	--	--	10	*	*
D	Syngnathus louisianae	--	--	--	1	*	*	--	--	—	5	*	*
	Citharichthys spilopterus	--	--	--	--	—	—	--	--	--	5	*	*
	Anguilla rostrata	13	*	*	1	*	*	3	1	1	13	*	*
	Paralichthys lethostigma	--	--	--	—	--	--	22	4	5	41	2	2
	Anchoa hepsetus	--	--	--	--	--	--	--	—	--	11	*	*

Table 14.8 Continued

Species Group	Species	Site Groups 1			2			3			4		
		n	$\bar{x}$	sd	n	$\bar{x}$	sd	n	$\bar{x}$	sd	n	$\bar{x}$	sd
E	*Diapterus auratus*	--	--	--	6	1	1	--	--	--	2	*	
	Eucinostomus harengula	--	--	--	9	1	2	--	--	--	9	*	*
	Mugil curema	5	*	*	16	1	2	--	--	--	9	*	*
	Cynoscion regalis	3	*	*	19	2	3	--	--	--	399	15	24
	Gobionellus hastatus	3	*	*	6	1	1	--	--	--	54	2	3
	Microgobius thalassinus	5	*	*	10	1	2	8	1	2	12	*	*
F	*Gobionellus shufeldti*	2	*	*	--	--	--	3	1	1	5	*	*
	Sciaenops ocellatus	1	*	*	--	--	--	2	*	*	3	*	*
	Lepomis macrochirus	1	*	*	--	--	--	2	*	*	--	--	--
G	*Prionotus tribulus*	--	--	--	2	*	*	--	--	--	1	*	*
	Etropus crossotus	--	--	--	1	*	*	--	--	--	1	*	*
	Cynoscion nebulosus	2	*	*	10	1	1	--	--	--	11	*	*
	Gobionellus boleosoma	3	*	*	5	*	*	--	--	--	4	*	*
	Symphurus plagiusa	13	*	*	8	1	2	2	*	*	27	1	3
	Gobiosoma ginsburgi	--	--	--	6	1	2	--	--	--	1	*	*
H	*Dormitator maculatus*	7	*	*	13	1	1	--	--	--	19	1	1
	Megalops atlanticus	46	2	2	40	3	5	--	--	--	15	1	1
	Fundulus confluentus	194	6	28	16	1	2	--	--	--	4	*	*
	Syngnathus scovelli	8	*	*	--	--	--	--	--	--	2	*	*

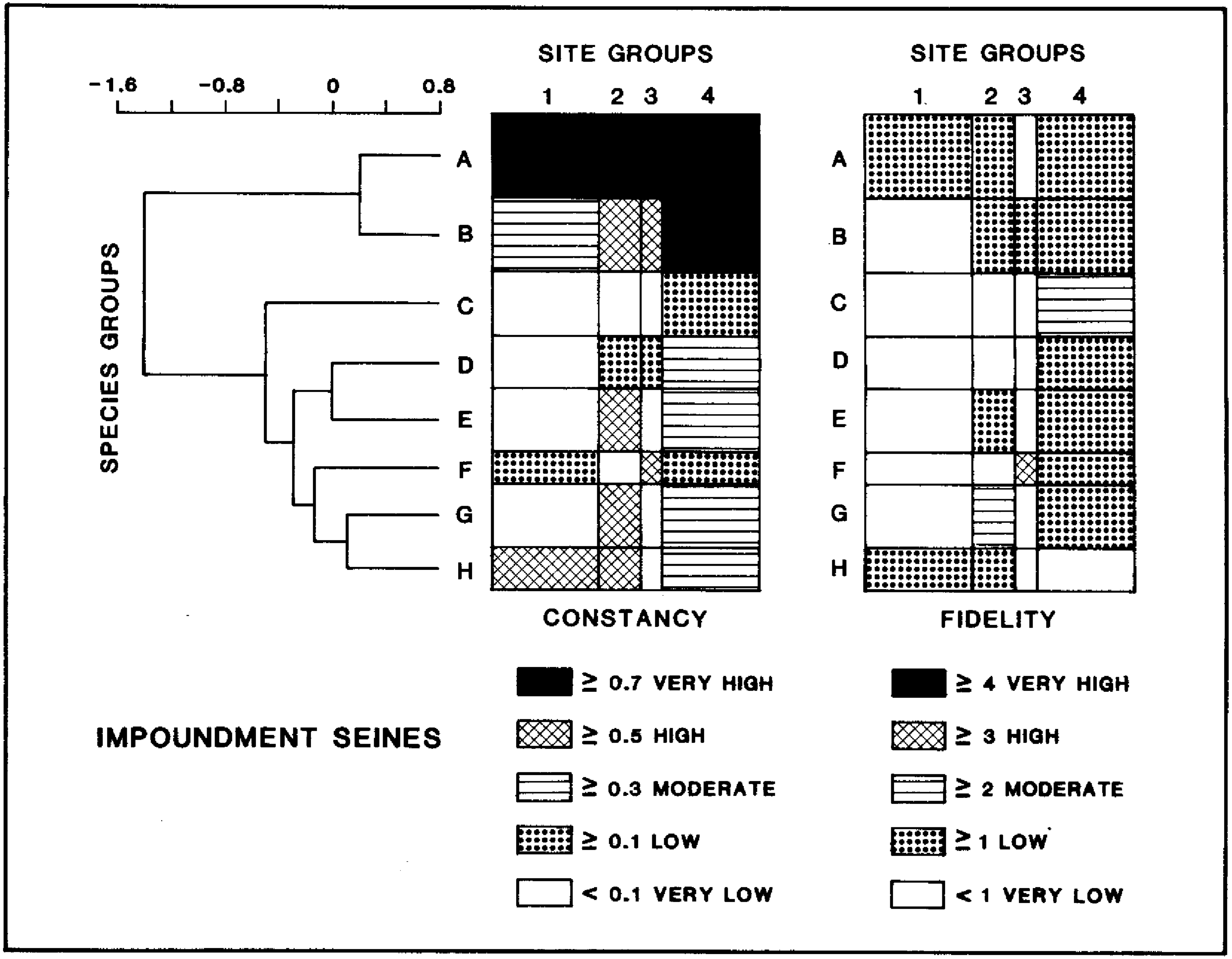

Figure 14.13 Nodal constancy and fidelity for site and species groups as defined by cluster analysis for the pooled seine collections in the study impoundments.

group of fishes that typified the ichthyofauna of the study impoundments. Group B had seven species that were mainly recruited to the impoundments during spring flooding and the subsequent tidal exchanges as permitted by the water-management scheme. Members of this group were found in all site groups (hence the low or very low fidelity values); however, highest constancy and abundance were in site group 4 (Fig. 14.13 and Table 14.8). The remaining six groups had species that generally had a lower abundance and frequency of occurrence in seine collections.

Cast-Net Collections. Cast-net sampling in the experimental impoundments and Chainey Creek caught 7081 individuals in 42 species (Table 14.9) with a total weight of 101.2 kg. The three most-numerous species (B. tyrannus, M. cephalus, and L. xanthurus) accounted for 83.8% and 85.3% of the total number and weight of fishes, respectively, taken with this gear. Samples in Chainey Creek yielded a greater number of species (34) than those from the experimental impoundments (28). Seasonal changes in the diversity of the ichthyofauna (as defined by the number of species) in all locations showed seasonal trends (Fig. 14.14). In Chainey Creek a greater number of species was taken in cast-net samples in spring of 1983 and late spring through early fall during 1984. Minimum values were observed in late fall and winter. The same general pattern was found inside the experimental impoundments, with lower numbers of species being found during the winter months except in impoundment 3, where low DO values in August and September 1983 caused a marked decline in the number of species.

The catch per unit effort was highest in Chainey Creek during 5 of the 11 sampling periods. The annual mean number CPUE was an order of magnitude higher in Chainey Creek ($\bar{x}$ = 411, sd = 698) than any of the impoundments (unit 2: $\bar{x}$ = 70 sd = 113; unit 3: $\bar{x}$ = 33 sd = 28; unit 4: $\bar{x}$ = 36 sd = 20). The annual mean weight CPUE was also higher in cast-net samples from the creek ($\bar{x}$ = 2.00 kg sd = 1.78) than the impounded sites (unit 2: $\bar{x}$ = 1.11 kg sd = 1.16; unit 3: $\bar{x}$ = 0.6 kg sd = 0.51; unit 4: $\bar{x}$ = 0.8 kg sd = 0.41). The relative abundance of Atlantic menhaden was generally higher in creek samples than inside the impoundments, where elevated catch rates were seen only during June 1984 in impoundment 2. Data for both years indicated that Chainey Creek is an important nursery area for young-of-the-year Atlantic menhaden. Striped mullet were absent

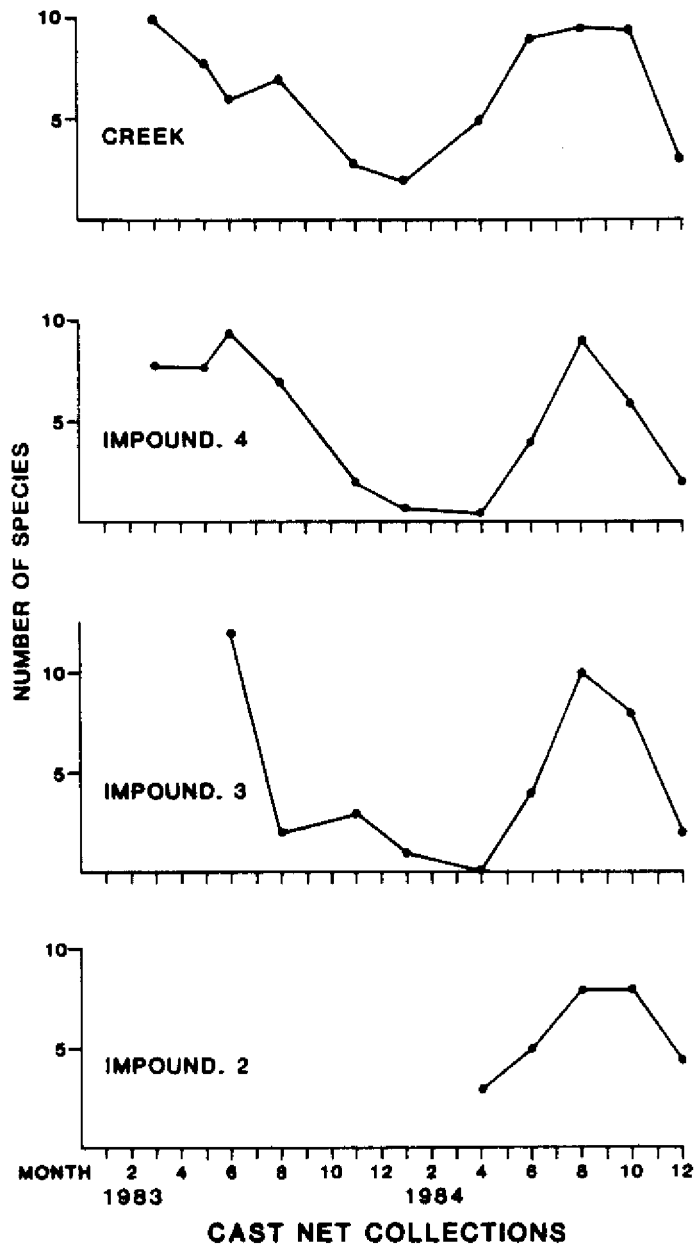

Figure 14.14 Number of species collected with 1.5 m, 0.95-cm-bar mesh cast nets in Chainey Creek and the study impoundments by sampling date.

Table 14.9

Numbers of fishes (total and by site)
taken with 1.5-m-radius, 0.95-cm bar mesh cast nets.

Species	Total Number	Unit 4	Unit 3	Unit 2	Chainey Creek
Brevoortia tyrannus	2781	3	8	320	2450
Mugil cephalus	1881	625	524	261	471
Leiostomus xanthurus	1272	96	73	30	1073
Menidia beryllina	211	5			206
Micropogonias undulatus	209	78	88	40	3
Mugil curema	184	6	10	1	167
Bairdiella chrysoura	160	95	37	13	15
Cyprinodon variegatus	84	33	3		48
Fundulus heteroclitus	67	39	18		10
Elops saurus	55	19	25	8	3
Cynoscion regalis	31	19	8	3	1
Lucania parva	25	21			4
Menidia menidia	24	3			21
Gambusia affinis	18				18
Lagodon rhomboides	16		1	14	1
Anchoa mitchilli	9		3	5	1
Opisthonema oglinum	6		1		6
Eucinostomus harengula	5		1	2	2
Gobiosomi bosci	5	5			
Poecilia latipinna	5		3		2
Dorosoma petenense	3				3
Pomatomus saltatrix	3				3
Anchoa hepsetus	2	2			
Citharichthys macrops	2	1			1
Dorosoma cepedianum	2				2
Paralichthys lethostigma	2				2
Pogonias cromis	2	1	1		
Sciaenops ocellatus	2				2
Symphurus plaguisa	2			1	1

Table 14.9 Continued

Species	Total Number	Unit 4	Unit 3	Unit 2	Chainey Creek
Trinectes maculatus	2	2			
Anguilla rostrata	1		1		
Caranx hippos	1				1
Citharichthys spilopterus	1				1
Cynoscion nebulosus	1				1
Diapterus auratus	1				1
Dormitator maculatus	1		1		
Etropus crossotus	1				1
Gobionellus hastatus	1	1			
Morone americana	1				1
Morone saxatilis	1				1
Paralichthys dentatus	1				1

only once (impoundment 3, April 1984) during the entire study. The annual mean numerical CPUE showed catch rates to be relatively similar in all sites (Chainey Creek: $\bar{x}$ = 24, sd = 24; unit 2: $\bar{x}$ = 17, sd = 24; unit 3: $\bar{x}$ = 23, sd = 27; unit 4: $\bar{x}$ = 21, sd = 14). Atlantic croaker occurred more frequently and generally in greater numbers (especially in spring and early summer) inside the impoundments than in Chainey Creek. A single collection made in the creek during March 1983 caught 83.5% of the total number of spot; however, other catches were much lower, and this species was not taken with our gear during November and January in any of the sites. Silver perch were taken almost exclusively during the late summer and early fall, primarily inside the impoundments.

Gill-Net Collections. The 1.27-cm bar mesh monofilament gill net caught 1365 individuals in 20 species with a weight of 9.5 kg. Juvenile Atlantic menhaden were two orders of magnitude more numerous than bluefish, the second most abundant species. Atlantic menhaden comprised 91.9% and 71.8% of the total number and weight, respectively, of fishes collected with this gear (Table 14.10). Plots of catch/set values showed that more species and more individuals with a greater total weight were taken during the late spring and summer (Fig. 14.15). Lowest catch rates were found from late fall through late winter. Young of the year Atlantic menhaden occurred in all but two collections (November 1983 and December 1984), and the highest catch rates were from May through August in 1983 and April through June in 1984. Juvenile bluefish were taken in small numbers during the late spring and summer.

Low catch rates (8 species, 29 individuals, total weight 19.1 kg) were found with the 3.81-cm bar mesh monofilament gill net. Striped mullet was the most numerous species; whereas the longnose gar, Lepisosteus osseus, contributed the greatest weight (Table 14.11). The large-mesh gill net was the only fishing gear that caught longnose gar.

Otter-Trawl Tows. Otter trawl tows in Chainey Creek caught 2088 fishes in 33 species with a total weight of 8.6 kg. The 10 most numerically abundant species accounted for 94.6% and 64.8% of the total number and weight, respectively, of fishes taken with the trawl gear. Spot ranked first in both numerical abundance and by weight (Table 14.12). The mean number of species was highest in the three trawl collections made in June 1984 and lowest in November 1983 (Fig. 14.16).

Table 14.10

Fishes taken in Chainey Creek with a 1.27-cm bar mesh monofilament gill net during 3-hr sets from March 1983 to December 1984.

Species	Number	Percentage of Catch	Weight (kg)	Percentage of Catch
Brevoortia tyrannus	1255	91.9	6.812	71.8
Pomatomus saltatrix	22	1.6	1.048	11.0
Bairdiella chrysoura	14	1.0	0.216	2.3
Lepomis macrochirus	11	0.8	0.062	0.7
Leiostomus xanthurus	8	0.6	0.054	0.6
Micropogonias undulatus	8	0.6	0.071	0.7
Mugil cephalus	8	0.6	0.113	1.2
Caranx hippos	7	0.5	0.037	0.4
Dorosoma petenense	7	0.5	0.140	1.5
Elops saurus	7	0.5	0.708	7.5
Mugil curema	4	0.3	0.034	0.4
Morone americana	3	0.2	0.039	0.4
Dorosoma cepedianum	2	0.1	0.008	0.1
Fundulus heteroclitus	2	0.1	0.028	0.3
Lagodon rhomboides	2	0.1	0.010	0.1
Cynoscion regalis	1	0.1	0.012	0.1
Dormitator maculatus	1	0.1	0.035	0.4
Opisthonema oglinum	1	0.1	0.008	0.1
Strongylura marina	1	0.1	0.049	0.5
Syngnathus scovelli	1	0.1	0.003	--
Total	1365		9.487	

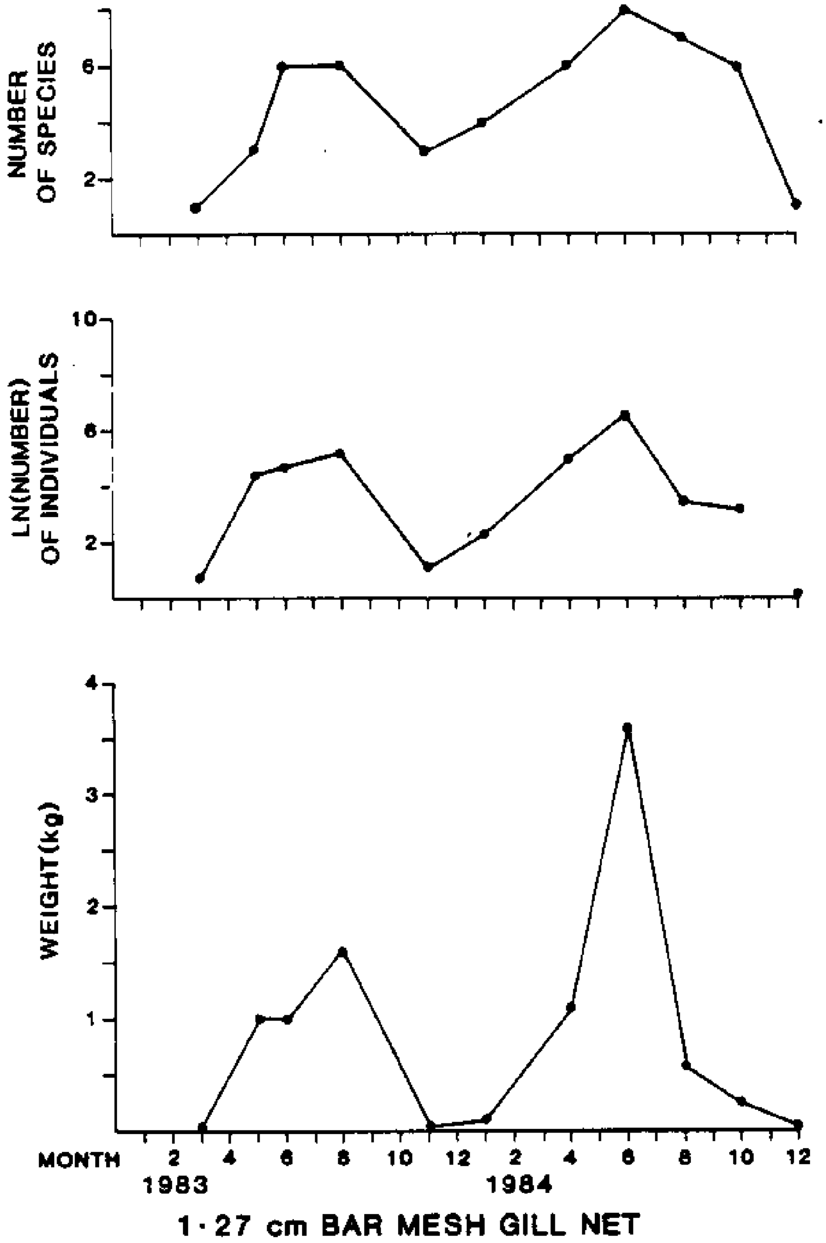

Figure 14.15 Plots of the number of species, natural log-transformed values of the number of individuals, and the weight of fishes collected in three-hour sets of a 1.27-cm-bar mesh gill net fished in Chainey Creek.

Table 14.11

Fishes taken in Chainey Creek with a 3.81-cm bar mesh monofilament gill net during 3-hr sets from March 1983 to December 1984.

Species	Number	Percentage of Catch	Weight (kg)	Percentage of Catch
<u>Mugil cephalus</u>	11	37.9	4.260	22.4
<u>Lepisosteus osseus</u>	8	27.6	12.936	67.9
<u>Ariopsis felis</u>	2	6.9	0.624	3.3
<u>Dorosoma cepedianum</u>	2	6.9	0.485	2.5
<u>Paralichthys lethostigma</u>	2	6.9	0.238	1.2
<u>Sciaenops ocellatus</u>	2	6.9	0.255	1.3
<u>Elops saurus</u>	1	3.4	0.211	1.1
<u>Pomatomus saltatrix</u>	1	3.4	0.047	0.2
Total	29		19.056	

There was a trend for fall collections to have fewer taxa available and to be vulnerable to the sampling gear. Late-spring collections had the greatest mean number of individuals, but they were also the most variable. The average weight was highest in October 1984 and lowest in November 1983 (Fig. 14.16). The standard deviations of both the number and weight of fishes taken with trawl gear were significantly correlated ($p = .01$) with their mean values (number: $r = 0.94$, $df = 9$; weight: $r = 0.94$; $df = 9$).

Normal cluster analysis (station cluster) of the trawl collections that were pooled by sampling date resulted in three seasonal site groups (Fig. 14.17). Site group 1 contained those samples from late fall, winter, and early spring. Site group 2 was a spring group, and the last group was a late summer/fall assemblage. Inverse analysis (species cluster) gave four groups containing from two to seven species each (Table 14.13). Species group A contained the relatively abundant species that were found during all seasons with the exception of <u>C. regalis</u> and <u>B. chrysoura</u> that were absent in site group 1. Group B had five species that

Table 14.12

Numbers and weights of fishes taken in 36 trawl tows made in Chainey Chainey from March 1983 to December 1984.

Species	Number	Percentage of Catch	Weight (kg)	Percentage of Catch
Leiostomus xanthurus	814	39.0	1.691	19.6
Anchoa mitchilli	409	19.6	0.273	3.2
Micropogonias undulatus	263	12.6	0.709	8.2
Bairdiella chrysoura	219	10.5	1.211	14.1
Brevoortia tyrannus	97	4.6	0.199	2.3
Cynoscion regalis	62	3.0	0.138	1.6
Gobiosoma bosci	33	1.6	0.023	0.3
Trinectes maculatus	30	1.4	0.087	1.0
Morone americana	26	1.2	1.202	14.0
Fundulus heteroclitus	24	1.1	0.046	0.5
Lagodon rhomboides	14	0.7	0.313	3.6
Mugil cephalus	12	0.6	0.546	6.3
Ictalurus catus	11	0.5	0.555	6.4
Symphurus plagiusa	9	0.4	0.028	0.3
Menidia beryllina	8	0.4	0.005	0.1
Gobionellus boleosoma	8	0.4	0.004	--
Etropus crossotus	8	0.4	0.011	0.1
Sciaenops ocellatus	7	0.3	0.177	2.1
Citharichthys macrops	5	0.2	0.005	0.1
Citharichthys spilopterus	5	0.2	0.013	0.2
Anguilla rostrata	4	0.2	0.882	10.2
Paralichthys lethostigma	4	0.2	0.029	0.3
Opsanus tau	3	0.1	0.247	2.9
Syngnathus scovelli	3	0.1	0.006	0.1
Cyprinodon variegatus	2	0.1	0.002	--
Opisthonema oglinum	1	--	0.003	--
Ariopsis felis	1	--	0.171	2.0

Table 14.12 Continued

Species	Number	Percentage of Catch	Weight (kg)	Percentage of Catch
Fundulus majalis	1	--	0.001	--
Lutjanus griseus	1	--	0.027	0.3
Chaetodipterus faber	1	--	0.004	--
Mugil curema	1	--	0.003	--
Stephanolepis hispidus	1	--	0.001	--
Dorosoma petenense	1	--	0.001	--
Total	2088		8.613	

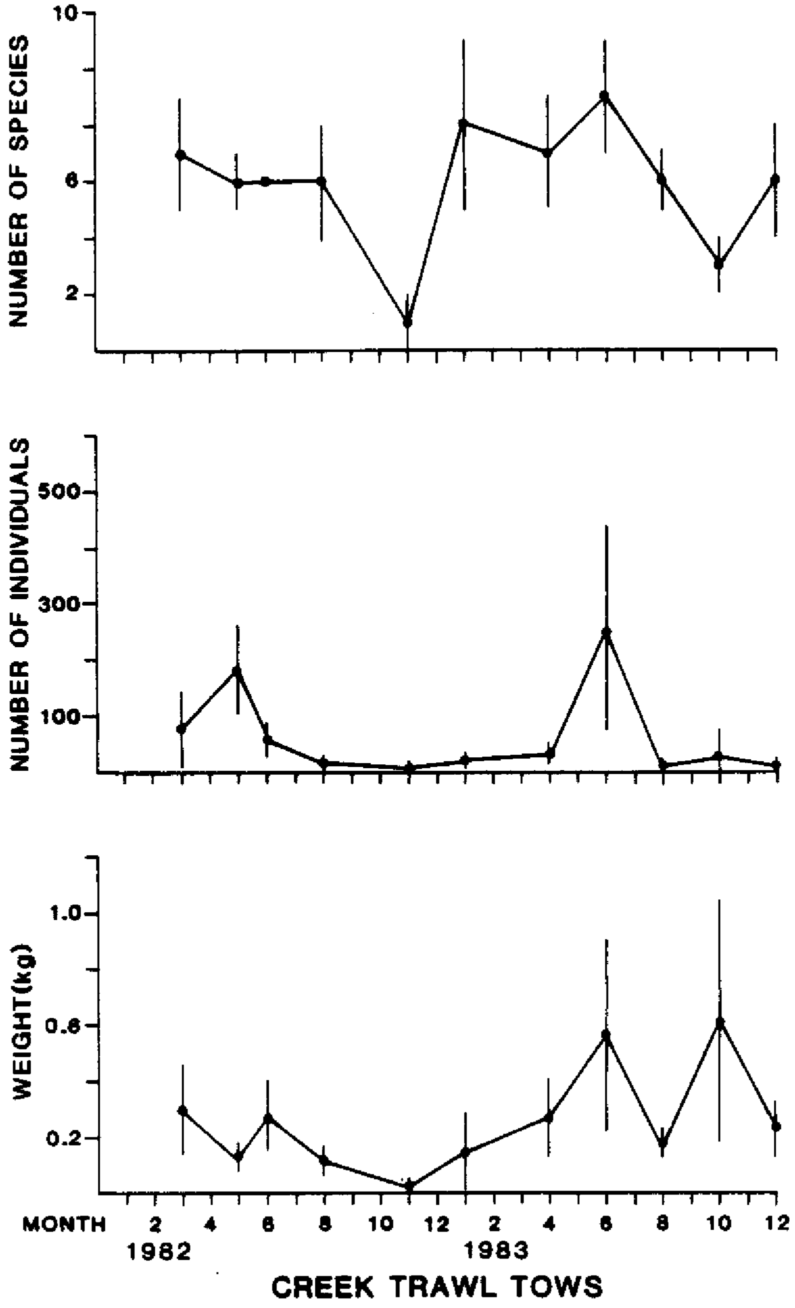

Figure 14.16 Plots of the mean (dot) and standard deviation (vertical bar) of the number of species, number of individuals, and total weight of fishes from trawl collections in Chainey Creek by month.

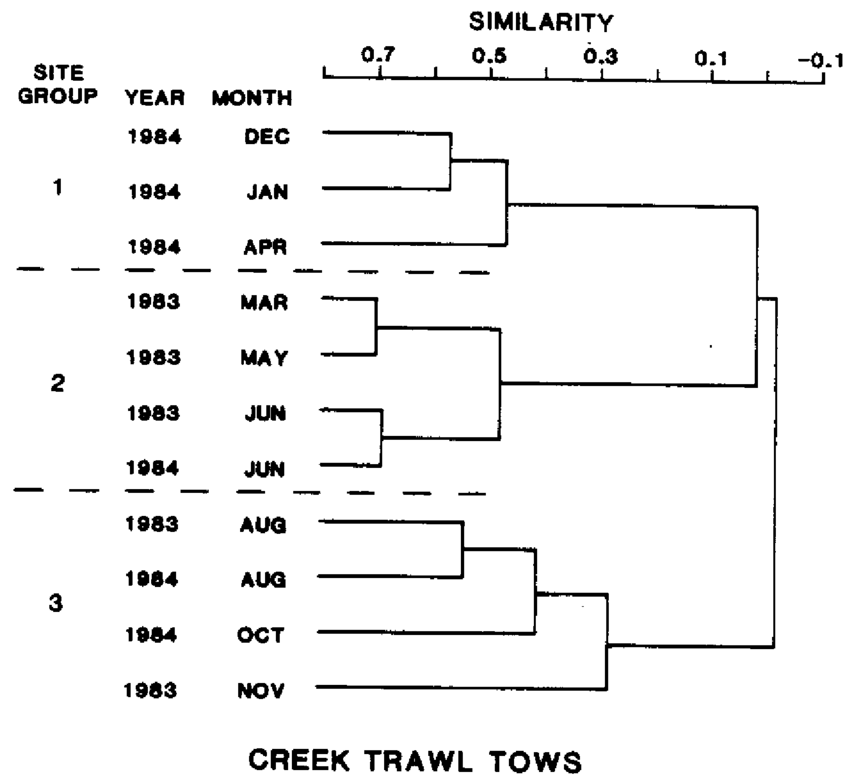

Figure 14.17 Normal cluster analysis for pooled trawl tows in [illegible] Chainey Creek. Bray-Curtis similarity coefficient, log-transformed data, flexible sorting with = 0.25.

Table 14.13 Two-way table (site groups across top; species groups down) showing the total number of individuals (n) and the mean and standard deviation of the number of each species taken in the trawl samples, that comprised the collections of a group as defined by the dendrogram. Site group 1 based on 9 samples whereas groups 2 and 3 have 12 each. *=<1.

Species Group	Species	Station Groups 1			2			3		
		n	$\bar{x}$	sd	n	$\bar{x}$	sd	n	$\bar{x}$	sd
A	Anchoa mitchilli	5	*	*	379	32	47	25	2	5
	Leiostomus xanthurus	11	1	2	790	66	89	13	1	1
	Micropogonias undulatus	80	7	13	193	16	9	10	1	1
	Trinectes maculatus	6	1	1	22	2	3	2	*	*
	Brevoortia tyrannus	1	*	*	94	8	11	2	*	*
	Cynoscion regalis	-	-	-	61	5	9	1	*	*
	Bairdiella chrysoura	-	-	-	148	12	29	71	6	15
B	Opsanus tau	-	-	-	1	*	*	2	*	*
	Citharichthys spilopterus	-	-	-	3	*	*	2	*	*
	Symphurus plagiusa	-	-	-	2	*	*	7	1	1
	Etropus crossotus	2	*	*	-	-	-	6	1	1
	Lagodon rhomboides	-	-	-	4	*	*	10	1	1
C	Gobionellus bolesosma	-	-	-	8	1	1	-	-	-
	Citharichthys macrops	-	-	-	5	*	*	-	-	-
D	Sciaenops ocellatus	5	1	1	2	*	*	-	-	-
	Mugil cephalus	11	1	1	1	*	*	-	-	-
	Gobiosoma bosci	17	2	1	6	1	1	10	1	3
	Morone americana	20	2	2	1	*	*	5	*	*
	Paralichthys lethostigma	4	*	*	-	-	-	-	-	-
	Syngnathus scovelli	2	*	*	1	*	*	-	-	-
	Anguilla rostrata	2	*	*	1	*	*	1	*	*

occurred mainly during spring, summer, and fall in relatively low numbers. Species in group C were taken only in spring samples, whereas fishes in group D occurred primarily in site group 1. Nodal analysis (Fig. 14.18) showed that species group A had its greatest constancy in site group 2, although it was an assemblage of fishes that occurred in trawl collections throughout the year, as demonstrated by its very low and low fidelity to any of the site groups. Group D had very high constancy and moderate fidelity to site group 1, indicating that it is an assemblage taken primarily during late fall, winter, and early spring in Chainey Creek.

Rotenone Collections. Rotenone sampling in the small subtidal creeks that drain the high marsh caught 23,660 fishes in 57 species with a total weight of 67.3 kg (Table 14.14). The 10 most-numerous fish species accounted for 94.5% and 89.1% of the total number and weight, respectively, of fishes taken with this gear. The mummichog was the most abundant species, whereas striped mullet contributed the greatest weight. The mean number of species of fishes taken in the three samples ranged from a low of 11 in December 1984 to a high of 22 in October 1984, and the variability within these collections was low, as evidenced by the small standard deviations (Fig. 14.19). Such was not the case with the values of the number and weight of fishes. The standard deviations were significantly correlated ($p = .01$, $df = 5$), with the means for each variable (mean number, $r = 0.90$; mean weight, $r = 0.99$). The mean number was highest in June and lowest in December, whereas the mean weight was highest in January and lowest in December (Fig. 14.19).

Temporal trends in catches of the 20 most-numerous species (Fig. 14.20) showed that several of these were present throughout the year. Some of these (*F. heteroclitus*, *M. beryllina*, *G. bosci*, *G. boleosoma*, *C. variegatus*, and *G. affinis*) were residents within the study area; that is, they were able to carry out their entire life history within the area. These were generally abundant and occurred at all sampling times. *Mugil cephalus* and *P. lethostigma* were found throughout the year, but neither species could be classified as a resident, because both move offshore to spawn at the appropriate size and age. Other transient species (*M. curema*, *B. chrysoura*, *E. saurus*) utilized these shallow-water habitats

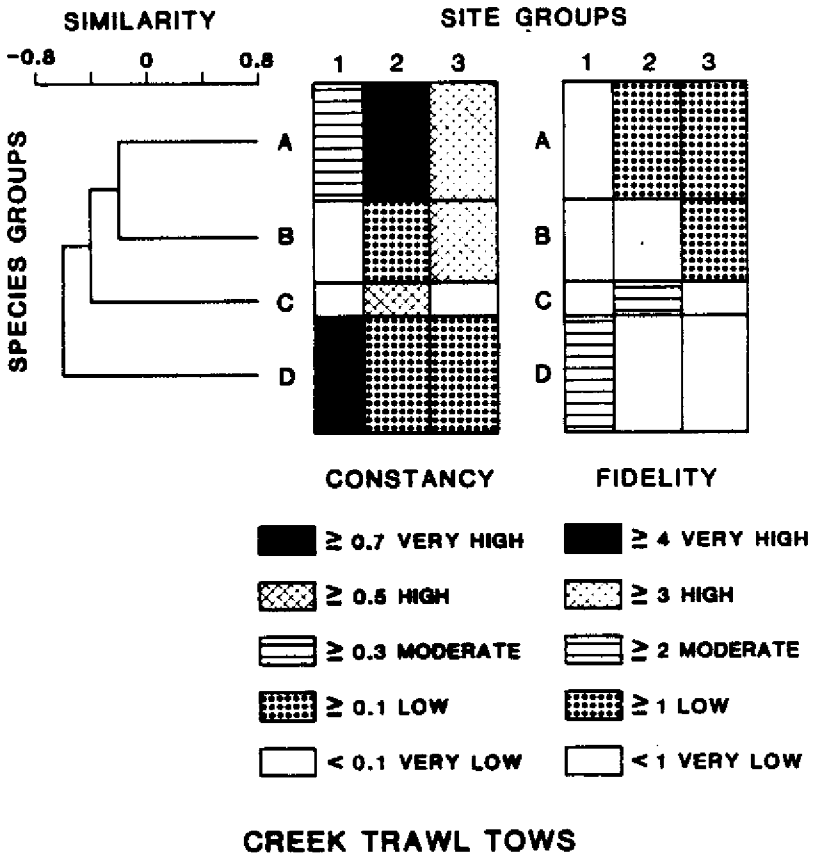

Figure 14.18 Nodal constancy and fidelity in a two-way table of site and species groups as defined by cluster analysis of trawl data in Chainey Creek.

Table 14.14

Fishes taken in small, subtidal feeder creeks that connect the high marsh to Chainey Creek with rotenone during late-ebb tide from August 1983 to December 1984.

Species	Number	Percentage of Catch	Weight (kg)	Percentage of Catch
Fundulus heteroclitus	9395	39.7	12.353	18.3
Mugil cephalus	3586	15.2	40.114	59.6
Leiostomus xanthurus	2202	9.3	4.535	6.7
Menidia beryllina	2177	9.2	0.715	1.1
Gobiosoma bosci	1590	6.7	0.408	0.6
Anchoa mitchilli	1148	4.9	0.075	0.1
Brevoortia tyrannus	1128	4.8	0.442	0.7
Gobionellus boleosoma	431	1.8	0.067	0.1
Mugil curema	396	1.7	1.238	1.8
Symphurus plagiusa	282	1.2	0.047	0.1
Myrophis punctatus	136	0.6	0.120	0.2
Menidia menidia	127	0.5	0.138	0.2
Micropogonias undulatus	122	0.5	0.360	0.5
Paralichthys lethostigma	108	0.5	1.549	2.3
Cyprinodon variegatus	101	0.4	0.060	0.1
Bairdiella chrysoura	95	0.4	0.603	0.9
Gambusia affinis	82	0.3	0.021	--
Eucinostomus sp.	81	0.3	0.004	--
Sciaenops ocellatus	63	0.3	0.044	0.1
Elops saurus	57	0.2	2.773	4.1
Lucania parva	53	0.2	0.014	--
Lagodon rhomboides	37	0.2	0.230	0.3
Morone americana	26	0.1	0.621	0.9
Syngnathus scovelli	26	0.1	0.013	--
Lutjanus griseus	20	0.1	0.029	--
Dormitator maculatus	18	0.1	0.003	--
Poecilia latipinna	17	0.1	0.010	--

Table 14.14 Continued

Species	Number	Percentage of Catch	Weight (kg)	Percentage of Catch
Syngnathus fuscus	16	0.1	0.007	--
Gobionellus shufeldti	16	0.1	0.008	--
Evorthordus lyricus	14	0.1	0.018	--
Gobiosoma ginsburgi	14	0.1	0.002	--
Gobionellus hastatus	13	0.1	0.010	--
Citharichthys spilopterus	9	--	0.037	0.1
Syngnathus louisianae	8	--	0.004	--
Dorosoma cepedianum	7	--	0.146	--
Gobiesox strumosus	7	--	0.012	--
Fundulus majalis	5	--	0.003	--
Anguilla rostrata	4	--	0.234	0.3
Cynoscion nebulosus	4	--	0.037	0.1
Microgobius thalassinus	4	--	0.004	--
Paralichthys dentatus	4	--	0.010	--
Dorosoma petenense	4	--	0.035	0.1
Caranx hippos	3	--	0.004	--
Pogonias cromis	3	--	0.131	0.2
Hypsoblennius hentzi	3	--	0.006	--
Fundulus luciae	3	--	0.002	--
Chasmodes bosquianus	2	--	0.003	--
Prionotus tribulus	2	--	0.001	--
Etropus crossotus	2	--	0.002	--
Lepomis macrochirus	2	--	0.003	--
Ictalurus catus	1	--	0.011	--
Rissola marginata	1	--	0.001	--
Archosargus probatocephalus	1	--	0.001	--
Chaetodipterus faber	1	--	0.010	--
Sphyraena guachancho	1	--	0.001	--
Hypleurochilus geminatus	1	--	0.001	--
Hypsoblennius ionthas	1	--	0.001	--
TOTAL	23,660		67.331	

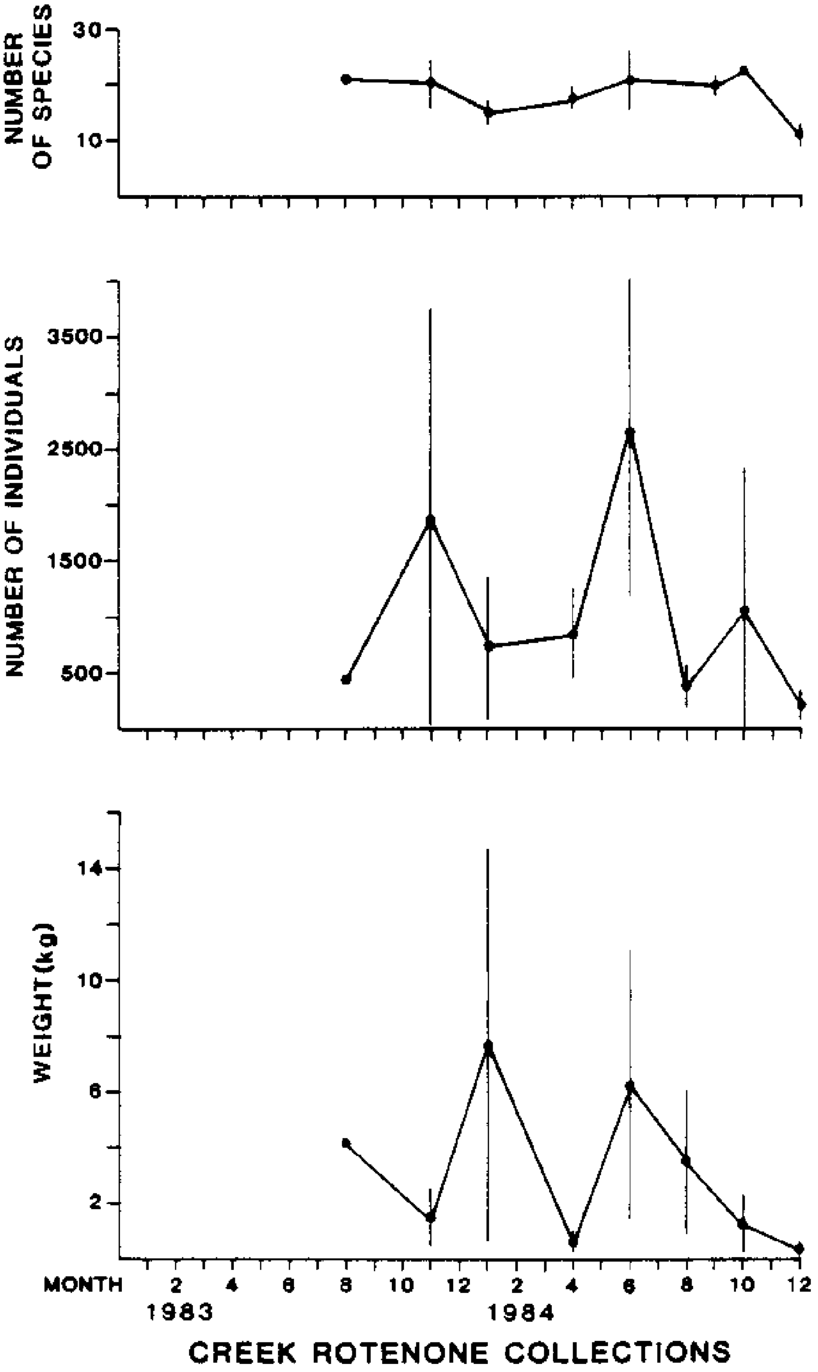

Figure 14.19 Plots of the means (dots) and standard deviations (vertical lines) of the number of species, number of individuals, and total weight of fishes by month from rotenone collections in the feeder creeks. August 1983, only a single sample taken; other months, n=3.

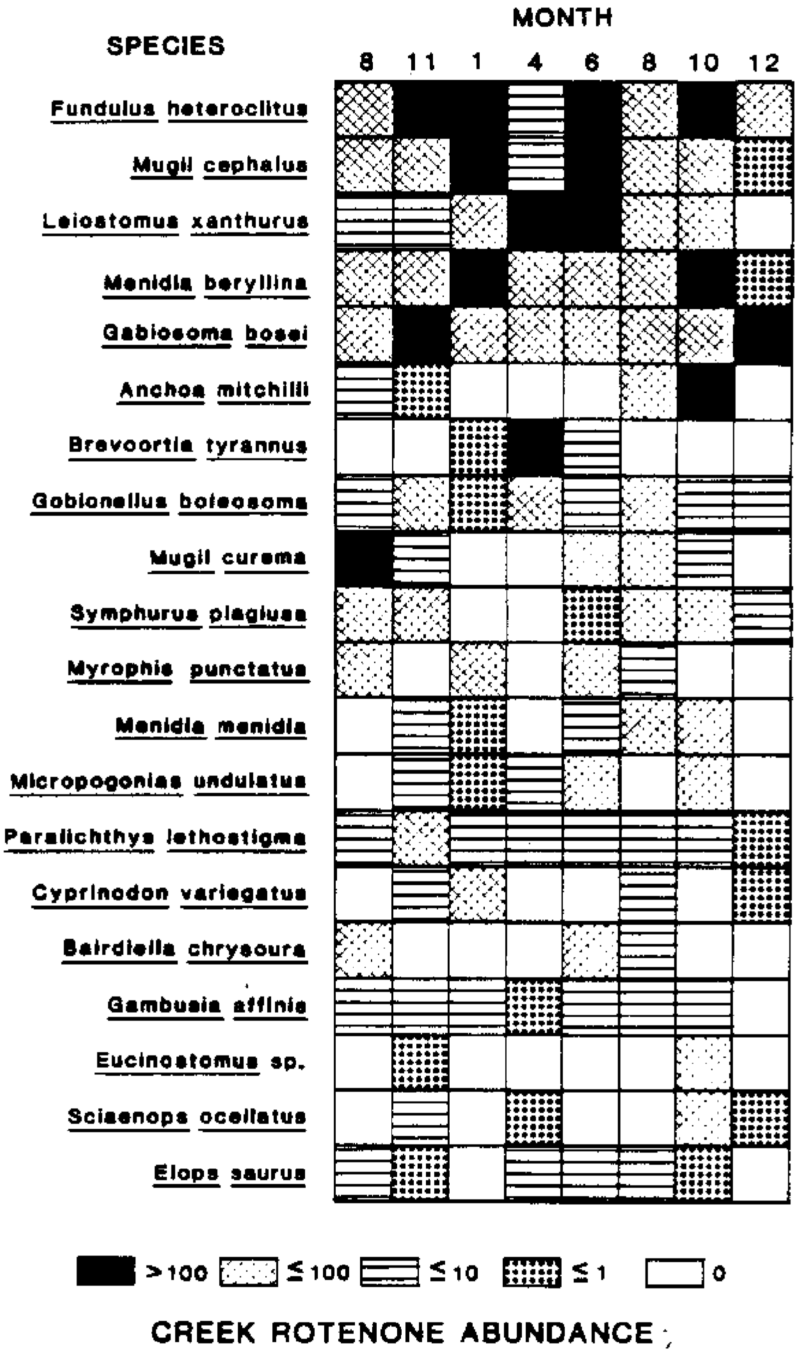

Figure 14.20 Temporal trends in the occurrences and abundance of the twenty most numerous fishes taken in rotenone collections. Coded values are the sums of the number of individuals of a given taxon divided by the number of 30.5 m-long sites samples.

during certain periods of the year and moved, presumably, down estuary and south during colder weather.

Comparisons of the assemblages of fishes in pooled rotenone collections from November 1983 to December 1984 (August 1983 was deleted from the analysis because of unequal effort) by cluster analysis gave three site groups that were largely seasonal (Fig. 14.21). Inverse analysis (species cluster) gave five groups containing from 3 to 15 species (Table 14.15). Nodal analysis showed that the species of group A were consistent members of the ichthyofauna of the shallow water feeder creeks in the study area throughout the year. This was shown by the high and very high constancy values of this species group in all site groups (Fig. 14.22). Species groups B, C, and D were absent from site group 1, and all had moderate-to-high constancy in the remaining site groups. Species group E had very high constancy in late summer and fall collections (site group 3) and high December values. Only three individuals (two S. ocellatus, one C. nebulosus) of this group were taken in the winter and spring rotenone collections. All species groups had low or very low fidelity values for all site groups (Fig. 14.22) which indicated that they generally do not have rigorously restrictive temporal distributions in the study area.

Between-Site Comparisons. Because the seine sites inside the experimental impoundments had comparable areas to those sampled by rotenone in small tributaries off Chainey Creek (~540 m^2), we compared the pooled monthly samples from each of the four locales (impoundments 2, 3, and 4 and marsh feeder creeks) by one-way analysis of variance. There was a significant difference in the total number of species between sites (Table 14.16). Linear contrasts by the Scheffe' method (Guenther, 1964) showed three groupings. Collections from the creek had significantly more species and greater species richness than all impoundments with the exception of impoundment 2. There were no significant differences in the log-transformed values of number of individuals or the total weight between the sites (Table 14.17). It should be pointed out, however, that the tidal creek has a continual turnover of species throughout the year, a phenomenon that does not occur on the same scale inside the impoundments, because of water-management strategies.

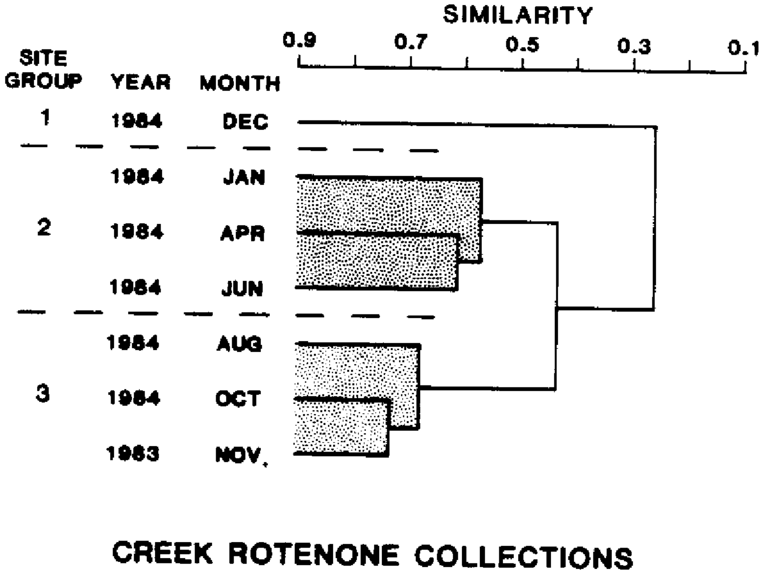

Figure 14.21 Normal cluster analysis of the rotenone collections in small feeder creeks. Bray-Curtis correlation, log-transformed data, flexible sorting with B = 0.25.

Table 14.15 Two way table (site groups across tops; species groups down) showing the total number of individuals (n), and the mean and standard deviation of the number of each species taken in the rotenone samples that comprised the collections of a group as defined by the dendogram. Site group 1 based on 3 samples whereas groups 2 and 3 have 9 each. *=<1

Species Group	Species	Site Groups								
		1			2			3		
		n	$\bar{x}$	sd	n	$\bar{x}$	sd	n	$\bar{x}$	sd
A	*Menidia beryllina*	3	1	1	954	106	251	1178	131	224
	Mugil cephalus	3	1	1	3260	362	811	299	33	38
	Fundulus heteroclitus	94	31	4	4035	448	574	5253	584	994
	Gobiosoma bosci	68	123	57	343	38	35	827	92	68
	Leiostomus xanthurus	-	-	-	2065	229	212	130	14	16
	Gobionellus boleosoma	12	4	2	104	12	24	305	34	52
	Gambusia affinis	-	-	-	32	4	4	48	5	4
	Menidia menidia	-	-	-	12	1	2	115	13	13
	Mugil curema	-	-	-	189	21	54	61	7	7
	Anchoa mitchilli	-	-	-	-	-	-	1146	127	247
	Symphurus plagiusa	7	2	3	1	*	*	233	26	36
	Lagodon rhomboides	1	*	*	28	3	6	3	*	*
	Paralichthys lethostigma	2	1	1	60	7	12	36	4	4
	Lucania parva	-	-	-	43	5	4	10	1	2
	Cyprinodon variegatus	1	*	*	81	9	26	19	2	3
B	*Myrophis punctatus*	-	-	-	105	12	24	10	1	2
	Bairdiella chrysoura	-	-	-	37	4	10	7	1	1
	Dorosoma cepedianum	-	-	-	1	*	*	6	1	1
C	*Morone americana*	-	-	-	23	3	4	3	*	*
	Gobionellus hastatus	-	-	-	12	1	2	1	*	*
	Elops saurus	-	-	-	20	2	3	29	3	6
	Micropogonias undulatus	-	-	-	108	12	19	14	2	3
	Syngnathus scovelli	-	-	-	9	1	1	17	2	5
	Brevoortia tyrannus	-	-	-	1128	125	203			
	Evorthodus lyricus	-	-	-	5	1	1	9	1	2
	Gobionellus shufeldti	-	-	-	2	*	*	14	2	2

Table 14.15 Continued

Species Group	Species	Site Groups								
		1			2			3		
		n	$\bar{x}$	sd	n	$\bar{x}$	sd	n	$\bar{x}$	sd
	Citharichthys spilopterus	-	-	-	3	*	*	6	1	1
	Syngnathus louisianae	-	-	-	6	1	1	1	*	*
D	*Dorosoma petenense*	-	-	-	1	*	*	2	*	*
	Paralichthys dentatus	-	-	-	3	*	*	1	*	*
	Fundulus majalis	-	-	-	4	*	*	1	*	*
	Anguilla rostrata	-	-	-	4	*	*	-	-	-
E	*Poecilia latipinna*	1	*	*	-	-	-	16	2	3
	Lutjanus griseus	1	*	*	-	-	-	16	2	2
	Sciaenops ocellatus	1	*	*	2	*	*	60	7	16
	Eucinostomus sp.	-	-	-	-	-	-	81	9	26
	Gobiesox strumosus	6	2	3	-	-	-	1	*	*
	Syngnathus fuscus	7	2	2	-	-	-	9	1	2
	Chasmodes bosquianus	-	-	-	-	-	-	2	*	*
	Microgobius thalassinus	-	-	-	-	-	-	4	*	*
	Cynoscion nebulosus	-	-	-	1	*	*	2	*	*

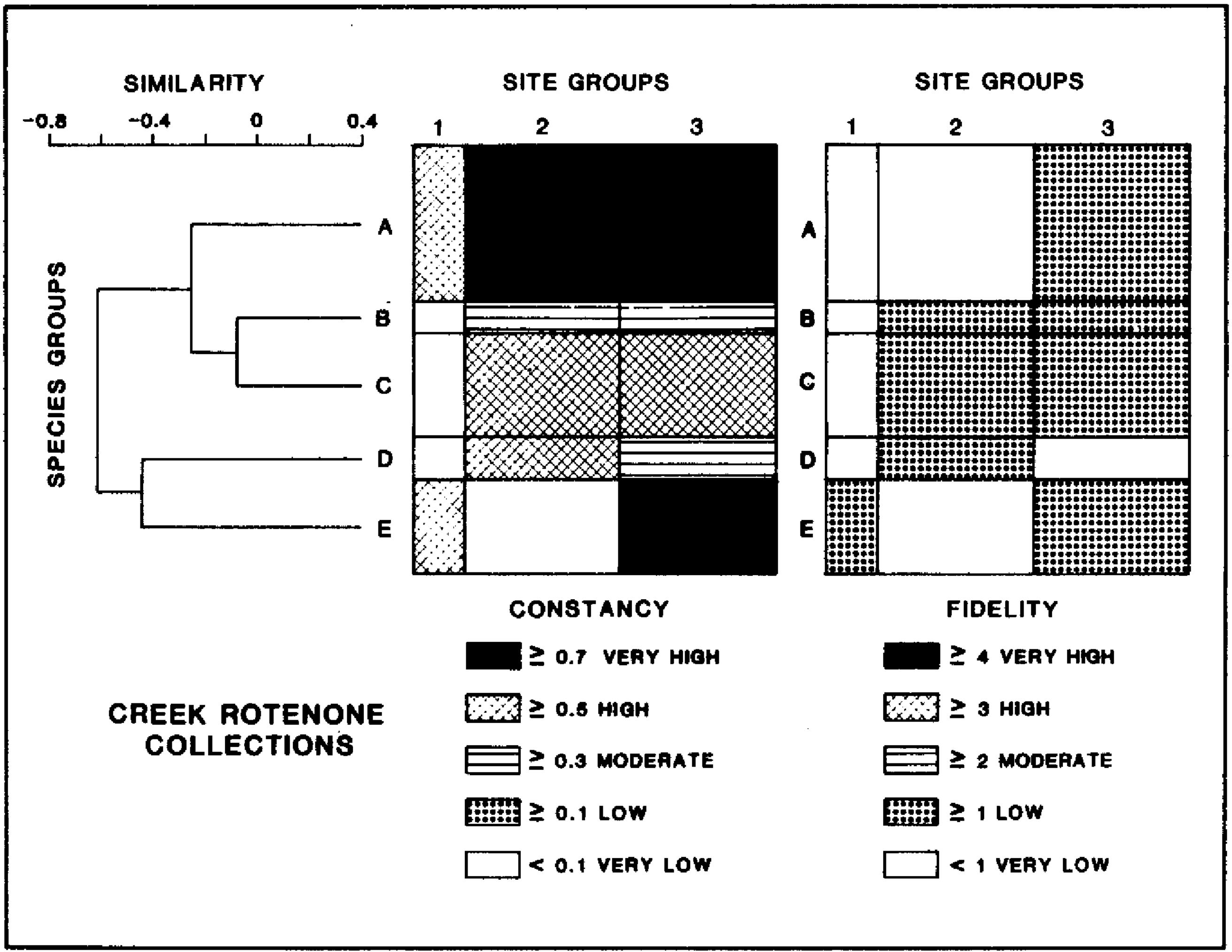

Figure 14.22 Nodal constancy and fidelity in a two-way table of site and species groups as defined by cluster analysis of rotenone collections in small feeder creeks.

Table 14.16

Results of one-way analysis of variance for comparisons of total number of species and species richness between sampling sites. Linear contrasts (Scheffe' method) were used to isolate significantly different means. IMP = impoundment; * = significant at p = 0.05

Number of Species:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Site	3	809.4	269.8	19.13*
Error	28	393.6	14.1	
Total	31	1,203.0		

Site	IMP 3	IMP 4	IMP 2	CREEK
Mean	17.6	19.1	24.2	26.3

Species Richness:

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Sites	3	8.499	2.833	5.469*
Error	28	14.516	0.518	
Total	31	23.015		

Site	IMP 3	IMP 4	IMP 2	CREEK
Mean	2.051	2.097	2.967	3.241

Table 14.17

Results of one-way analysis of variance for comparisons of log-transformed values of the number of individuals and total weight (grams) between sampling sites.

ns = not significantly different at p = 0.05

Number of Individuals (log number):

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Sites	3	0.511	0.170	1.133 ns
Error	28	4.204	0.150	
Total	31	4.715		

Total Weight (log weight [g]):

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Sites	3	0.419	0.139	1.058 ns
Error	28	3.696	0.132	
Total	31	4.115		

Presence-absence cluster analysis of the species lists derived from all fishing gears in each of the four sites gave six groups that contained from 2 to 11 collections (Fig. 14.23). The main division of the dendrogram separated most of both the creek and impoundment 2 collections from those in impoundments 3 and 4. Within the major division that contained the creek collections, four groups were formed. Three of these were seasonal groups from the creek system (5 = winter-early spring; 6 = late spring; 4 = summer-fall). A single collection from impoundment 2 from April 1984 was included in group 5. The remaining group was from impoundments 2, 3, and 4. The other main division had two groups, one of which was composed primarily of collections from late summer through early spring and the other of those from spring through late summer. Only 2 of 20 collections in these two groups were not from impoundments 3 and 4.

Inverse analysis resulted in eleven species groups that contained from 2 to 11 species (Table 14.18). Examination of the frequency of occurrence of members of species group A in the collections that comprised the six site groups clearly demonstrated their ubiquity during the study. Seven of the ten species (*F. heteroclitus*, *M. beryllina*, *G. bosci*, *G. affinis*, *L. parva*, *C. variegatus*, *P. latipinna*) were estuarine endemics. Their widespread occurrence in all site groups resulted in this species assemblage having high and very high constancy and low fidelity (Fig. 14.24). This species group contained the most abundant and frequently occurring taxa in the study area. They comprised 88.0% of the 171,822 fishes taken with all gear types in all sampling locales.

Dormitator maculatus was the only species in group B that was collected in the Chainey Creek system. This group had high and moderate constancy to site groups 1, 2, and 3 which were, with one exception, all inside the impoundments. The low-fidelity values showed that these fishes did not have a strong affinity for any one site group. Species group C had two species of gerreids plus a third type that we were unable to identify to species, plus the chain pipefish and the seaboard goby. Members of this group were taken in summer and fall collections both inside the impoundments and in the creek system. The highest constancy and fidelity values were in site group 3 which were collections made inside the impoundments during the late summer and fall of 1984.

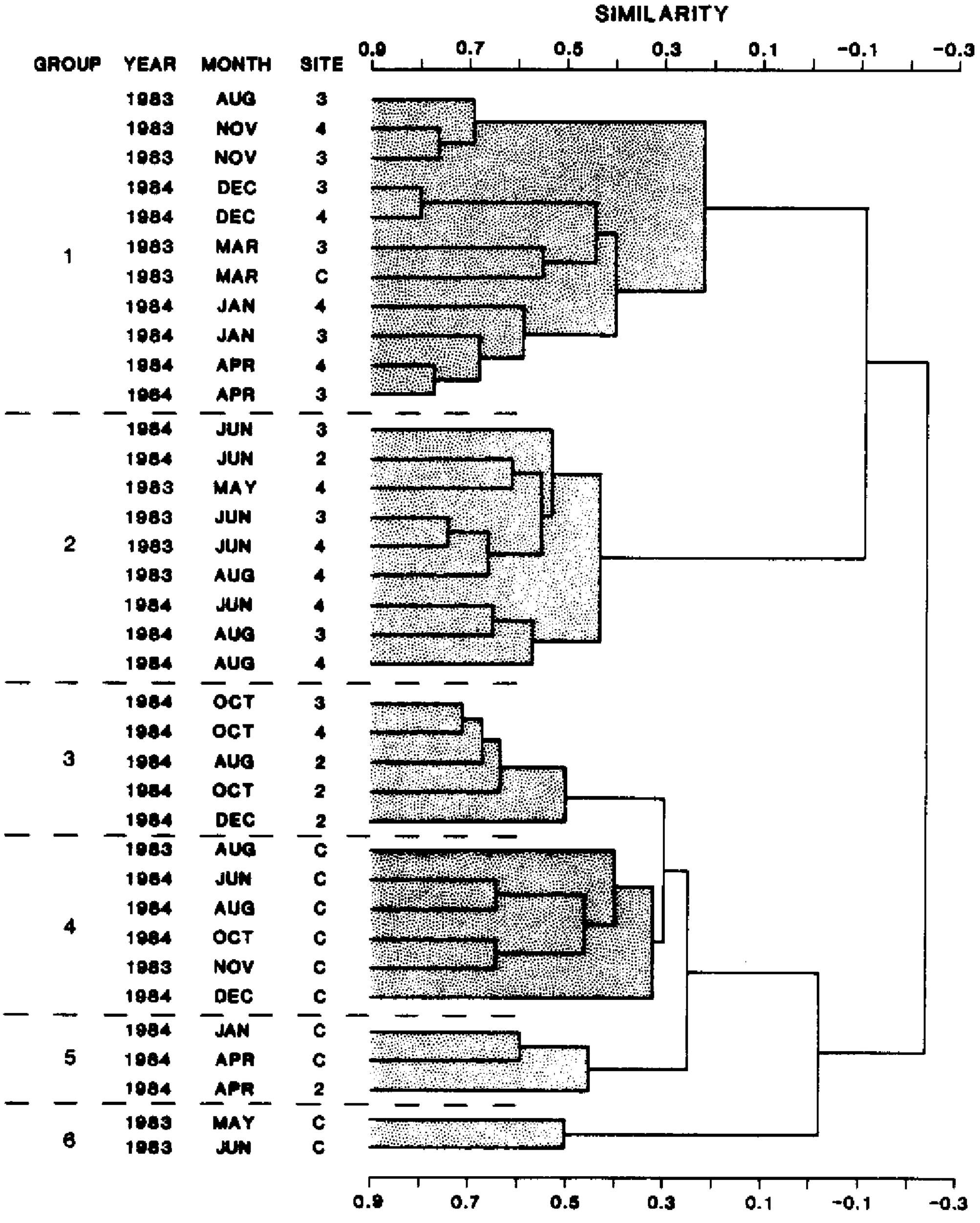

Figure 14.23 Normal cluster analysis of fishes collected by all gear types at each site by sampling date. Jaccard similarity coefficient, flexible sorting, B = 0.25. Sites: 2 = impoundment 2; 3 = impoundment 3; 4 = impoundment 4; C = open tidal creek system.

Table 14.18

Species groups as defined by inverse presence-absence cluster analysis and the number of occurrences of each species in N samples comprising each site group.

Species Groups	Species	Site Groups					
		1	2	3	4	5	6
		N = 11	N = 9	N = 5	N = 6	N = 3	N = 2
A	*Fundulus heteroclitus*	11	9	5	6	3	1
	Mugil cephalus	11	9	5	6	3	2
	Menidia beryllina	11	9	5	6	3	-
	Gobiosoma bosci	10	9	5	6	3	-
	Gambusia affinis	11	9	5	5	3	1
	Leiostomus xanthurus	8	9	5	6	3	2
	Micropogonias undulatus	8	9	5	5	3	2
	Lucania parva	11	7	5	3	3	-
	Cyprinodon variegatus	10	9	5	3	1	-
	Poecilia latipinna	11	8	5	3	-	1
B	*Dormitator maculatus*	2	4	3	1	1	-
	Megalops atlanticus	3	3	4	-	-	-
	Fundulus confluentus	7	6	2	-	-	-
C	*Eucinostomus* sp.	--	1	3	2	-	-
	Diapterus auratus	--	2	2	1	-	-
	Syngnathus louisianae	--	2	2	3	-	-
	Eucinostomus harengulus	--	3	2	1	-	-
	Gobiosoma ginsburgi	--	-	2	1	-	-
D	*Symphurus plagiusa*	2	1	5	6	1	1
	Gobionellus boleosoma	2	-	5	6	2	2
	Cynoscion nebulosus	2	2	5	3	1	-
	Lagodon rhomboides	4	4	3	6	3	1
	Paralichthys lethostigma	--	4	2	6	3	-
	Sciaenops ocellatus	1	1	2	4	3	1

Table 14.18 Continued

Species Groups	Species	Site Groups 1	2	3	4	5	6
		N = 11	N = 9	N = 5	N = 6	N = 3	N = 2
	Syngnathus scovelli	5	1	1	3	2	-
	Anguilla rostrata	3	4	3	2	3	-
	Gobionellus shufeldti	2	1	1	4	2	-
E	*Anchoa hepsetus*	-	4	-	-	-	-
	Pogonias cromis	-	4	-	1	1	-
	Gobionellus hastatus	-	8	1	2	1	-
	Morone americana	-	6	-	4	2	-
	Brevoortia tyrannus	4	8	5	4	3	2
	Anchoa mitchilli	2	8	5	6	1	2
	Elops saurus	2	9	4	5	1	-
	Bairdiella chrysoura	2	8	5	5	-	1
	Cynoscion regalis	-	9	3	2	-	1
	Mugil curema	-	6	3	6	-	2
	Microgobius thalassinus	1	7	2	3	1	1
F	*Prionotus tribulus*	-	1	2	1	-	-
	Fundulus luciae	-	1	-	1	-	-
	Chasmodes bosquianus	-	-	-	2	-	-
	Citharichthys spilopterus	-	1	2	3	-	-
G	*Dorosoma petenense*	1	1	-	3	2	1
	Dorosoma cepedianum	-	-	-	4	2	-
	Paralichthys dentatus	-	-	-	1	1	1
	Fundulus majalis	-	-	-	1	1	-
H	*Gobiesox strumosus*	-	-	-	2	-	-
	Syngnathus fuscus	-	-	-	3	-	-
	Lutjanus griseus	-	-	-	5	-	-
	Etropus crossotus	-	-	2	4	-	-
	Lepisosteus osseus	-	-	-	3	-	2

Table 14.18 Continued

Species Group	Species	Site Groups					
		1	2	3	4	5	6
		N = 11	N = 9	N = 5	N = 6	N = 3	N = 2
I	Ictalurus catus	1	--	-	-	1	-
	Lepomis macrochirus	1	--	-	-	2	-
J	Pomatomus saltatrix	-	---	-	2	-	2
	Ariopsis felis	-	--	-	1	-	1
	Citharichthys macrops	-	1	-	-	-	2
K	Menidia menidia	3	2	-	4	1	-
	Trinectes maculatus	1	2	-	3	2	2
	Opisthonema oglinum	1	2	-	2	-	-
	Opsanus tau	-	1	-	3	-	-
	Evorthodus lyricus	-	33	-	4	-	-
	Archosargus probatocephalus	-	2	-	1	-	-
	Myrophis punctatus	-	-	-	3	1	-
	Caranx hippos	-	-	-	2	-	-
	Morone saxatilis	-	1	-	1	-	-

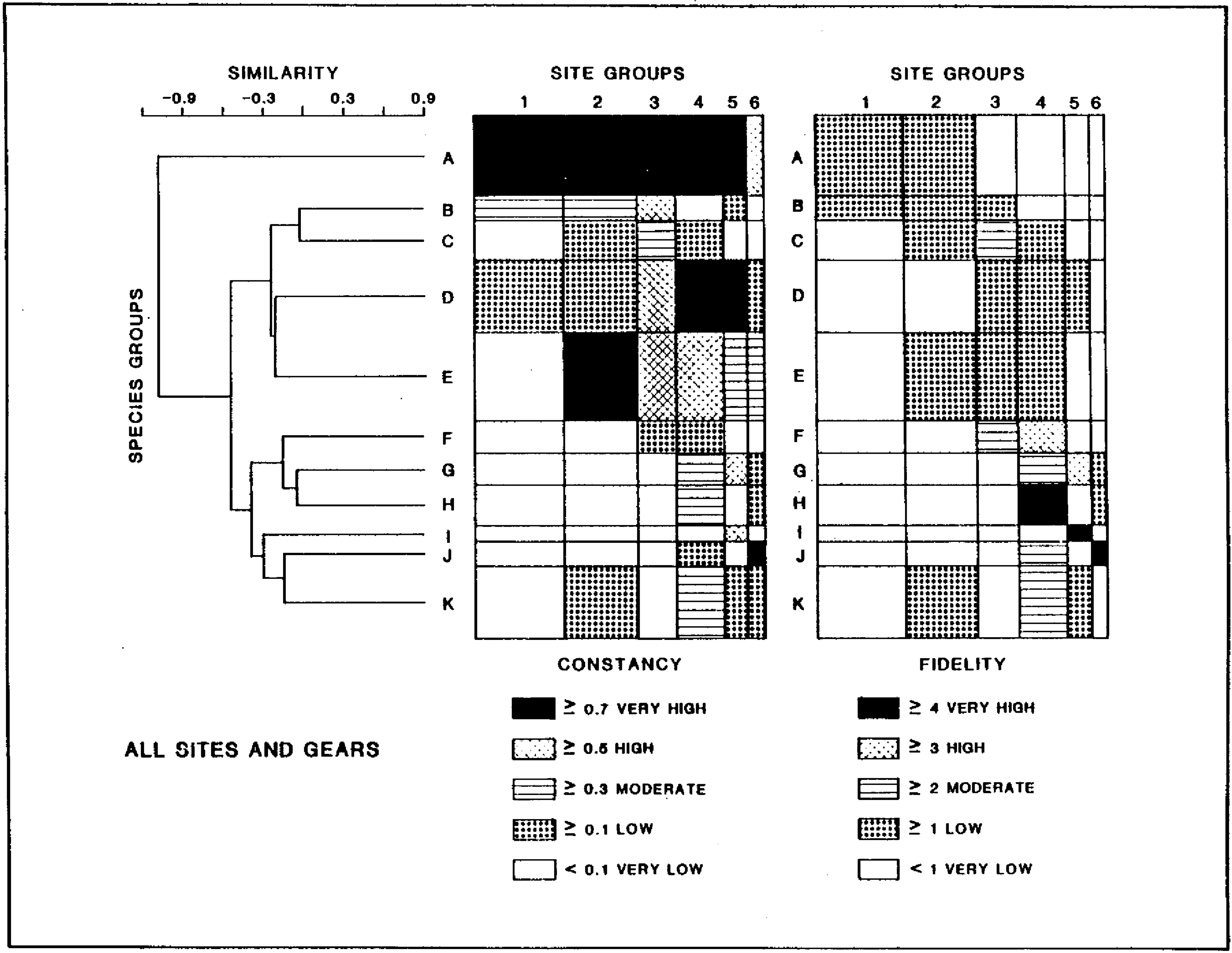

Figure 14.24 Nodal constancy and fidelity in a two-way table of site and species groups as defined by cluster analysis of fishes collected by all gear types at a sampling site by month.

Although the nine species of group D were encountered in all six site groups (hence this group's overall very low and low fidelity), they had highest constancy in site groups 4 and 5 which were, with one exception, collections from Chainey Creek. Of these nine species, six were estuarine transients, two were estuarine gobies, and there was a single pipefish species. These latter taxa were probably estuarine endemics. Seven of the eleven species in group E were estuarine transients. The exceptions were the whiteperch, _M. americana_; two species of gobies; and the bay anchovy, _A. mitchilli_. This group had highest constancy in site group 2 (late spring and summer collections inside the impoundments), whereas moderate constancy was seen in site groups 5 and 6, which were collections from Chainey Creek. Because the species of this group were widely occurring in all site groups except 1, low fidelity was observed. Because species in group F were rare, they displayed very low or low constancy in all site groups. These species had a higher frequency of occurrence in collections from the tidal creek, and this group had highest fidelity to site group 4 (all creek samples). We feel that we underestimated the occurrence and abundance of the marsh killifish, _Fundulus luciae_. This species was a resident of the small pools of standing water in the high marsh and was, therefore, spatially separated from our collecting efforts. Group G also comprised relatively rare species that were primarily collected in the tidal creek system.

With the exception of _Etropus crossotus_, all species in group 4 were taken exclusively in the tidal creek. This resulted in these species having very high fidelity to site group 4, which had six collections; all from the creek habitat. Group I contained two freshwater species; all but one _Lepomis macrochirus_ were caught in Chainey Creek during low-salinity conditions of January and April 1984. Of the three species in group J, only a single _Citharichthys macrops_ occurred inside the impoundments. The remaining fishes were collected by trawl tows and gill net sets in Chainey Creek. This species group had its highest constancy and fidelity to site group 6 (1983 spring creek samples). The last species group had nine species that had moderate constancy and fidelity to collections made in Chainey Creek (site group 4); however, members of this group were encountered in all site groups with the exception of three.

Food Habits

We determined the diets of the 15 dominant species of fishes in the impoundments. These species accounted for 97% of the total number and 94% of the total biomass of fishes inside the impoundments. Of the 1060 individuals utilized in this study, 914 stomachs (86%) contained food items. Descriptions of the diets of these species follow in phylogenetic order.

Family Elopidae: Elops saurus, Ladyfish. Ladyfish occurred in moderate numbers in the impoundments during the spring and summer. All sizes ate relatively large food items, with decapods (Palaemonetes pugio and Penaeus duorarum) and other fishes (L. parva, F. heteroclitus, G. affinis, P. latipinna, and M. beryllina) making up most of the diet (Appendix Table 14.4A). Nereid polychaetes, Nereis succinea, contributed significantly to the total number and volume of food items; however, they occurred in only two individuals, which suggest these ladyfish had encountered a breeding swarm. Thus the importance of polychaetes in the diet was probably a random event. The occurrence of smaller food items (insects, amphipods, and gastropods) was incidental (Appendix Table 14.4A).

We were able to collect only larger E. saurus (164 to 216 mm SL) in creek samples. Fifteen of these twenty-two ladyfish had food, and two species of decapods (P. pugio and P. duorarum) comprised the diet.

Family Clupeidae: Brevoortia tyrranus, Atlantic Menhaden. Juvenile Atlantic menhaden were abundant in collections made during the spring. Little seasonal variability was observed in their diet (Appendix Table 14.4B). Detritus, blue-green algae, and diatoms were consistently encountered in fishes both from the tidal creek and inside the impoundments. All three items were present in all stomachs, although relative volumes of each differed. Detritus accounted for approximately 62% of the total volume, blue-green algae 31%, and diatoms 7%.

Family Engraulidae: Anchoa mitchilli, Bay Anchovy. Bay anchovies were recruited into the impoundments during the spring flooding as small juveniles and remained throughout the summer. Inside the impoundments, their diet was restricted to few prey items, with copepods and decapod larvae (Palaemonetes spp. and Grapsidae zoea) constituting the greatest part of their diet (Appendix Table 14.4C). Bay anchovies taken in the tidal creek had a more-diverse diet. In addition to copepods, which continued to be a dominant food item, Palaemonetes larvae, ostracods, isopods, and gastropods were consumed.

Family Cyprinodontidae: Cyprinodon variegatus, Sheepshead Minnow. In the impoundments, sheepshead minnows were abundant throughout the year. Stomachs of C. variegatus showed this species to be primarily but not exclusively herbivorous. Green algae, the dominant food item in every stomach, accounted for 99% of the total food volume, whereas copepods, the only other prey item, occurred in less than 3% of the stomachs (Appendix Table 14.4D). Cyprinodon variegatus was less abundant in collections from the tidal creek than inside the impoundments, and examination of the few sheepshead minnows from the creek showed them to be totally herbivorous.

Family Cyprinodontidae: Fundulus heteroclitus, Mummichog. The mummichog, one of the most-abundant fishes in the impoundments, was a year round resident, with a diverse, seasonally variable diet. During summer, detritus accounted for over 80% of the total volume of all stomach contents. Foraminifera and decapods (Palaemonetes larvae and P. pugio) were also important, whereas nematodes, the polychaete, Capitella capitata, and gastropods were minor food items. Fundulus heteroclitus from fall samples consumed detritus, foraminifera, and decapods, in addition to green algae, which was found in 50% of the fishes examined from inside the impoundments during this season. In the winter, the occurrence and importance of detritus and foraminifera decreased greatly; at this time decapods (Palaemonetes larvae and P. pugio) were the dominant food items. Nematodes, polychaetes, copepods, and insects were also consumed but were of minor importance. Stomachs from spring were dominated by insects and insect larvae; detritus, decapods, and polychaetes were also eaten in small quantities.

Mummichogs collected in the tidal creek ate many of the same food items as fishes from the impoundments, but their relative importance differed. Detritus and insects, both major dietary items in impoundment fishes, were of only minor importance in the creek. Decapods, secondary food items in the impoundments, were the dominant food source in the creek, and all other prey items had about equal importance (Appendix Table 14.4E). These included foraminifera, polychaetes, nematodes, fishes, amphipods, copepods, and mysids.

Family Cyprinodontidae: Lucania parva, Rainwater Killifish. Rainwater killifish were abundant members of the fish community inside the impoundments during all seasons except summer. Because they were rare in fish collections from the tidal creek, no dietary information was obtained from this habitat. The diet of L. parva was not diverse but did show seasonal changes. Although green algae and detritus were found in some of the stomachs of L. parva, the main food source was ostracods, which were in every stomach during the fall. In the winter the diet consisted of blue-green algae and copepods, each occurring in 50% of the stomachs. Insect larvae became the major food source in spring, although ostracods were also eaten in addition to foraminifera and palaemonid eggs (Appendix Table 14.4F).

Family Poeciliidae: Gambusia affinis, Mosquitofish. Mosquitofish were very abundant in the impoundments during all seasons, and since they were rare in creek samples and those captured had empty stomachs, habitat comparisons were not made. Few individuals had food, limited to small bits of detritus, in their stomachs during the summer. This may have resulted from the fact that 90% of the fishes sampled at this time were females with developing young. Mosquitofish collected during the fall had the greatest diversity of food items, with 83% of the stomachs containing small mats of blue-green algae. Insects, copepods, and ostracods were found in small percentages of the stomachs (Appendix Table 14.4G). During the winter, only 12% of the fish examined had food in their stomachs; these contained blue-green algae and insects. With the exception of some palaemonid body parts, G. affinis ate only insects and insect larvae during spring.

Family Poeciliidae: Poecilia latipinna, Sailfin Molly. All stomachs from seasonal collections of sailfin mollies inside the impoundments contained only diatoms and detritus in about equal proportions (Appendix Table 14.4H). Poecilia latipinna was collected rarely in the tidal creek; however, these also contained only diatoms and detritus.

Family Atherinidae: Menidia beryllina, Inland Silverside. Inland silversides occurred in the impoundments throughout the year, indicating they may have been permanent residents. In all inland silversides sampled, in all seasons, copepods were by far the most-preferred food (Appendix Table 14.4I). Seasonality was found in the consumption of secondary food items. In the spring, insect larvae and adults were the second most important food source, whereas these were replaced by decapod larvae during summer. Decapods and detritus were consumed in the autumn, and mysids were important in winter. Additionally, during the spring, summer, and fall, at least one individual had consumed blue-green algae. Fishes taken in the tidal creek also primarily fed on copepods, with insects and amphipods as secondary food items. Cirripedia, chlorophyta, and diatoms were also eaten.

Family Sciaenidae: *Bairdiella chrysoura*, Silver Perch. Although large numbers of larvae and small juveniles were present inside the impoundments during spring, smaller numbers of silver perch were caught in the summer and fall, and this species was absent in winter. Because of the large size differential between seasons, it is difficult to attribute dietary changes to size or season alone. There was, however, a decline in the number of prey species in the fall, a trend that was found in other predatory species. Ninety-five percent of the diet of *B. chrysoura* (32 to 49 mm SL) from summer collections inside the impoundments was made up of *Palaemonetes* larvae, adult *P. pugio*, and copepods (Appendix Table 14.4J). Minor prey items were insects, mysids, and grapsid crabs. Silver perch taken in the fall ate only adult *Palaemonetes* spp., capitellid polychaetes, fishes, and detritus that was probably ingested incidentally with items such as the infaunal polychaetes. Analysis of the diets of different size classes of *B. chrysoura* indicated that, with increasing size, a preference was exhibited for larger prey items. Silver perch collected in the tidal creek were either small juveniles (<30 mm SL) or large individuals (>100 mm SL), and of these only two had stomach contents. These consumed food similar to that of the larger silver perch from inside the impoundments, with adult *P. pugio*, fishes, crab zoea, and amphipods comprising the diet.

Family Sciaenidae: *Cynoscion regalis*, Weakfish. Juvenile weakfish (<30 mm SL) entered the impoundments in the spring and grew to 50 to 105 mm SL by summer. Inside the impoundments their diet consisted mainly of decapods, both larval and adult, and fishes. Copepods, isopods, insects, and mysids were minor constituents (Appendix Table 14.4K). The diet of weakfish changed with size. Smaller fish (<80 mm SL) fed mostly on *Palaemonetes* larvae, with small quantities of adult palaemonids. With increased size, the consumption of larvae diminished and adult palaemonids became more important. Fish greater than 100 mm SL did not eat Palaemonetes sp., but changed preference to crab zoea and fishes, which became the dominant prey items. Cynoscion regalis in tidal creek samples had eaten adult Palaemonetes spp. which occurred in 94% of the individuals. The only other food item was fishes, which was found in 11% of the specimens.

Family Sciaenidae: Leiostomus xanthurus, Spot. Spot were present inside the impoundments throughout the year. Winter sampling caught postlarval spot (<20 mm SL). During the spring, stomach contents of juvenile spot (20 to 50 mm SL), which dominated the catches, showed that the most-important food item was insect larvae. These were in all stomachs examined and accounted for over 85% of the total volume of food during this season. Copepods also were an important food source; minor dietary items included adult insects, nematodes, and polychaetes. Spot from summer samples had a greater size range (50 to 100 mm SL) and a corresponding greater diversity of prey items. Insect larvae, absent from the diets of these fish, were replaced by foraminifera as the dominant food source. Foraminifera occurred in 90% of the stomachs and represented over 80% of the total volume of food. Other major food items were copepods, Palaemonetes larvae, polychaetes, and nematodes; ostracods, gastropods, cirripedia, and insects were of lesser importance. Detritus was probably ingested during benthic browsing. As predator size increased in the fall (90 to 135 mm SL), the diversity of prey items decreased, and a more-even distribution of food items resulted in lack of dominance of the diet by a single prey taxa. Copepods, polychaetes, insects, and amphipods were all represented in the diet. Additionally, more detritus was consumed, occurring in 75% of the stomachs. Stomach contents of spot from the tidal creek had both a greater number of prey taxa and a greater mean number of taxa per stomach than spot in the impoundments (Appendix Table 14.4L). The most-important food items were polychaetes, copepods, amphipods, decapods, and cirripedia. Nematodes, pelecypods, ostracods, cumaceans, tanaidaceans, isopods, fishes, and insects were also eaten. Detritus was consumed, but it was probably ingested incidentally with benthic infauna.

Family Sciaenidae: Micropogonias undulatus, Atlantic Croaker. Atlantic croaker were present inside the impoundments throughout the year. Larvae (<20 mm SL) entered during the fall and winter, and during the fall both larvae and fish from the previous year's spawn were caught. Only juveniles (28 to 55 mm SL) were taken during spring sampling, and by summer M. undulatus ranged in size from 44 to 100 mm SL. Some seasonal variations as well as strong differences between size classes were seen in the diet. Smaller juveniles (<50 mm SL) fed almost exclusively on insect larvae. Juvenile Atlantic croaker of this size were present during the spring, the same period during which insect larvae were abundant and the only time insect larvae were found in the diet of any species. During other seasons, however, juveniles fed mainly on decapod larvae, and they tended to consume more polychaetes as they grew. Copepods, mysids, fishes, and foraminifera comprised only a small percentage of the total diet (Appendix Table 14.4M). Atlantic croakers from the tidal creek had both a more-diverse diet as well as a more-even distribution in the importance of taxa that comprised the diet than those from the impoundments. The major prey items in fishes sampled in the creek were decapods, polychaetes, mysids, amphipods, and pelecypods. Other food items were cumaceans, fishes, foraminifera, insects, and detritus (probably ingested while browsing on benthic infauna).

Family Mugilidae: Mugil cephalus, Striped Mullet. Striped mullet were abundant in both the impoundment and the tidal creek during all seasons. Regardless of size, season, or location, their diet remained constant. Diatoms and detritus occurred in all stomachs and contributed about equally to the diet. Blue-green algae were only slightly less abundant, occurring in 94% of the stomachs; foraminifera were found infrequently (4% of the stomachs) (Appendix Table 14.4N).

Family Bothidae: Paralichthys lethostigma, Southern Flounder. Although southern flounder differed in size in spring (54 to 71 mm SL) and summer (92 to 265 mm SL) samples from the impoundments, size-related changes in the diet were absent. In all size classes, palaemonid shrimp and fishes were of approximately equal importance in the diet (Appendix Table 14.40). Southern flounder from the tidal creek had a greater size range, but this appeared to have no effect on dietary preference, because Palaemonetes spp. and fishes were consumed by all size classes.

Palaemonetes spp. were the most-important food item in creek specimens, whereas southern flounder from the impoundments ate more fishes.

Between-Habitat Comparisons Of Food Habits. Comparisons of the food items in the diets of fishes from Chainey Creek and the experimental impoundments showed two differences that could be related to prey availability and abundance in the two habitats. Large predators that primarily ate decapods inside the impoundments also had these crustaceans as their main food in the tidal creek. Ladyfish, *E. saurus*, ate only decapods, and palaemonids had a much greater index of relative importance in *P. lethostigma* from the creek than those from the impoundment. Fishes were about 10 times more important in the diet of southern flounder from the impoundments than fishes from the creek.

Fishes that were primarily benthic foragers had a more-diverse diet in the tidal creek than inside the impoundment. The food of spot from Chainey Creek was more diverse and contained more taxa that made significant contributions to the overall diet than was true for fishes from inside the impoundment. Spot from the latter habitat essentially preyed on three main taxa (Foraminifera, Copepoda, and Insecta), whereas spot from the tidal creek consumed copepods, decapods, ostracods, two species of amphipods, barnacle larvae, and two species of polychaetes in significant amounts. Atlantic croaker, another benthic-foraging species, showed the same basic pattern.

The diets of planktivores differed little between creek and impoundment samples. Copepods and decapod larvae were the primary food items and were approximately equally abundant in stomachs from both locations. The only difference in the diets was the presence of relatively large amounts of cypris larvae in fishes collected in the creek. Herbivorous fishes consumed the same food items in both habitats.

Four groups of fishes with similar diets were found in the impoundments (Fig. 14.25). Although fishes in group I (*B. chrysoura*, *A. mitchilli*, *C. regalis*, *M. beryllina*, and *L. xanthurus*) generally consumed a variety of items, they all ate *Palaemonetes* spp. larvae and calanoid copepods. Fishes in group II (*L. parva* and *G. affinis*) consumed insects and zooplankton, whereas group III contained the larger predators (*P. lethostigma* and *E. saurus*) that ate decapods and other fishes. The

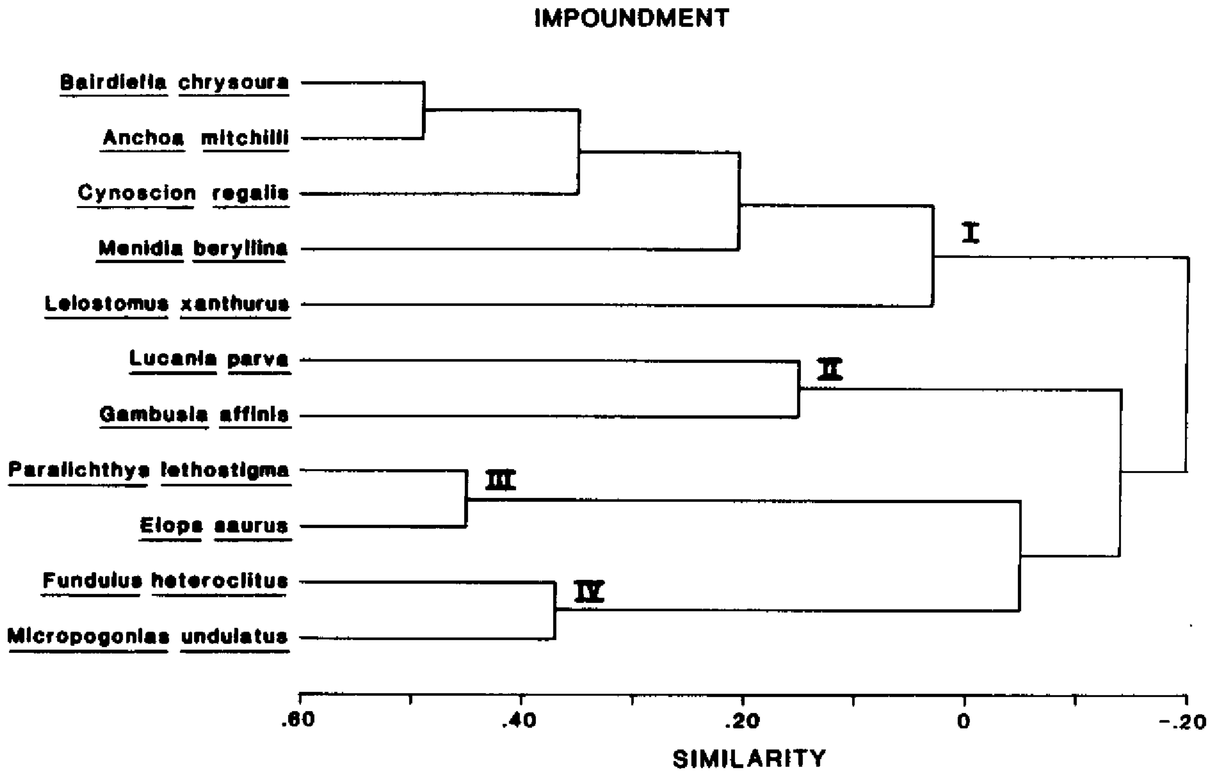

Figure 14.25 Dendrogram showing results of cluster analysis depicting groups of fishes with similar diets inside the experimental impoundments.

remaining group (F. heteroclitus and M. undulatus) were foraging species that consumed a variety of prey items.

Fishes from Chainey Creek formed three groups with similar diets (Fig. 14.26). Group I fed almost exclusively on adult Palaemonetes spp. Inside the impoundments, C. regalis consumed mainly larval and adult decapods. Thus this species went from the plankton-feeding group inside the impoundments to the decapod-feeding group in Chainey Creek. Group II contained those fishes that foraged on a variety of prey items. As was found inside the impoundments, F. heteroclitus and M. undulatus had similar diets. All had varied diets, however; decapods, amphipods, polychaetes, and mysids were present in their diets. Group III species ate barnacle larvae, insects, and copepods in addition to decapods and amphipods that were eaten by group II fishes.

DISCUSSION

Ichthyoplankton

We had the highest catch rates of larval fishes during February and March (see Fig. 14.9 and Appendix Table 14.1), when maximum freshwater discharge in the Santee River system depressed salinities to 0.0 to 10.0 ppt in the study area. Significant recruitment of larval and juvenile fishes to the shallow waters of the Ogeechee River-Ossabow Sound salt-marsh estuarine system of Georgia occurred during winter and spring, when maximum water discharge produced freshwater conditions (Rogers et al., 1984). It has been suggested that the larvae and juveniles of some estuarine transient species (e.g., L. xanthurus, M. undulatus, and B. tyrannus) do not select habitats strictly on the basis of salinity. Rather, they may utilize these habitats to take advantage of an abundance of food, reduced competition, and a lack of predators (Chao and Musick, 1977; Weinstein, 1979; Subrahmanyam and Coultas, 1980).

Our study collected more species (n = 60) of estuarine larval and juvenile fishes than those of previous investigators. Cain and Dean (1976), in monthly samples over a year in a tidal creek in North Inlet estuary, South Carolina, caught 51 species of fishes. Other studies (Burns, 1974; Subrahmanyam and Drake, 1975; Shenker and Dean, 1979; Weinstein, 1979; Bozeman and Dean, 1980; Rogers et al., 1984; Rozas and

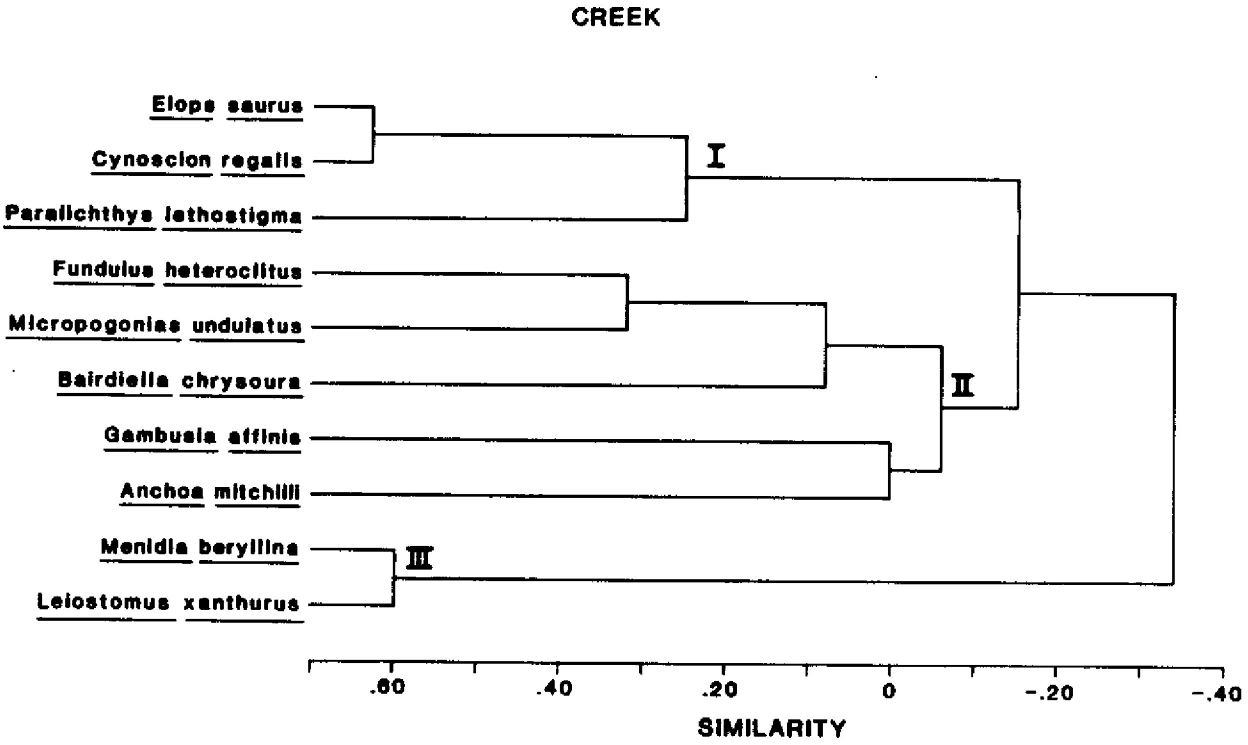

Figure 14.26 Dendrogram showing results of cluster anslysis depicting groups of fishes with similar diets in the tidal creek system.

Hackney, 1984) found fewer species. Although our large number of species may have resulted from the intensive and long-term sampling effort, which increased the probability of encountering rare species, the presence of some species may have been attributable to the "edge effect" (Odum, 1971). Fishes from various salinity regimes occurred in our sampling site because the area had a wide annual salinity range and frequently became a transition area from oligohaline to higher-salinity waters. This annual variability resulted in the collection of freshwater taxa (*Ictalurus catus*, *Lepomis gulosus* and *Eleotris pisonis*) as well as polyhaline and euhaline species (*Menidia menidia*, *Prionotus carolinus*, *P. scitulus*, *P. tribulus*, *Mycteroperca microlepis*, *Caranx hippos*, *Orthopristis chrysopterus*, *Archosargus probatocephalus*, *Diplodus holbrooki*, *Stellifer lanceolatus*, *Chaetodipterus faber*, *Hypsoblennius* spp., *Paralichthys albigutta*, *Symphurus civittatum*, *Stephanolepis hispidus*, and *Sphoeriodes* spp.). Our most-abundant taxa were commonly occurring species in other studies along the southeastern coast of the United States (Burns, 1974; Thayer et al., 1974; Subrahmanyam and Drake, 1975; Cain and Dean, 1976; Shenker and Dean, 1979; Weinstein, 1979, Bozeman and Dean, 1980; Rogers et al., 1984; Rozas and Hackney, 1984; Ruple, 1984; Cowan and Birdsong, 1985).

Spot, the numerically dominant species in ichthyoplankton samples from the tidal creek during both years, was not abundant in impoundment samples because the water-control structures were closed during the time of maximum recruitment of spot into the creeks. During the second year significant numbers of larval spot were caught at the trunk of impoundment 2 because this pond was managed as a weir with constant tidal exchange.

Ladyfish, the most-numerous species in the impoundment samples during the first year (n = 1516), was a minor component of the ichthyoplankton collections in Chainey Creek (n = 39) during the same period. Most ladyfish were stage II leptocephali ($\bar{x}$ SL = 28 mm) that were probably able to avoid the nets fished in the creek. Net avoidance at the water-control structures was eliminated because all water entering or leaving the impoundments was filtered during a sampling event.

Atlantic croaker was the second most abundant species and occurred more frequently than any other species. Its spawning season extends over a protracted period from September through March, and possibly as late as

May or June (Pearson, 1929; Hildebrand and Cable, 1934). During the second year we collected larvae (6 to 9 mm SL) as early as September, indicating that spawning may have occurred as early as August off the coast of South Carolina.

In the Cape Fear River of North Carolina, Weinstein et al. (1980) found that the shallow-water marsh habitats in this estuarine system were not a major nursery for Atlantic croaker. This species preferred estuarine areas with deep channels and, generally, were not taken in the shallows (Welsh and Breeder, 1923; Wallace, 1941; Suttkus, 1955; Haven, 1957; Nelson, 1969; Chao and Musick, 1977; Weinstein et al., 1980). Our data show that the Atlantic croaker utilize shallow-water habitats in a manner similar to findings in estuaries along the Gulf of Mexico and North Carolina (Herke, 1971; Arnoldi et al., 1974; Yakupzack et al., 1977; Currin et al., 1984).

Collections during 1984 at the water-control structure of impoundment 2 (which functioned as a weir) were dominated by striped mullet, *Mugil cephalus* (n = 2142). Because only five prejuvenile *M. cephalus* were taken in plankton samples from the creek during the same period, we felt that the species was able to avoid the plankton nets in the creek. The water-control structures were closed during the peak ingress of striped mullet in 1983, and thus few individuals of this species were taken.

Discrete depth sampling in the main channel of the Cape Fear River estuary (depth, 12 m) showed that *L. xanthurus*, *M. undulatus*, and *Paralichthys* spp. exhibited distinct behavioral responses to photoperiod and tide that allowed these species to maintain a position in the estuary and avoid being flushed out (Weinstein et al., 1980). *Leiostomus xanthurus* and *Paralichthys* spp. moved to the surface at night and used tidal currents to move into the marshes. *Micropogonias undulatus* was caught in greater numbers in deep water at the head of the estuary. Ruple (1984) found greater densities of larvae in night collections, and Lewis and Wilkins (1971) caught more *L. xanthurus*, *B. tyrannus*, and *L. rhomboides* at night than during the day. Our diel comparisons showed many more larval and juvenile fishes were collected in night samples and that ebb-tide collections generally had fewer larvae for most taxa (see Fig. 14.9). The abundance of *L. xanthurus* and *G. bosci* was not affected by tidal stage, and we failed to demonstrate any vertical movement of larval fishes, as found by Weinstein et al. (1980). This was probably a result of the shallow depth (1.6 m) of Chainey Creek and the homogeneity of the water column caused by the strong tidal currents.

At the impoundment stations during 1983, more fishes were caught during flood tide, when water entered the pond through the water-control structure, than during ebb tide, when water flowed over the flash boards into the creek. M. undulatus was an exception to this general pattern. When catches at the water-control structures were greatest in May, the average size of this species was 16 mm SL. At this size M. undulatus may still be planktonic and not ready to settle out of the water column.

Although the utilization of estuarine habitats as nurseries for many species of sciaenids has been well-documented, few studies have found larval C. nebulosus, P. cromis, and S. ocellatus in shallow-water marsh habitats. We collected 44 larval spotted seatrout, C. nebulosus, from June to September 1983 and two additional specimens in May 1984. Thirty-four larval black drum, P. cromis (5 to 7 mm SL), were taken in May and June 1983. Joseph et al. (1964) reported that black drum spawn in the lower Chesapeake Bay during April and May, even through their ichthyoplanklon collections failed to catch larval black drum over a three-year period. Frisbie (1961) speculated that larval black drum may move offshore, but others have stated that offshore movement would be inconsistent with the typical up-bay movement of most other sciaenids (Joseph et al., 1964). Joseph et al. (1964) postulated that black drum larvae moved into tidal creeks, where they were spatially separated from the sampling effort. Our collection of larval black drum in the Chainey Creek system tends to support their explanation. Larval red drum, S. ocellatus, (n = 136; SL = 3 to 9 mm) were caught from August to October 1983, and four additional specimens (5 to 7 mm SL) were taken during the same months in 1984. We caught one 46-mm-SL juvenile in nets fished in March 1983. Spawning of red drum was reported to occur outside estuaries in nearshore coastal waters (Pearson, 1929; Mansueti, 1960; Jannke, 1971), and our collection of small larvae confirmed this. Along the Atlantic Coast spawning season ranged from August to November in Virginia waters (Hildebrand and Schroeder, 1928; Mansueti, 1960; Joseph et al., 1964), and between September and February in Florida (Jannke, 1971), and our data indicated that red drum may spawn as early as late July in South Carolina waters.

Fishes of the estuarine shallow-water marsh habitat can be separated into two broad groups: transients, those that utilize these areas as nursery grounds; and residents, those that complete their life cycle in the estuary. Cluster and nodal analyses clearly demonstrated the seasonality of the ichthyoplankton community in Chainey Creek. This seasonality resulted from the temporal separation of periods of recruitment of the larvae and juveniles of the dominant species. This may have prevented niche overlap. Although several studies have been conducted to examine the relationships between available food supply and survival of the year class (Hjort, 1914; Marr, 1956; May, 1974; Houde, 1978), very little is known about species interactions among postlarval fishes in estuaries (Weinstein et al., 1980). Seasonal changes, that is, the "waves of recruitment" (Weinstein, 1979), in the abundance of postlarval and juvenile fishes with similar diets would spread the trophic demands on the resource over a longer time period. The presence of numerous larvae and juveniles that were spawned in marine waters shows the importance of tidal marsh areas as nursery grounds. Species that use shallow-water marsh habitats as nurseries are important in the transfer of energy to higher trophic levels (Weinstein, 1979). Because these species are only temporary residents of the estuary, they may also be an important vehicle for the transfer of energy to nearshore coastal waters (Bozeman and Dean, 1980).

Seasonal variation in community structure was not observed at the impoundment stations during the first year. With the exception of May 1983, the water-management strategy prevented significant water exchange between Chainey Creek and the impoundments. Samples taken at the water-control structures during reduced flow conditions caught few larval and juvenile fishes. However, samples collected from the water-control structure of impoundment 2 during the second year (where the trunk and flashboards were set to act as a weir) showed that fishes moved into the impoundments when tidal exchange was permitted and that the resulting species composition depended on what species were present in the tidal creek. Thus the most-important factor in determining the species composition and abundance of larval and juvenile fishes that entered the impoundments was the water-management strategy. The prevention of tidal exchange in the impoundments during times of abundance of taxa in Chainey Creek resulted in either reduced catch rates or the total absence of these species in plankton samples at the water-control structures. For example, larval and juvenile spot were very abundant in samples from the tidal creek (n = 28,622); however, only 830 individuals were collected at the trunks. This resulted from reduced or no tidal exchange during the period when spot were very abundant in the plankton. This was demonstrated for other species such as summer and southern flounder, red drum, and spotted seatrout. Because the seasonal peaks in abundance of these species did not coincide with periods when tidal exchange was permitted between the impoundments and Chainey Creek, they were unable to utilize the impoundments as nursery areas.

Juvenile and Adult Fishes

Sampling Techniques and Diversity. Before making comparisons of the ichthyofauna in the experimental impoundments and the adjacent open tidal creek system, some information on the fishing characteristics of the various types of gear needs to be presented. Preliminary seine hauls in the perimeter ditch of the experimental impoundments showed the importance of using block nets to effectively close in an area and inhibit the escapement of both fishes and decapods from the sampling site. When blocknets were not used, the fauna was composed of relatively small-sized, slow-moving fishes in the families Cyprinodontidae, Atherinidae, and Engraulidae. During initial tests to determine appropriate sampling methodology, we saw larger fishes such as *Mugil cephalus* avoid the seine net and dart out of the sampling site. After using blocknets, we felt that our catches were representative, in that they accurately described the species composition and abundance of fishes in a given site. To define the ichthyofauna we needed to use two mesh sizes, 6.4- and 0.8-mm bar mesh. We made three pulls of the coarse-mesh seine and a single pull of the fine-mesh seine. The coarse-mesh seine caught larger fishes and decapod crustaceans and only a small amount of detritus. The fine-mesh seine caught small fishes and crustaceans as well as significant quantities of detritus. Sorting fishes from the contents of the fine mesh net was very labor-intensive (up to 24 hr), and thus we did not make multiple hauls with this net.

Cast-net collections provided qualitative information on the species composition of fishes; however, there were two problems with this gear. First, there was the age-old difficulty of mesh selectivity that is present in nets not constructed out of fine mesh. Small fishes, such as postlarval spot, Atlantic croaker, mosquitofish, and inland silverside, for the most part passed through the 0.95-cm bar mesh net with little difficulty. In addition, we do not know how well fishes avoid the net. A strong-swimming species of fish would have little difficulty in avoiding the 1.5-m-radius cast net as it descended through the water column.

Mesh selectivity also was a problem with gill nets. Very small fishes passed through both sizes of gill nets. Large fishes generally were not entangled by the 2.54-cm stretch mesh net, and the catches of the large-mesh net for such taxa as large striped mullet, M. cephalus, were not indicative of their abundance in the tidal creek. We have seen striped mullet swim to the net and then jump over it. Another difficulty was the inability to quantify the catches in terms of area. We limited our discussion of gill nets, therefore, to general trends in catch per set and the presentation of a faunal list.

Otter trawl nets generally have been considered to be a relatively inefficient sampling gear. Problems associated with trawl nets include mesh selectivity, the availability and vulnerability of target species, and consistency in net configuration and towing methodology during each sampling event. Our trawl net was constructed of 1.25-cm stretch mesh netting and permitted the escapement of some postlarval spot and Atlantic croaker, as well as other small fishes that utilize Chainey Creek. Atlantic menhaden were frequently seen in large schools in the creek during trawl sampling. These fishes were in the upper part of the water column and were, therefore, unavailable to the trawl gear, being spatially separated from the net. Because our net was a small sampling device (headrope length = 3.4 m), large fishes were easily able to avoid the net and therefore were invulnerable to the fishing gear.

Rotenone collections inside blocknets that surround a given area were very effective in sampling fishes in the small subtidal creeks that drain the high marsh. Although Weinstein and Davis (1980) found that this technique resulted in greater species richness than seine collections in the same areas, they found that rotenone sampling gave lower estimates of the standing crop of fishes than seine hauls. This was caused by the failure of some fishes to surface and be captured. We found that not all taxa of fishes reacted to rotenone in the same fashion. For example, striped mullet rose to the surface and swam about in respiratory stress, whereas members of the family Blenniidae generally did not come to the surface.

The species diversity, defined as the number of species taken at each site, was dependent on both the sampling technique and the location. Inside the experimental impoundments, seine hauls collected almost twice as many species as cast nets (Table 14.19). We felt that seining gave an accurate picture of the species composition, because only one species was added to the faunal list with cast-net sampling.

Table 14.19

Total number of species collected by each gear type in the various sampling sites

Gear	Site	Total Species
Seine net	Impoundment	52
Cast net	Impoundment	28
	Main Creek	34
Trawl net	Main Creek	33
2.5 cm gill net	Main Creek	20
7.6 cm gill net	Main Creek	8
Rotenone	Feeder Creek	57

An important point that needs to be highlighted is the very distorted picture of the ichthyofauna of the tidal creek system that is obtained by the exclusive use of the otter trawl net. This gear collected a total of only 33 species, a total of 1 less than the number taken by cast nets in the creek. By far the most-efficient sampling technique in the unimpounded marsh habitat was rotenone (Table 14.19). For all sampling dates and all gears, we collected 16 more species in the tidal creek system (n = 69) than inside the experimental impoundments (n = 53) (Appendix Table 14.5). Prior to the use of rotenone in our sampling, the ichthyofauna inside the impoundments, as defined by seine and cast-net collections, was more diverse than that of the tidal creek as described by gill, cast, and trawl nets (Fig. 14.27). However, after the initiation of rotenone sampling, the total number of species was higher in the tidal creek than inside the impoundments.

Annual Cycle of the Fish Community in the Impoundments. To summarize the dynamic events that occurred in the experimental impoundments during the course of the two-year study, we divided the annual cycle of the ponds into discrete periods, each of which had phenomena that impacted the fish community.

During the spring flooding of the impoundments, fishes that were abundant either as larvae or juveniles in Chainey Creek were recruited into the impoundments. The fish community after flooding was comprised of the core group of species (*G. affinis*, *M. beryllina*, *M. cephalus*, *G. bosci*, *C. variegatus*, *F. heteroclitus*, *P. latipinna*, and *L. parva*) plus taxa in the Sciaenidae, Engraulidae, Sparidae, and Clupeidae that entered during flooding. In June and July, larval fishes that were present in the ichthyoplankton of Chainey Creek were recruited into the impoundments at high tide, when water flowed into the units across the sill. *Elops saurus*, *M. atlanticus*, *B. chrysoura*, and *C. regalis* entered during this period. As the water levels in the ponds were raised, the amount of tidal circulation decreased, thereby reducing the possible level of larval recruitment from the tidal creek.

Tidal exchange was reduced further in late summer by placing additional flashboards in the water-control structure. Water temperatures were very high in the impoundments at this time, and they were accompanied by reduced levels of dissolved oxygen (see Fig. 14.6). In a classic dissolved oxygen (DO) sag, values are at a minimum around sunrise, which is a period of major feeding activity for many species of birds that are predators on fishes. On 17 August 1983, of approximately 400 birds observed in impoundment 3, about 25% were actively feeding (M. Epstein, personal communication; see Chapter 15). This was one week prior to our August sampling trip, during which we collected few estuarine transient

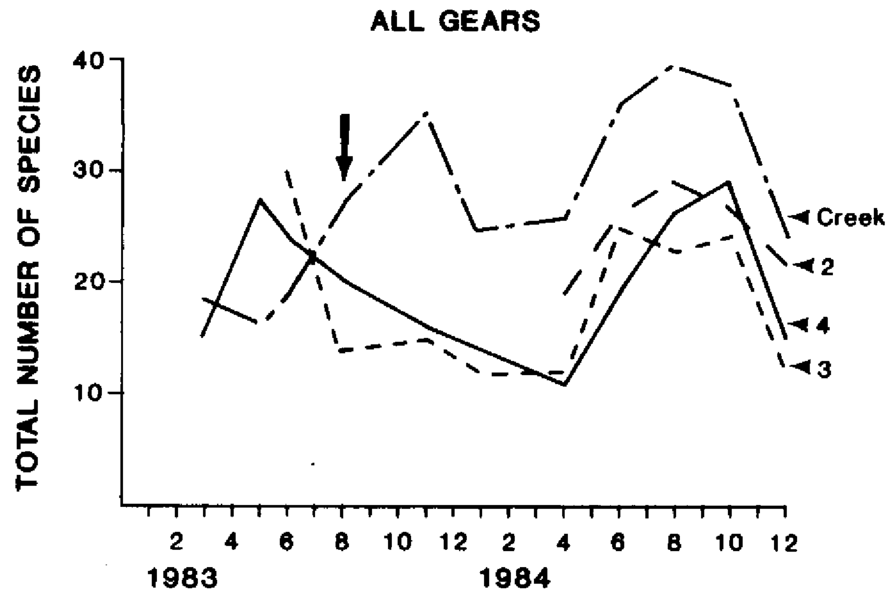

Figure 14.27 Total number of species collected monthly with all gear types at each sampling site (2 = impoundment 2; 3 = impoundment 3; 4 = impoundment 4; creek = Chainey Creek). Arrow denotes time when we initiated rotenone sampling in the feeder creeks.

species and found DO concentrations as low as 0.5 mg/liter in this impoundment. Fishes that were recruited into the impoundments during spring flooding and subsequent tidal exchange in June and July of 1983 were exposed to very low levels of DO at this time. The results of the cluster analysis showed that seine hauls in impoundments 3 and 4 from late summer and fall of 1983 were similar in faunal composition to that sample from March 1983 made prior to flooding. There was a definite change in the ichthyofauna of these sites from May and June 1983 to August 1983.

Many species of fishes have been shown to exhibit behavioral patterns, termed the low oxygen syndrome, in nonfavorable habitats (Chittenden, 1971). As DO levels decline to unsuitable concentrations, fishes become restless and actively swim about. The concentration at which this occurs is termed the oxykinetic level (Fry, 1960) and is interpreted as being the initiation of the avoidance response to adverse environmental conditions. As oxygen concentrations decline further, the frequency and amplitude of ventilation increase as the fishes attempt to compensate for lower oxygen concentrations by passing a greater volume of water over the gills. Many fishes then rise to the surface to gulp air or to obtain water with a greater oxygen concentration at the surface microlayer; however, only those species that are morphologically adapted, that is, possess flattened crania and dorsally-oriented mouths, are able to effectively use the oxygen-rich water at the air-water interface without greatly altering their usual swimming posture (Lewis, 1970). Fishes unable to employ this strategy generally become disoriented and then die.

If DO levels reached oxykinetic level inside an impoundment, increased swimming would not result in fishes being able to avoid these unfavorable conditions, because they were confined to the ponds. All species that comprised the core of the impoundment ichthyofauna (species group A of the seine data, see Table 14.8), with the exception of _G. bosci_ and _C. variegatus_, are morphologically adapted to utilize the surface microlayer. When fishes are stressed by low concentrations of DO and either utilize the surface microlayer or gulp air at the surface, however, they are much more vulnerable to predation by birds. In this case, death would not be directly caused by hypoxia. Feeding by avian predators would have been made much easier.

To further illustrate the changes in the fish community over an annual cycle inside the impoundments, we expressed the abundance of fishes at a given time within an experimental unit as the catch per trip, which was the pooled catches of a species in the three seine sites. This was the catch per unit effort and was interpreted as an index of relative abundance. We used the seven dominant estuarine transient species inside the impoundments for this presentation.

Between June and August of 1983, the abundance of these species declined in both impoundments sampled (Table 14.20). Estuarine transient species disappeared in impoundment 3 during this period, whereas their abundance was reduced by 62% in impoundment 4 during the same time interval. DO concentrations were lower than 0.5 mg/liter in unit 3 and as low as 1.2 mg/liter in unit 4. A similar trend in abundance of these species was seen in 1984, with the lowest observed DO concentrations (0.8 mg/liter) and the greatest decline in unit 3 (Table 14.21). We believe the decline in the abundance of these species may have been attributable to low DO concentrations which either killed the fishes or made them more vulnerable to predation.

Annual Cycle of the Fish Community in the Tidal Creek. We found the shallow-water habitat of the Chainey Creek area to be used extensively by numerous species of fishes that were both residents and transients. Transient species of fishes have been shown to be a significant component of the ichthyofauna in the shallow-marsh habitat of estuaries along the South Atlantic coast (Cain and Dean, 1976; Weinstein, 1979; Weinstein et al., 1980). In the Chainey Creek area, peak periods of recruitment of the larvae and postlarvae of estuarine transients occurred during the winter months, when spot, Atlantic croaker, pinfish, Atlantic menhaden, summer and southern flounders, and striped mullet were very abundant (Fig. 14.28).

Recruitment of the transient species to the tidal creek system was not limited to the winter. Spring and early summer brought ladyfish, weakfish, silver perch, gerreids, whitings, spotted seatrout, black drum, and tarpon. Several of these species had protracted spawning seasons and continued to be recruited to the study area throughout the summer into early fall. August brought red drum larvae, which peaked in abundance in September. The larvae and postlarvae of the dominant winter group first

Table 14.20

Changes in relative abundance of dominant estuarine transient species collected in seine hauls during 1983 in experimental impoundments.

Species	Impoundment	Catch/Trip		
		June	August	November
Leiostomus xanthurus	3	550	0	0
	4	212	235	0
Micropogonias undulatus	3	727	0	0
	4	381	56	34
Brevoortia tyrannus	3	29	0	0
	4	9	0	0
Lagodon rhomboides	3	7	0	0
	4	5	0	0
Bairdiella chrysoura	3	28	0	0
	4	46	0	0
Elops saurus	3	90	0	0
	4	152	20	3
Cynoscion regalis	3	177	0	0
	4	24	3	0
Totals	3	1608	0	3
	4	829	314	37

Table 14.21

Changes in relative abundance of dominant estuarine transient species collected in seine hauls during 1984 in experimental impoundments.

Species	Impoundment	Catch/Trip			
		June	August	October	December
Leiostomus xanthurus	2	319	20	76	21
	3	16	0	6	1
	4	57	22	5	0
Micropogonias undulatus	2	140	4	2	0
	3	123	0	0	0
	4	16	2	0	4
Brevoortia tyrannus	2	195	101	163	14
	3	46	0	16	0
	4	5	0	1	2
Lagodon rhomboides	2	63	50	90	29
	3	0	0	0	0
	4	0	0	0	0
Bairdiella chrysoura	2	300	148	16	25
	3	127	0	73	5
	4	20	51	58	63
Elops saurus	2	17	11	41	0
	3	217	61	47	0
	4	550	33	22	0
Cynoscion regalis	2	79	2	0	0
	3	102	0	12	0
	4	1	7	0	0
Totals	2	1113	336	388	89
	3	631	61	154	6
	4	649	115	86	69

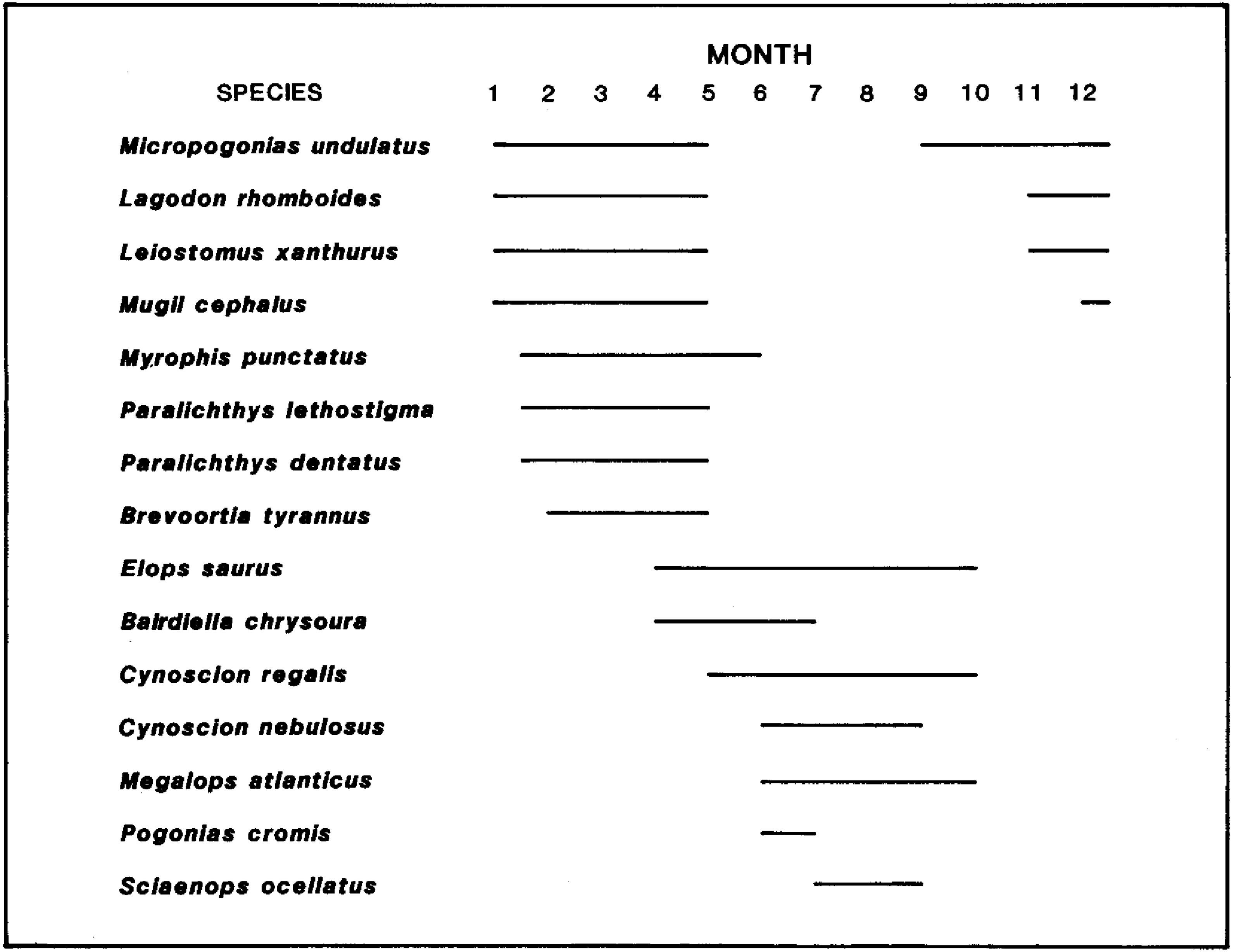

Figure 14.28 Months of recruitment of the early life history stages of estuarine transient species in the Chainey Creek complex.

appeared in late autumn. Thus there were continued waves of recruitment of the early-life-history stages of the estuarine transient species in the open tidal creek. As these grew, they moved down estuary, where they either took up residence in deeper estuarine waters or moved into the coastal habitat.

Food Habits. Diets of fishes that were collected in sufficient numbers for comparisons showed various levels of similarity between the two habitats. Some species consumed the same food items in the creek and the impoundments. Among these were the Atlantic menhaden, sheepshead killifish, and striped mullet. These three species consumed algae and detritus in both habitats.

Two species consumed approximately the same taxa in both habitats, but the importance of these items in the diet differed. Southern flounder ate palaemonid shrimp in each site; individuals from the creek ingested far more grass shrimp and fewer fishes inside the impoundments. Although calanoid copepods dominated the diet of bay anchovies from both habitats, in the impoundments they ate far more decapods than fishes from the creek.

Other fishes, such as the inland silverside, ladyfish, silver perch, and weakfish, had a more-diverse diet inside the impoundments than in the creek. The most-important food items in the diets of inland silversides from both habitats were copepods and insects. Decapod larvae, a frequently occurring and moderately important food for impoundment fishes, were absent in the diet of the inland silverside from the creek. Ladyfish from the creek ate only decapods (*Palaemonetes pugio* and *Penaeus duorarum*). Inside the impoundments, four species of fishes as well as polychaetes, gastropods, and insects were consumed by ladyfish in addition to the two-previously mentioned decapods. Silver perch had a much more diverse diet inside the impoundments than in the creek, but this was probably a reflection of sample size, because only 2 of 14 fishes examined from the creek had stomach contents. Although the dominant items in the diet (palaemonid shrimp and fishes) of weakfish were similar in both habitats, individuals in the impoundments consumed grapsid zoea, copepods, isopods, mysids, and insects. These were not eaten by weakfish in the creek.

Mummichogs, spot, and Atlantic croaker (all generalized benthic feeders) had more-diverse diets. In addition, many more taxa were shown to be relatively important food items in fishes from the creek.

Because new ecological systems develop when portions of an estuary are impounded (Copeland, 1974), it is not unexpected to find differences in feeding dynamics between the two habitats. Although differences in feeding habits appear subtle, they result from larger changes in prey populations. Fishes that consumed benthic or planktonic organisms in Chainey Creek had a wider range of food items than similar feeders in the impoundments. The macrofaunal diversity was higher in the creek than inside impoundments (see Chapter 12), and Knott (1980) found that zooplankton diversity was lower in impoundments than in the natural estuarine habitat. The prey species able to survive the rigorous habitat inside the impoundments flourished, especially *Palaemonetes* spp. All predators took advantage of their abundance and ate significant quanitites of these shrimp.

CONCLUSIONS

The experimental impoundments impacted estuarine transient species in three main ways. First, because of the water-management strategy, these structures removed shallow-water marsh habitat from the estuarine nursery system. During periods of no tidal exchange (November to April), all species were denied access to the impoundments. In late summer and early fall, the increased water level in the beds (caused by the addition of flash boards at the water-control structures) reduced tidal exchange and therefore permitted limited access. Second, because water-management practices prevented the movement of many species of fishes from the impoundment to the tidal creek system, those individuals inside these units could not move from adverse environmental conditions such as high or low temperatures and low DO. Thus, mortality due to exceeding limits of tolerance of environmental factors and predation, was increased. Finally, those estuarine transient species of fishes that entered the impoundments were denied the opportunity to complete their life cycles. These organisms were not permitted to move down estuary with growth. Not only did this prevent these species from reproducing, but it also stopped the annual export of the living biomass of these species, thus breaking the important energy link between the marshes and the coastal marine environment (Weinstein et al., 1980).

The presence of wetland impoundments in coastal South Carolina is a reality, and their adverse impact on estuarine fishes has been supported by our data. From our experience, we feel that the initiation of two simple practices by impoundment managers would reduce the magnitude of their negative impacts on estuarine fishes. First, during hot summer months, water levels in the impoundments should not be raised to the extent that tidal circulation is greatly reduced. Increased circulation would help moderate high temperatures and also reduce the probability of severe DO sags. Secondly, instead of removing flash boards at the water-control structure to lower the impoundment water level during late fall (December), the inside gate should be raised so that water flows out through the bottom rather than over the sill. On December 5, 1984, we lowered the water levels in two impoundments by two methods. In one, two flash boards were removed, and all water leaving the impoundment was strained through a 1-mm mesh net for 3.5 hr. Palaemonetes spp. and mosquito fish were the only organisms that went over the sill. In a second pond, a 6.1-m shrimp trawl net was attached to the trunk, and the inside gate was raised. Even though the trawl net was not completely efficient, we caught 720 individuals in nine species with a weight of 33.4 kg during the 3.5-hr set. Estuarine transient species accounted for 95% of the number of fishes.

If these two procedures were followed, perhaps the poor water quality encountered in summer would be improved, thus reducing the associated mortality, and those organisms that survived until fall would be able to move down estuary and complete their life cycle. We would like to point out that the only way to prevent the reduction of shallow-water marsh habitat in South Carolina estuaries by impoundments is not to construct any more of these structures.

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SECTION VIII

WILDLIFE COMMUNITY

Chapter 15

Use of Managed and Open Tidal Marsh by Waterbirds and Alligators

M. B. Epstein and R. L. Joyner

INTRODUCTION

Palustrine forested wetlands previously cleared and impounded during the eighteenth and nineteenth centuries for the cultivation of rice and indigo are significant ecological features in the South Carolina intertidal coastal zone. The majority of the impoundments occupy freshwater estuaries; however, some occur in saline environments. Historically, impoundments made up about 29% of the 204,146 ha of coastal marshland of South Carolina (Tiner, 1977; Aichele, 1984). Today, 51% of these have been abandoned or are no longer impounded; the remainder are managed mainly for wintering waterfowl (Miglarese and Sandifer, 1982).

Most wildlife investigations in South Carolina impoundments have focused on wintering waterfowl (Alexander and Hair, 1977; Prevost et al., 1978; Prevost and Gresham, 1981; Swiderek, 1982; Miglarese and Sandifer, 1982); although fish and other wildlife values have been recognized (Newsom, 1967; Morgan et al., 1975). The southern bald eagle, _Halaeetus l. leucocephalus_, osprey, _Pandion haliaetus_, and American alligator, _Alligator mississippiensis_ utilize South Carolina's impounded marshes for feeding and nesting (Henry and Notemeier, 1975; Murphy and Coker, 1978; Wilkinson, 1983). In contrast, little quantitative information exists concerning use of South Carolina open tidal marshes by birds (Christy et al., 1981; Bildstein et al., 1982a; Bildstein et al., 1982b).

In this study, waterbird and alligator use of managed and open tidal wetlands was analyzed to provide information for managers to assess, select, and preserve or maintain coastal habitats that are vital to wetland wildlife communities. The research generated baseline information on the response of selected wildlife to waterfowl management on brackish wetlands. We determined waterbird use of managed and open tidal marsh on the Tom Yawkey Wildlife Center, Georgetown, South Carolina during 1983-1984. Our objectives were to: (1) characterize waterbird use of the study area, (2) compare waterbird and alligator use of managed and unmanaged marshes, (3) estimate widgeongrass, Ruppia sp., production and utilization by waterfowl in managed impoundments, and (4) make observations on the potential impact of waterbirds on the natural productivity of the study impoundments.

METHODS AND STUDY AREA

Sampling

The experiment was a simple random design with six managed units and two unmanaged sites. We addressed the second objective with the null hypothesis that waterbird and alligator use of managed and unmanaged marshland are equal.

The managed impoundments were a series of five units (average = 5.3 ha, 13 acres); and Cooperfield, a 13.8-ha (34-acre) managed impoundment (Fig. 15.1). The unmanaged sites included a 13.6-ha (33.5-acre) section of salt marsh adjacent to Cooperfield and one tidal impoundment (unit 6, 7.9 ha, 19.4 acres).

During the first field season (January through December 1983), the open marsh, unit 6 (tidal impoundment), Cooperfield, and two of the five managed impoundments (units 1 to 5) were randomly selected for censusing and observation; that is, five (two unmanaged, three managed) of the eight sites were sampled each time, approximately four times per week. During the second field season (January through July 1984), observation periods were modified from four to two per week, and all eight sites were sampled on each occasion.

Counts and behavioral observations were made from four towers (4m high) on study impoundment dikes between units 1 and 2, 3 and 4, 5 and 6

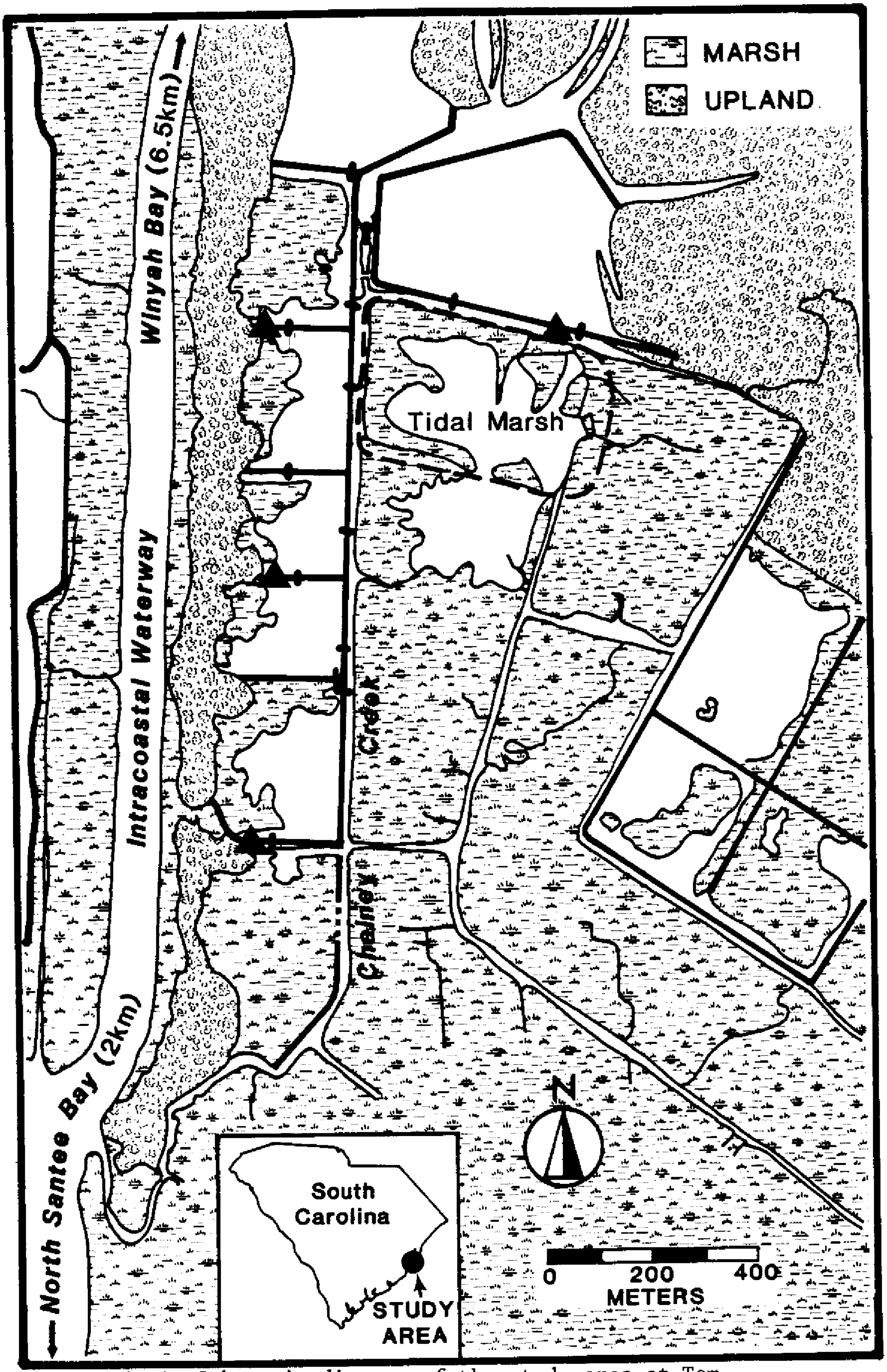

Figure 15.1 Schematic diagram of the study area at Tom Yawkey Wildlife Center. Triangles indicate location of observation towers.

(tidal impoundment) and Cooperfield and the open marsh site (Fig. 15.1). Tower location allowed subsequent or intermittent observations of contiguous impoundments and saltmarsh. We minimized disturbance while sampling by accessing the towers through the upland area behind the impoundments. Relative use was determined by direct observation and counts of birds and alligators using each study site during each season of the year. The general method of sampling is similar to a station index (Mannan and Meslow, 1981). To compensate for the limitations of sampling of some species in dense emergent vegetation (e.g., moorhens, *Gallinula chloropus*, and least bitterns, *Ixobrychus exilis*), vocalizations were used to locate and count birds. An index for the number of calls was used exclusively to monitor clapper rail, *Rallus longirostris*, abundance.

Counts were made during periods of high avian activity (morning and evening), beginning 1 hr after sunrise and about 3 hr before sunset (Robbins, 1981a). No counts were made at midday, during heavy rain or fog, or when temperatures were less than $-5^{\circ}C$ (Robbins, 1981b). Sampling periods at each station lasted a minimum of 10 min or until all birds were counted using 7 X binoculars and a 16 to 35 X spotting scope. The starting observation site was randomly chosen (random numbers table). The same observer (M. Epstein) conducted all censuses. Birds were identified to species when possible. Because of the difficulty in distinguishing sandpiper, *Calidris* spp., species in winter plumage (Carter, 1984), selected species (white-rumped sandpiper, *C. fusciocollis*; least sandpiper, *C. minutilla*; semipalmated sandpiper, *C. pusillus*; and the western sandpiper, *C. mauri*) were grouped as peeps. Similarly, long-billed dowitchers, *Limnodromus scolopaceus*, and short-billed dowitchers, *L. grizeus*, were counted as dowitchers. Immature and unidentifiable gulls and yellowlegs were categorized as gulls and yellowlegs, respectively.

Individual birds were counted by species when possible. The number of individuals in large flocks was estimated by counting the number of individuals in small groups and then determining the number of similar-sized groups in the concentration. In concentrations with no discernible groups, the field in view as seen through the spotting scope was used to group the birds. The spotting scope was then shifted over the concentration until all birds were counted. After the initial scan was completed, additional birds (not previously recorded) arriving in the area were counted for the remainder of the 10-min observation period.

Alligators were enumerated by size classes: (1) small alligators < 1.5 m (5 ft) and (2) large alligators $\geq$ 1.5 m. Late evening (> 1830 hr) counts of birds roosting in trees or snags in a freshwater zone adjacent to Cooperfield were made during September and October 1983.

Date, time, temperature, low and high wind speed and direction, percent cloud cover, water level, and precipitation were recorded at each station. An index of precipitation (none, drizzle, or light rain) and weekly salinity and rainfall measurements were recorded (Robbins, 1981b). Salinity was measured using a refractometer. Water-level gauges were established at each study site. Zero water level was established when impoundment beds were completely dewatered. Water level in the perimeter ditches at this time was even with the edge of the impoundment bed. Water levels in the salt marsh and unit 6 were governed by tidal pulse and other natural factors.

To assess widgeon grass, _Ruppia_ _maritima_, use by waterfowl, three 1-m^2 exclosures were randomly placed in each of units 2, 4, 5, and Cooperfield. Vegetative samples were taken inside and outside the exclosures every other month starting in August 1983 and ending in February 1984. Sampling procedures were adopted from Prevost et al. (1978). Widgeon grass samples were not taken during the 1984 growing season.

Analysis

Before morning and evening counts were analyzed by study site for each observation period, species occurring fewer than 10 times overall were omitted from the calculations (Kessler and Milne, 1982). Data (total number of birds/census) were normalized with log (ln) transformation for homogeneous variance for ANOVA because of the large sample and wide range of numbers (Steel and Torrie, 1980). Before pooling morning and evening counts, we used a t-test to investigate the hypothesis that the means of the two groups were equal (Helwig and Council, 1979). Paired t-tests were performed on morning and evening samples occurring on the same day to determine whether the mean difference varied significantly from zero (Helwig and Council, 1979).

Before pooling the 1983 and 1984 data, a t-test procedure was performed to look for differences between the means of the two groups. We used a one-way ANOVA to test for differences between study sites. When comparing study sites, all data were converted to log (ln) (birds/0.4 ha + 1). Duncan's multiple range test was used to detect differences in sample means (Helwig and Council, 1979).

Simple correlation analysis was used to measure multicollinearity among environmental varables for the overall data set and by season before testing for associations with bird numbers using stepwise multiple regression (Helwig and Council, 1979). These procedures were performed on Cooperfield and the adjacent salt-marsh site. We set a criterion to use only one variable of an interrelated ($r \geq .7$) set of variables for the multiple regression analysis (Kaminiski and Prince, 1984). The regression procedure was performed on the log (ln) (birds/ha + 1) counted by census period for each of the two sites. Models having high R^2 values ($\geq .5$) were retained for descriptive purposes.

Seasonal periods were adopted from Bildstein et al. (1982a) and include: fall, 1 October to 31 December; winter, 1 January to 15 March; spring, 16 March to 31 May; and summer, 1 June to 30 September. Analysis of variance was performed on the number of birds and species by season and study site. Bird species occurring fewer than 10 times overall were not omitted from calculations on the number of bird species, because differences in habitat diversity can influence species richness (Tramer, 1969); however, unidentified species (i.e., gulls and yellowlegs) were omitted from these calculations, as were clapper rails. We used square-root transformations to normalize species data, because they consisted of relatively small whole numbers (Steel and Torrie, 1980). Again, all data were converted to birds per area before transformation when comparing study sites.

Calculations of bird use-days were made by multiplying the mean number of individuals of a species recorded on two consecutive samples by the number of days between those samples (Rundle and Fredrickson, 1981). Use-days were calculated for all species, study sites, and seasons. Annual use-days were averaged by season and year; however, fall is representative of only one field season.

RESULTS

Waterbird Utilization

During the 19-month study period, a total of 141,426 individual birds comprising 81 species was recorded among the 1544 censuses taken on the eight study sites (Tables 15.1 and 15.2). A total of 416,709 bird use-days (6763 use-days/ha) was recorded for 80 species (excluding clapper rails). Of 77 wetland birds (75 species plus peeps and dowitchers,) 56 (72.7%) were recorded using unmanaged sites versus 76 (98.7%) using the managed sites. Average species richness was higher for the managed sites (57) versus the unmanaged sites (43) (Table 15.2). Species occurring fewer than 10 times are listed in Table 15.3. Of the 81 species identified using the study area, 78 wetland birds were grouped in the overall analysis (including peeps, dowitchers, gulls, and yellowlegs and excluding clapper rails) unless otherwise noted (Appendix 15.1). Of the 78 birds, 44 (56.4%) met the minimum criteria ($\geq$ 300 use-days overall) for calculation of average annual use-days (AUD) which totaled 222,043 average annual use-days (3603 AUD/ha).

Abiotic Factors

Environmental factors deleted from the multiple regression analysis because of high intercorrelations ($\geq .7$) with other variables were low wind speed (open marsh and Cooperfield) and salinity (Cooperfield). Also removed were wind direction and date; wind direction data were categorical, and seasonality is discussed later in the chapter.

Bird use was inversely correlated to water level on Cooperfield and the open-marsh site. Environmental factors explained 35% of the variation in the regression model for the open marsh; 63% of the variation in the number of birds was explained in the model for Cooperfield (Table 15.4). Temperature and salinity correlated with bird numbers but explained less than four percent of the variation on both sites.

Regression analysis performed by season resulted in low R^2 values for summer (.03), fall (.37), and winter (.42) for Cooperfield. Similarly, the open marsh had low R^2 values in summer (.21), fall (.38), and winter (.38). For these seasons, environmental factors explained less

Table 15.1

Waterbird groups and species utilizing Tom Yawkey Wildlife Center experimental impoundments and salt-marsh area, 1983-1984.

Bird Group	Species Code
Surface Divers	
Pied-billed Grebe (*Polilymbus podiceps*)[1]	PBG[2]
Double-Crested Cormorant (*Phalacrocorax auritus*)	DCC
Anhinga (*Anhinga anhinga*)	ANHI
Aerial Divers	
Brown pelican (*Pelecanus occidentalis*)	BPEL
Laughing Gull (*Larus atricilla*)	LGUL
Bonaparte's Gull (*L. philadelphia*)	BONE
Ring-billed Gull (*L. delawarensis*)	RBG
Herring Gull (*L. argentatus*)	HERG
Gull-billed Tern (*Sterna nilotica*)	GBT
Caspian Tern (*S. caspia*)	CAST
Royal Tern (*S. maxima*)	ROYL
Common Tern (*S. hirundo*)	COMT
Forster's Tern (*S. forsteri*)	FORT
Least Tern (*S. antillarum*)	LTRN
Black Skimmer (*Rynchops niger*)	SKIM
Belted Kingfisher (*Ceryle torquata*)	KING
Raptors	
Osprey (*Pandion haliaetus*)	OSPY
Bald eagle (*Haliaeetus leucocephalus*)	BLDE
Northern Harrier (*Circus cyaneus*)	NOHA
Red-Tailed Hawk (*Buteo jamaicensis*)	RTH
American Kestrel (*Falco sparverius*)	KEST
Peregrine Falcon (*F. peregrinus*)	PFAL

Table 15.1 Continued

Bird Group	Species Code
Waders	
American Bittern (*Botauris lentiginosus*)	ABIT
Least Bittern (*Ixobrychus exilis*)	LBIT
Great Blue Heron (*Ardea herodias*)	GBH
Great Egret (*Casmerodius albus*)	GEGT
Snowy Egret (*Egretta thula*)	SNOW
Little Blue Heron (*E. caerulea*)	LBH
Tricolor Heron (*E. tricolor*)	TRIC
Cattle Egret (*Bubulcus ibis*)	CATL
Green-backed Heron (*Butoride striatus*)	GREH
Black-crowned Night Heron (*Nycticorax nycticorax*)	BCNH
Yellow-crowned Night Heron (*N. violaceus*)	YCNH
White Ibis (*Eudocimus albus*)	WIBS
Glossy Ibis (*Plegadis falcinellus*)	GIBS
Roseate Spoonbill (*Ajaia ajaia*)	SBIL
Wood Stork (*Mycteria americana*)	WSTK
Rails	
Yellow Rail (*Coturnicops noveboracensis*)	YELO
Clapper Rail (*Rallus longirostris*)	MHEN
Virginia Rail (*R. limicola*)	VIRG
Sora (*Porzana carolina*)	SORA
Common Moorhen (*Gallinula chloropus*)	GALL
American Coot (*Fulica americana*)	COOT
Shorebirds	
Black-bellied Plover (*Squatarola sqwuatarola*)	BBPL
Wilson Plover (*Charadrius wilsonia*)	WPLV
Semipalmated Plover (*C. semipalmatus*)	SPPL
Killdeer (*C. vociferus*)	KILD
Black-necked Stilt (*Himantopus mexicanus*)	BNST
American Avocet (*Recurvirostra americana*)	VOT

Table 15.1 Continued

Bird Group	Species Code
Greater Yellowlegs (*Tringa melanoleuca*)	GYLG
Lesser Yellowlegs (*T. fauipes*)	LYLG
Solitary Sandpiper (*T. solitaria*)	SOLS
Willet (*Catoptrophorus semipalmatus*)	WLET
Spotted Sandpiper (*Actitis macularia*)	SPOT
Marbled Godwit (*Limosa fedora*)	MGOD
Semipalmated Sandpiper (*Calidris pusilla*)	PEEP
Western Sandpiper (*C. mauri*)	PEEP
Least Sandpiper (*C. minutilla*)	PEEP
White-rumped Sandpiper (*C. fuscicollis*)	PEEP
Dunlin (*C. alpina*)	DUNL
Stilt Sandpiper (*C. himantopus*)	STLT
Short-billed Dowitcher (*Limnodromus griseus*)	DOWI
Long-billed Dowitcher (*L. scolopaceus*)	DOWI
Common Snipe (*Gallinago gallinago*)	SNPE
Waterfowl	
Wood Duck (*Aix sponsa*)	WOOD
Green-winged Teal (*Anas crecca*)	GWT
American Black Duck (*A. rubripes*)	BLAK
Mottled Duck (*A. Fulvigula*)	MOTD
Mallard (*A. platyrhynchos*)	MALD
Northern Pintail (*A. acuta*)	PINT
Blue-winged Teal (*A. discors*)	BWT
Northern Shoveler (*A. clypeata*)	SHOV
Gadwall (*A. strepera*)	GADW
American Widgeon (*A. americana*)	WIDG
Canvasback (*Aythya valisineria*)	CANB
Ring-necked Duck (*A. collaris*)	RND
Lesser Scaup (*A. affinis*)	LSCP
Common Goldeye (*Bucephala clamgula*)	CGE
Bufflehead (*B. albesla*)	BUFF

Table 15.1 Continued

Bird Group	Species Code
Hooded Merganser (*Lophodytes cucullatus*)	HMER
Red-breasted Merganser (*Mergus serrator*)	RBME

---

[1] Common and scientific names of birds after AOU (1982).

[2] Species code by authors for convenience

Table 15.2

Comparison of total bird numbers and species richness by study site, 1983-1984.

	STUDY SITE[1]							
	No.1	No.2	No.3	No.4	No.5	TI	OM	CF
(n[2])	(138)	(138)	(143)	(150)	(135)	(280)	(280)	(280)
Bird numbers	2348	6063	5266	8015	12,843	937	5452	100,502
% Total	1.7	4.3	3.7	5.7	9.1	0.7	3.9	71.1
Birds/ha	302	1274	1492	1955	2052	119	402	7304
%/ha	2.0	8.6	10.0	13.1	13.8	0.8	2.7	49.0
Species richness[3]	51	56	50	54	60	33	53	69
Relative diversity[4]	0.66	0.73	0.65	0.70	0.78	0.43	0.69	0.90

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[1] TI, tidal impoundment; OM, open marsh; CF, Cooperfield.

[2] Sample Size.

[3] Number of species.

[4] Species richness/(75 species + PEEP + DOWI).

Table 15.3

Species observed fewer than 10 times during the 1983-1984 field seasons.

Species	Number of Occurrences
American Bittern (*Botaurus lentiginosus*)	1
Cattle Egret (*Bubulcus ibis*)	4
Roseate Spoonbill (*Ajaia ajaja*)	1
Wood Duck (*Aix sponsa*)	9
Canvasback (*Aytha valisineria*)	1
Lesser Scaup (*A. affinis*)	6
Ring-necked Duck (*A. collaris*)	2
Common Goldeneye (*Bucephala clangula*)	8
Bufflehead (*B. albeola*)	4
Red-breasted Merganser (*Murgus serrator*)	4
Peregrine Falcon (*Falco peregrinus*)	1
Yellow Rail (*Coturnicops noveboracensis*)	1
Virginia Rail (*Rallus limicola*)	2
Wilson's Plover (*Charadrius wilsonia*)	1
Marbled Godwit (*Limosa fedoa*)	4
Stilt Sandpiper (*Calidris himantopus*)	6
Gull-billed Tern (*Sterna nilotica*)	2
Common Tern (*S. hirundo*)	8

than 50% of the observed variation in the number of birds utilizing both sites. Water level was the most important variable; however,

Table 15.4

Environmental variables influencing bird numbers on Cooperfield and the the open marsh site, 1983-1984.

Site	Variable	B(100)[1]	x	SE	Range	F	R^2(x100)
Cooperfield							63
	Water level (cm)	-4.4	32.9	1.22	0-73	249.1*	
	Temperature (°C)	-3.0	17.6	0.53	-5-34	21.1*	
Open Marsh							35
	Water level (cm)	-0.1	92.0	2.13	1-152	122.7*	
	Salinity (ppt)	-0.1	15.6	0.59	0-32	15.5*	
	Temperature (°C)	-0.1	17.8	0.53	-4-34	9.6*	

[1] Standardized regression coefficient.

* P > F = .0001

** P > F = .002

environmental factors accounted for less than 3% of the variation in bird numbers on Cooperfield during summer. A higher percentage of the variation was explained for both sites in spring (Table 15.5). Water level explained 85% of the variation in bird numbers on Cooperfield and 47% of the variation on the open marsh.

Spring water level was the most important variable correlated with bird use on both sites. Significantly fewer birds (F = 236.7, df = 63) used the open marsh as water level and percent cloud cover increased. Fifty-one percent of the variation in the number of birds was explained by the model for the open marsh and 88% by the model for Cooperfield (Table 15.5).

The number of birds did not differ significantly (P < .05) in the t-test for morning and evening counts except in unit 5 (P < .05, t = 3.34, df = 103) during the 1983-1984 field season. However, bird numbers differed significantly (P < .05) in units 3 and 5 during morning and evening counts in

1983. The tidal impoundment (unit 6) was the only unit to differ significantly ($P < .05$, $t = 2.52$, $df = 60$) in the paired t-tests conducted on days and sites having both morning and evening counts. Sample size limited the paired t-test comparison for units 1 to 5.

The results of the t-test conducted by study site for the same time period in 1983 and 1984, January through July, were nonsignificant ($P > .05$) for all sites except unit 5, which had significantly fewer birds ($t = 2.69$, $P = .008$) and species ($t = 3.23$, $P = .001$) in 1983.

Table 15.5

Environmental factors influencing bird numbers on Cooperfield and the open marsh site during the spring 1983 and 1984.

Site	Variable	B(100)[1]	$\bar{x}$	SE	Range	F	R^2(x100)
Cooperfield							88
	Water level (cm)	-9.4	14.1	0.84	1-47	333.3*	
	Salinity (ppt)	-4.5	6.0	1.88	0-22	15.1**	
Open Marsh							51
	Water level (cm)	-1.0	90.8	5.18	1-147	60.0*	
	Cloud cover (%)	-0.3	35.2	5.23	0-100	6.1***	

[1] Standard regression coefficient.

* P > F = .0001

** P > F = .0002

*** P > F = .0164

Seasonality

Bird numbers differed significantly ($F = 74.97$, $P < .05$) in the ANOVA conducted between seasons. Bird numbers did not differ ($P > .05$) during the winter and spring but differed significantly during the fall and summer. Although an analysis of variance of the number of species by season differed significantly ($F = 11.87$, $P < .05$), Duncan's multiple comparison separated only the summer, when there were fewer numbers of individual birds and species. Appendix Table 15.2 shows the total number of birds counted by season, site and site area. The spring season had the largest number of birds, followed by winter, fall, and summer periods (Fig. 15.2). There was much annual variation in bird numbers by season and bird group (Table 15.6). More monthly use-days were recorded for surface diver, waterfowl, wader, and rail groups in 1983, and there was a 41% increase in shorebird use-days in 1984.

Shorebirds contributed 54.8% of the average annual use of the study area (Fig. 15.3), with highest numbers occurring in spring (Fig. 15.4). Included in the calculations were 13 of the 17 shorebirds (including peeps and dowitchers), and 10 species provided 97.5% of the group's average annual use (Table 15.7). Peeps contributed the most (28.6%), followed by dowitchers, dunlins, yellowlegs, and semipalmated plovers, respectively.

Waterfowl were the second largest contributor (26.8%) to the average annual use. As expected, waterfowl increased during the fall, became the predominate group during the winter (35,792 average winter use-days), and declined during the spring (Fig. 15.4.). Five species (American green-winged teal, blue-winged teal, American wigeon, hooded merganser, and coots) contributed 95.6% of the group's average annual use (Table 15.7). Coots were included with waterfowl and contributed only 8% to the group's average annual use. The common moorhen contributed 92.1% of the average annual use by rails.

Nine of fifteen species accounted for 97.6% of wading bird use. As a group, wading birds had much higher average annual use-days (AUD) during the summer (7787 AUD) and fall (9933 AUD) than the other groups (Figs. 15.4 and 15.5). White ibis, great blue heron, great egret, little blue heron, snowy egret, and the tricolor heron contributed 82.6% of the wader group average annual utilization.

Of the 13 aerial diver species, 5 provided 91.6% of the group's use (Table 15.7). Laughing and ring-billed gulls were the most numerous, contributing 40.7% of the group's average annual use. Laughing gulls were more common during the spring through fall; ring-billed gulls were more abundant during the fall and winter. Similarly, caspian terns were predominant during the fall through winter, and royal terns during the summer.

Pied-billed grebes, double-crested cormorants, and anhingas contributed 100% of the surface diver group utilization. Both the surface and aerial diver groups were more prevalent during the summer and fall periods, and both became less numerous during the winter and spring (Figs. 15.4 and 15.5).

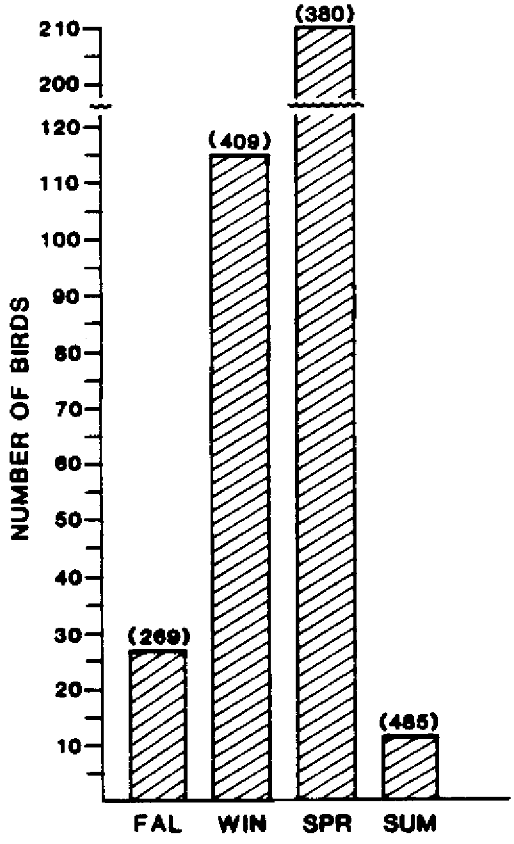

Figure 15.2 Relative number of birds counted per sample (N) by season, 1983 to 1984.

Table 15.6 Annual bird use-days by month and bird group, 1983-1984.

	Surface Divers		Aerial Divers		Waders		Raptors		Shorebirds		Rail		Waterfowl	
	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984
January	222	424	401	941	272	1521	23	61	494	8027	42	48	8628	16,607
February	787	118	428	420	3517	1454	110	100	4469	7004	398	1	10,562	12,218
March	647	177	279	757	2285	1346	94	138	8184	19,093	169	0	26,282	16,876
April	188	183	530	141	5656	599	90	50	40,488	56,605	340	106	20,707	1796
May	86	44	251	195	1364	1897	61	4	16,134	75,700	323	51	656	132
June	247	47	132	33	1040	638	25	23	364	410	353	42	353	38
July	513	96	152	118	2282	1092	25	18	115	185	221	89	62	38
August	500	-[1]	612	-	2839	-	44	-	464	-	76	-	2	-
September	365	-	638	-	2420	-	30	-	281	-	52	-	0	-
October	479	-	291	-	3584	-	62	-	446	-	50	-	2	-
November	1950	-	1128	-	3179	-	50	-	1046	-	34	-	547	-
December	918	-	1116	-	3142	-	53	-	1747	-	8	-	1952	-

[1] No data collected from August to December 1984.

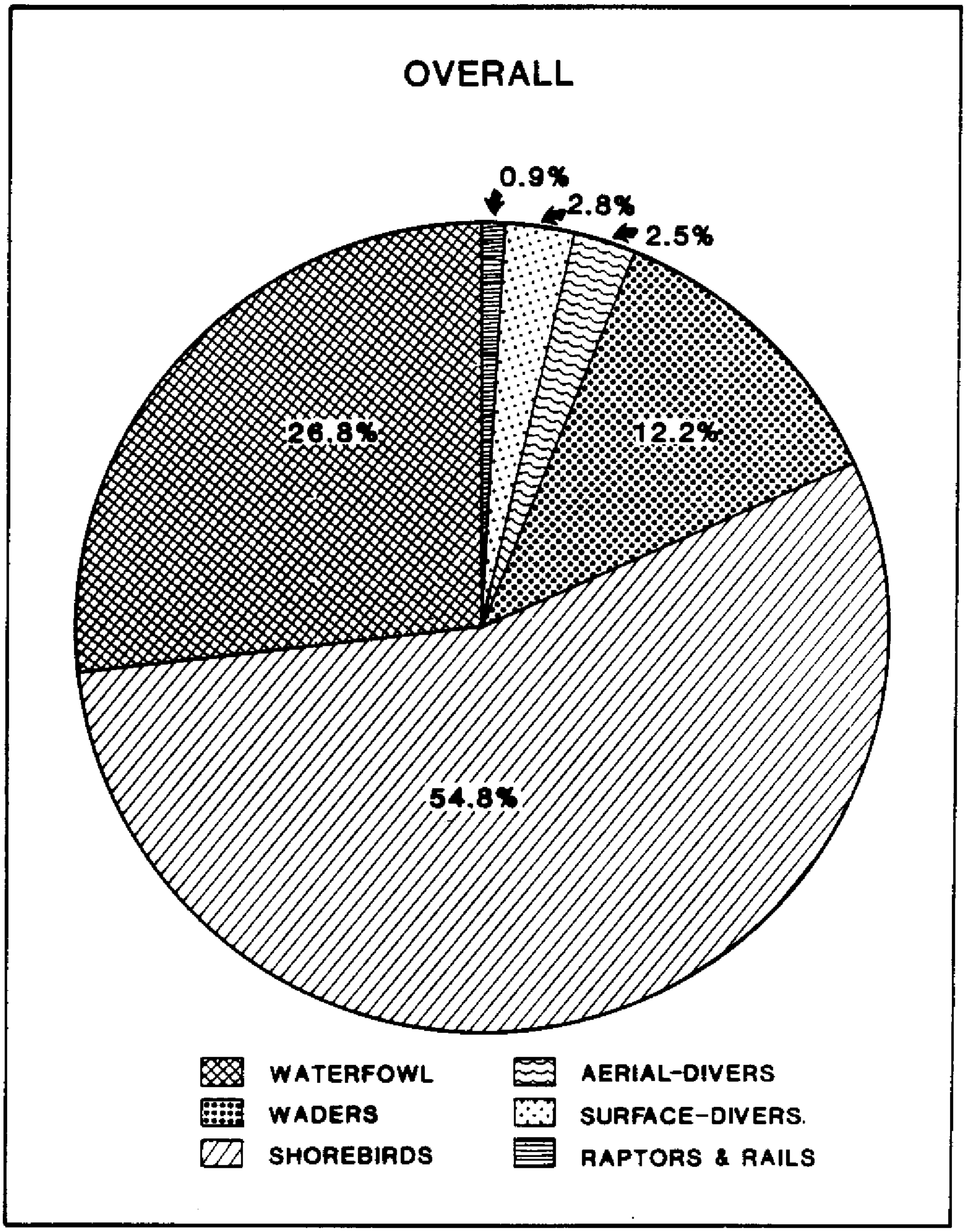

Figure 15.3 Relative average annual use-days for seven waterbird groups, 1983 to 1984.

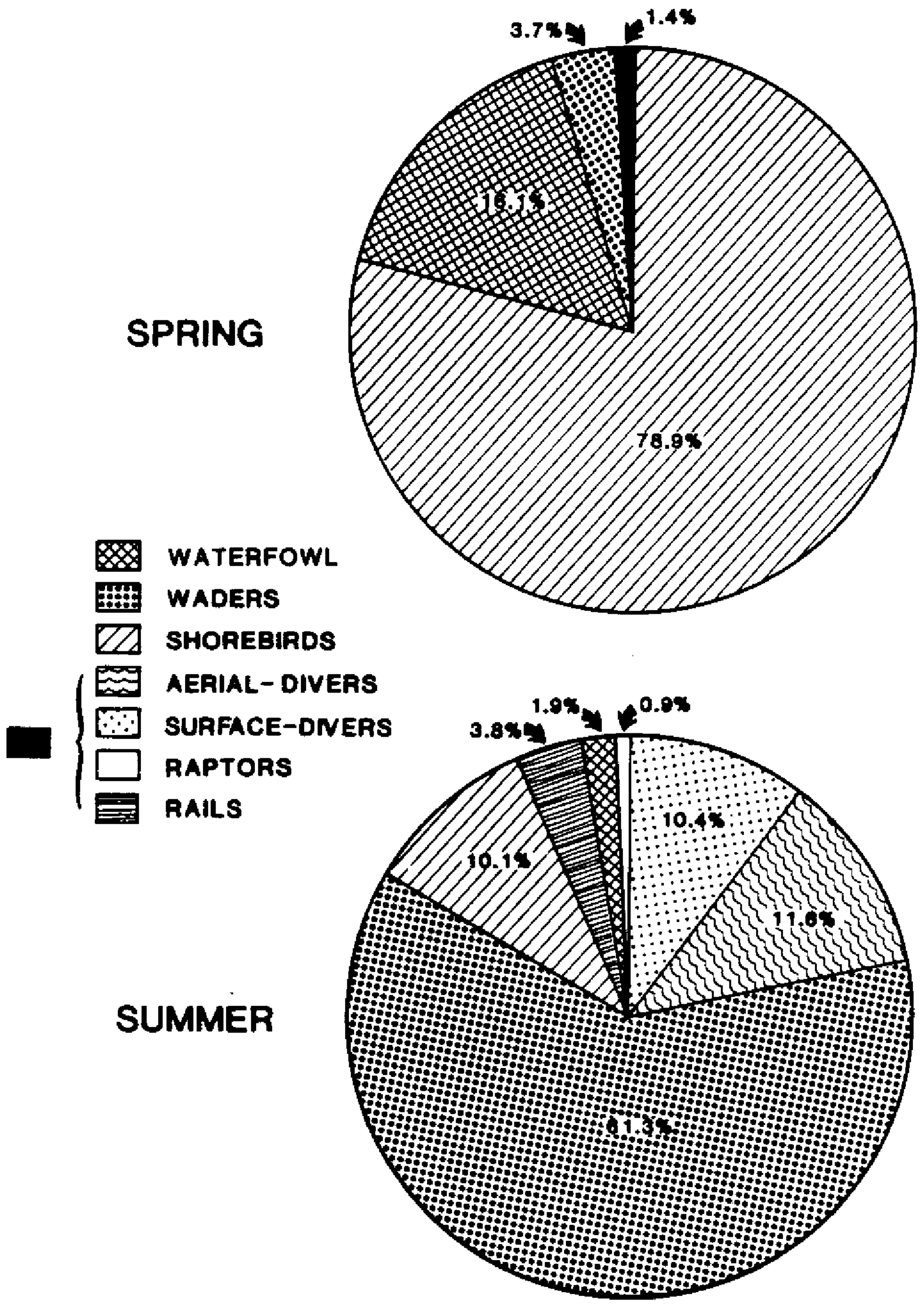

Figure 15.4 Average spring and summer utilization by seven waterbird groups, 1983 to 1984.

Table 15.7

Average annual and seasonal bird use-days for selected wetland-associated birds, 1983-1984.

	Winter	Spring	Summer	Fall[1]	Average Annual	Grand Total
Surface Divers						
PBG[2]	792	178	442	1339	2751	-
DCC	150	253	19	1842	2264	-
ANHI	4	55	991	166	1216	6231
Aerial Divers						
LGUL	38	300	331	588	1257	-
RBG	540	123	0	375	1038	-
CAST	77	25	8	832	942	-
GULL[3]	310	116	32	290	748	-
KING	169	48	63	379	659	-
ROYL	0	2	476	37	515	-
Other Divers[4]	197	132	112	33	474	5633
Waders						
WIBS	1266	473	887	3093	5719	-
GBH	676	447	1102	3156	5381	-
GEGT	408	1018	2706	971	5103	-
LBH	760	958	920	744	3382	-
SNOW	1162	586	516	1012	3276	-
TRIC	249	358	622	735	1964	-
BCNH	50	374	196	176	796	-
LBIT	108	424	6	0	538	-
GIBS	0	90	542	62	694	-
Other Waders	1	56	263	11	331	27,184

Table 15.7 Continued

	Winter	Spring	Summer	Fall[1]	Average Annual	Grand Total
Raptors						
OSPY	32	96	113	24	265	-
NOHA	88	53	2	77	220	-
Other Raptors	80	18	6	52	156	641
Shorebirds						
PEEP[5]	847	32,858	994	93	34,792	-
DOWI[6]	4882	23,515	115	846	29,358	-
DUNL	4986	19,485	0	264	24,735	-
LYLG	570	14,488	28	495	15,581	-
SPPL	36	5886	70	36	6028	-
GYGL	1332	2568	11	571	4482	-
YLG[7]	1471	2026	0	98	3595	-
BBPL	202	672	16	24	914	-
BNST	0	491	22	0	513	-
AVOT	392	5	0	0	397	-
WLET	18	306	14	0	338	-
SPOT	0	208	4	42	254	-
KILD	80	148	0	0	228	-
SPE	132	64	0	12	208	-
Other Shorebirds	23	115	10	0	148	121,571
Rails[8]						
GALL	296	341	473	87	1197	-
Other Rails	14	74	8	6	102	1299

Table 15.7 Continued

	Winter	Spring	Summer	Fall[1]	Average Annual	Grand Total
Waterfowl						
GWT	21,526	11,260	4	209	32,999	-
BWT	3733	7838	11	550	12,132	-
WIDG	4604	966	0	42	5612	-
IMER	2003	12	0	1576	3591	-
COOT	2347	62	18	96	2523	-
SHOV	554	296	0	0	850	-
MOTD	46	386	200	5	637	-
GADW	393	92	0	0	485	-
PINT	488	8	0	0	456	-
Other Waterfowl	138	33	14	14	199	59,484
	Total average annual use-days			=		222,043

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[1] Reflects fall 1983.

[2] See Table 1 for species codes.

[3] Immature and unidentified gulls (Laurs spp.).

[4] Includes other waterbird (group) species with < 300 use-days overall (Appendix 15.1).

[5] Includes least, semipalmated, western, and white-rumped sandpipers.

[6] Includes short- and long-billed dowitchers.

[7] Unidentified yellowlegs (Tringa spp.).

[8] See Fig. 15.7 for clapper rails. American coots are grouped with waterfowl.

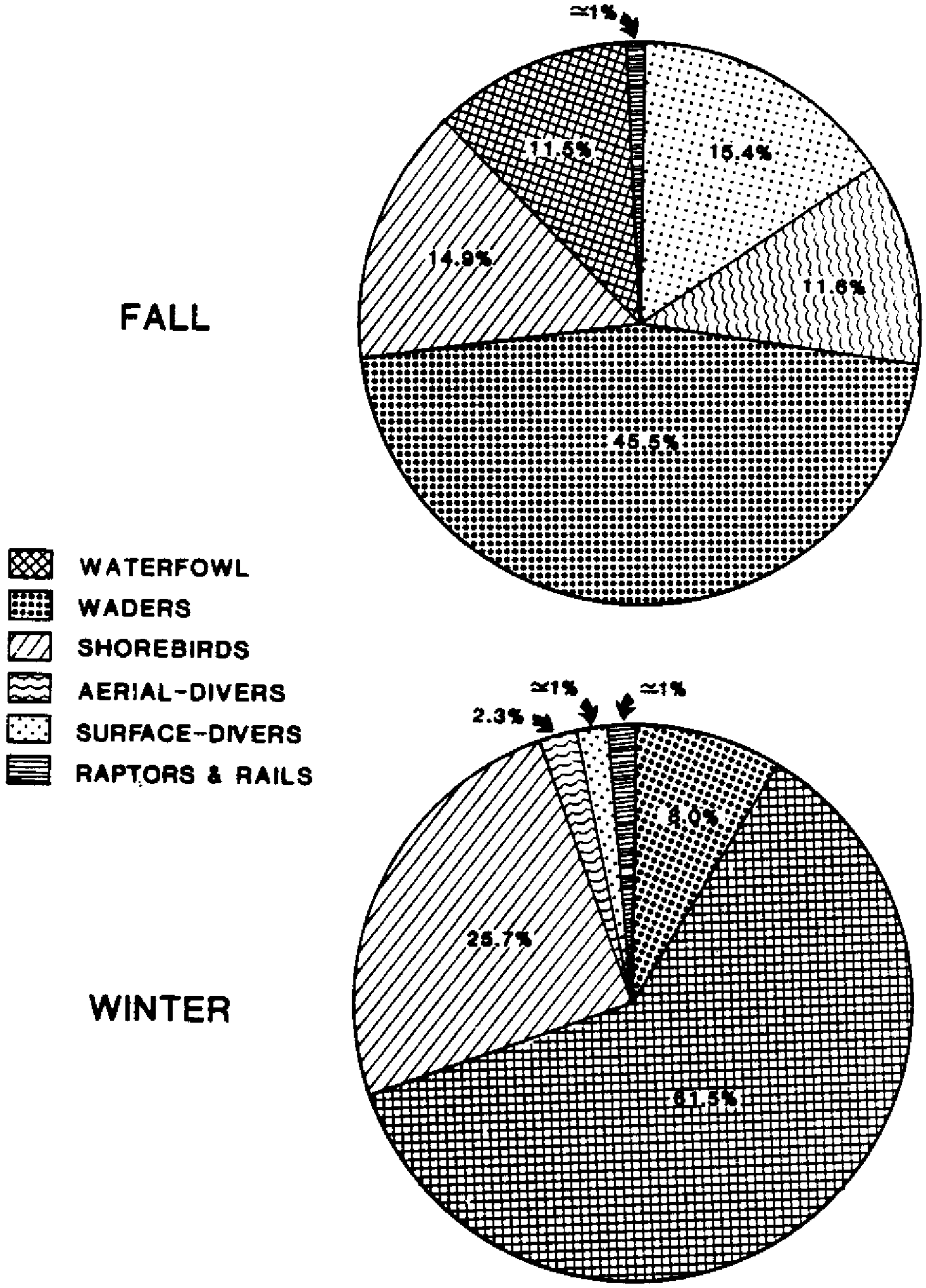

Figure 15.5 Average fall and winter utilization by seven waterbird groups, 1983 to 1984.

Two of the six raptor species (osprey and northern harrier) contributed 75.7% of the group's use. Southern bald eagles average 81 AUD and were more common on the study area from January through April. Similarly, the northern harrier occurred most frequently from September through April. Although the osprey was recorded during every month except January, it occurred predominantly from March through September.

Seasonal Site Utilization

The number of birds recorded among study sites differed significantly ($P < .05$) during fall ($F = 44.5$), winter ($F = 62.7$), spring ($F = 44.5$), and summer ($F = 19.1$). Generally, there was much seasonal variation in bird use among study sites (Table 15.8). The most used sites were the managed ones: unit 2 during the fall; Cooperfield and unit 4 during winter; Cooperfield again in the spring, and unit 3 during summer. The tidal impoundment was least used in all seasons. Similarly, fewer birds used the open marsh in all seasons except summer. During summer, bird use of the open marsh did not differ ($P > .05$) from units 2, 4, 5, or Cooperfield, but had significantly more birds per area than unit 1 and the tidal impoundment. The regression analysis indicated that bird numbers increased in the open marsh with increasing air temperature. Significantly fewer species of birds were observed on the open marsh during the summer, although the number of birds remained generally high (Tables 15.8 and 15.9). Wading birds were predominant (61.3%) during the summer (Fig. 15.4, Table 15.6). Although the regression procedure did not correlate bird numbers with the summer water level in Cooperfield, we feel that increasing the water level during the summer may have inhibited some bird use of impoundments.

The number of species differed significantly ($P < .05$) by study site for fall ($F = 62.1$), winter ($F = 62.2$), spring ($F = 47.0$), and summer ($F = 65.3$). Duncan's multiple comparison indicated high seasonal variation in the number of species using each site (Table 15.9). The relative number and diversity of birds using each site during the study are presented in Table 15.2. Approximately 71% of the total number of birds (49% birds/ha) and 90% of the species richness were recorded on the larger impoundment (Cooperfield). The tidal impoundment (unit 6) ranked lowest in all cases. The general distribution of site utilization is shown in Fig. 15.6.

Table 15.8 Multiple comparison of the number of birds per observation by season and site, 1983-1984.

Study Site[1]	Fall			Winter			Spring			Summer		
	N[2]	Mean[3]	Group[4]	N	Mean	Group	N	Mean	Group	N	Mean	Group
1	22	1.83	c	38	2.16	c	36	1.62	e	42	1.25	c
2	23	4.02	a	39	5.34	b	37	2.44	d	39	1.62	b
3	22	2.84	b	38	5.19	b	41	2.95	cd	42	2.03	a
4	20	2.47	b	38	8.11	a	41	3.72	c	51	1.65	b
5	21	1.77	c	34	5.77	b	33	7.90	b	47	1.48	b
TI	53	1.15	d	74	1.12	d	64	1.16	e	88	1.12	c
OM	53	1.36	d	74	1.52	d	64	1.54	e	88	1.53	b
CF	53	2.58	b	74	8.42	a	64	13.31	a	88	1.63	b

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[1] TI, tidal impoundment; OM, open marsh; CF, Cooperfield.

[2] Number of samples.

[3] Mean number (log) of birds per 0.4 ha (acre).

[4] The same letter(s) (grouping) are not significantly different.

Table 15.9 Multiple comparison of the number of species per observation by season and study site, 1983-1984.

Study Site[1]	Fall			Winter			Spring			Summer		
	N[2]	Mean[3]	Group[4]	N	Mean	Group	N	Mean	Group	N	Mean	Group
1	22	0.60	c	38	0.54	c	36	0.47	d	42	0.44	d
2	23	1.11	a	39	0.86	a	37	0.79	bc	39	0.70	b
3	22	0.95	b	36	0.77	b	41	0.72	c	42	0.80	a
4	20	0.87	b	38	0.93	a	41	0.78	bc	51	0.70	b
5	21	0.65	c	34	0.76	b	33	0.86	ab	47	0.56	c
TI	53	0.29	d	74	0.26	e	63	0.28	e	88	0.27	e
OM	54	0.38	d	74	0.43	d	64	0.40	d	88	0.44	d
CF	54	0.66	c	74	0.72	b	64	0.91	a	88	0.52	c

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[1] TI, tidal impoundment; OM, open marsh; CF, Cooperfield.

[2] Number of samples.

[3] Means reflect the average number (log) of species per 0.4 ha (acre).

[4] The same letter(s) are not significantly differenct.

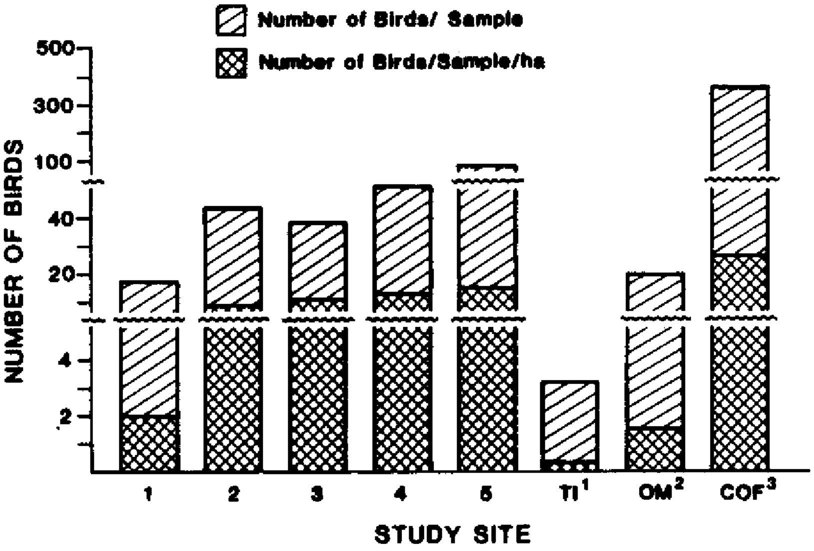

Figure 15.6 Number of birds by sample and site area, 1983 to 1984.

Bird use among study sites differed significantly ($F = 77.86$, $P < .05$). The mean number of birds per area (85.6) was significantly higher ($P < .05$) for Cooperfield (Duncan's multiple range test). The mean number of birds per area for units 2 to 5 (19.3 to 26.1) did not differ significantly ($P > .05$) but differed from unit 1 (5.2) and the open marsh (4.4); the latter two areas were similar (Fig. 15.6). Significantly fewer birds (3.1) and species used the tidal impoundment. The same pattern of site use is reflected in the percent-utilization figures (Table 15.10). There was, however, much higher use of the unmanaged sites by clapper rails (Fig. 15.7).

As a group, shorebirds preferred the managed units, particularly Cooperfield (43.8%) and unit 5 (24%), to the unmanaged sites (Table 15.10). The average annual use of managed units by shorebirds was 2224.5 use-days/ha; it was 124 use-days/ha for the unmanaged sites. Unit 2 had relatively fewer shorebird use-days (4.6%) per hectare than the other managed units, which probably resulted from the lack of drawdown of unit 2 in 1984 (Table 15.5).

Similarly, there was higher waterfowl use of the managed sites, particularly Cooperfield (41.5%). The average use of managed units by waterfowl was 1141 use-days/ha; it was 30 use-days/ha for the unmanaged sites (Table 15.10). Unit 2 had relatively high (15.6%) waterfowl (particularly mottled ducks), surface diver (25.3%), and wader (27.8%) use (Table 15.10).

Waders provided relatively high (12.2%) use of the study area (Fig. 15.3). Annual use of the managed units by waders average 580 use-days/ha; the unmanaged sites averaged 186 annual use-days/ha (Table 15.10). Similarly, there was higher use of managed sites by surface and aerial diver and rail (excluding clapper rail) groups; there was similar use of managed and unmanaged sites by the raptor group (Table 15.10).

Roosting Counts

Our evening counts did not include roosting birds; however, during September and October of 1983, six late-evening counts (1800 to 1900 hr) were made to determine the number and composition of waterbirds roosting in the trees and snags adjacent to Cooperfield, mainly in the Reserve Pond area. A total of 3192 birds (average = 532) of eight species were recorded during the six counts. The white ibis (45.9%) and great egret (42.3%) comprised the greater porportion (88.2%) of eight species (Table 15.11). From these data a total of 15,734 use-days (average 3146.7 ± 1163) was calculated between 13

Table 15.10

Average annual bird use-days per hectare by study site for wetland-associated birds having ≥ 300 use-days overall, 1983-1984.

	Study Site[1]							
	1	2	3	4	5	TI	OM	CF
Surface Divers								
PBG[2]	35	107	64	109	47	1	5	58
DCC	28	82	11	8	39	1	17	81
ANHI	3	17	10	13	8	4	2	68
AUD[3]/ha	66	206	85	130	94	2	24	207
Aerial Divers								
LGUL	7	23	69	30	25	0.4	11	30
RBG	2	12	17	10	16	1	9	47
CAST	6	8	21	10	14	0	3	62
GULL[4]	4	9	5	26	13	1	6	28
KING	13	21	24	41	6	4	9	15
ROYL	3	2	28	11	7	0	1	20
Other Divers[5]	2	12	11	8	9	2	6	14
AUD/ha	37	87	175	136	90	8	45	216
Waders								
WIBS	21	307	55	63	25	27	111	127
GBH	70	238	124	68	73	14	29	148
GEGT	30	138	304	96	58	11	53	115
LBH	21	145	112	90	21	1	4	113
SNOW	19	126	56	50	20	18	65	72
TRIC	13	74	69	82	22	7	12	41
BCNH	4	6	24	10	5	2	4	37

Table 15.10 Continued

	Study Site[1]							
	1	2	3	4	5	TI	OM	CF
LBIT	10	21	19	10	23	4	2	14
GIBS	0	11	0	11	2	2	0.1	30
Other								8
Waders	1	6	12	1	9	1	5	8
AUD/ha	189	1072	775	481	258	87	285	705
Raptors								
OSPY	3	2	4	2	2	1	3	12
NOHA	5	0.4	3	3	4	8	5	1
Other								
Raptors	4	3	1	3	2	2	0.2	4
AUD/ha	12	5	8	8	8	11	8	17
Shorebirds								
PEEP[6]	37	52	216	280	1259	34	105	1655
DOWI[7]	72	189	599	499	624	28	20	1484
DUNL	17	104	337	378	535	0	9	1301
LYLG	40	92	77	174	483	7	3	779
SPPL	0	1	51	140	163	6	7	298
GYLG	29	107	67	84	64	6	10	188
YLG[8]	37	43	141	77	49	4	3	139
BBPL	0	6	12	27	32	0	3	36
BNST	0.4	4	3	6	7	0	0.2	30
AVOT	0	0	0	0	2	0	0	28
WLET	0	0	1	28	28	0	2	1
SPOT	5	44	9	7	1	0	0.1	8
KILL	0	8	8	21	9	0	0	2
SNPE	8	15	7	6	0	1	0	1
Other								
Shorebirds	0.3	0	0.3	2	5	0	0.3	8
AUD/ha	246	625	1528	1729	3261	86	163	5958

Table 15.10 Continued

				Study Site[1]				
	1	2	3	4	5	TI	OM	CF
Rails[9]								
GALL	31	17	30	26	22	0	0.2	38
Other Rails	8	1	1	1	7	0	0	0
AUD/ha	39	18	31	27	29	0	0.2	38
Waterfowl								
GWT	126	630	353	859	653	26	2	1448
BWT	30	109	11	17	37	0	1	745
WIDG	9	59	2	234	3	0	0.3	310
HMER	4	249	216	112	28	0.1	27	44
COOT	11	4	0	1	2	0	1	174
SHOV	1	1	0	25	21	0	0.1	44
MOTD	7	20	7	9	7	1	1	26
GADW	0	0	0	1	6	0	0	32
PINT	0	1	0	0	0	0	0	33
Other Waterfowl	2	7	0.6	1	6	0	1	8
AUD/ha	290	1080	590	1259	763	27	33	2864
TOTAL AUD/ha	879	3093	3192	3770	4503	221	558	10,005
% Utilization	3.4	11.8	12.2	14.4	17.2	0.8	2.1	38.2

Table 15.10 Continued

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[1] TI, tidal impoundment; OM, open marsh; CF, Cooperfield.

[2] See Table 15.1 for species codes.

[3] AUD = average annual bird use-days.

[4] Unidentified or immature <u>Larus</u> spp.

[5] Other category includes species having <300 use-days overall.

[6] Includes least, semipalmated, western and white-rumped sandpipers.

[7] Includes short- and long-billed dowitchers.

[8] Unidentified yellowlegs (<u>Tringa</u> spp.)

[9] See Fig. 15.7 for clapper rails; American coots are grouped with waterfowl.

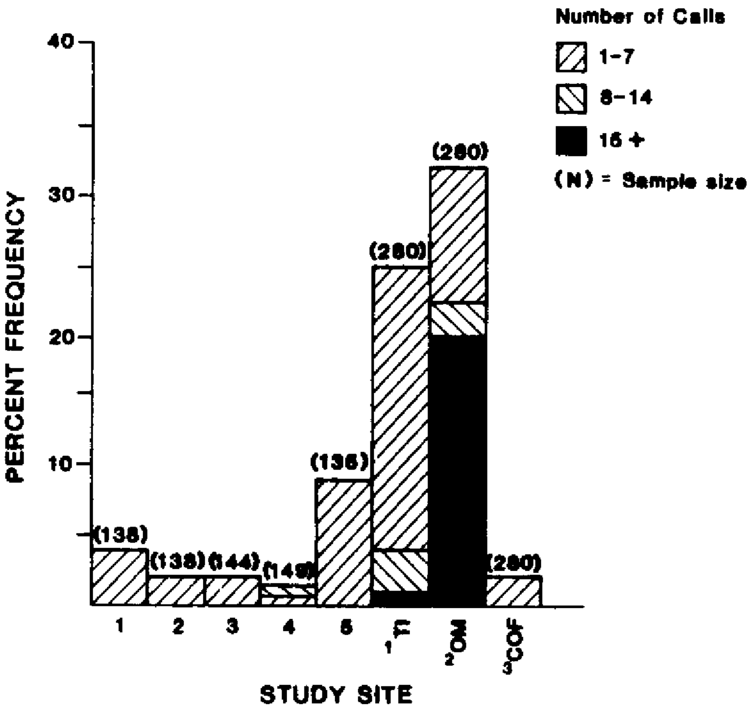

Figure 15.7 Percent frequency of clapper rail calls recorded by study site, 1983 to 1984.

September and 17 October. The main flight directions to the roost were from the southeast, south, and southwest, respectively.

Table 15.11

Evening counts of birds roosting behind Cooperfield, September-October, 1983.

Species	9/13	9/16	9/23	10/3	10/13	10/17	Total	X	± one SD
ANHI	31	6	10	3	7	7	64	10.7	10.2
WIBS	5	47	177	139	440	57	1465	244.2	253.2
GEGT	451	488	170	26	181	34	1350	255.0	200.6
GBH	1	4	6	0	0	4	15	5.0	2.5
WSTK	3	5	2	0	0	0	10	1.7	2.1
SNOW	0	0	7	61	82	99	249	41.5	44.6
LBH	0	0	0	0	19	3	22	3.7	7.6
TRIC	0	0	0	0	9	8	17	2.8	4.4
Totals	491	550	372	229	738	12	3192	532.0	219.2

Widgeon Grass Production

Measurement of widgeon grass production is summarized in Table 15.12 and reflects weights of stems, leaves, and seeds remaining on plants at the time of sampling. Because of extreme drought conditions, high diurnal water temperature during late July ranged from 30 to 34°C in the impoundments and about 28 to 29°C in the tidal creek.

Salinities generally ranged from 23 to 30 ppt during this period, and a decline in widgeon grass was observed. Widgeon grass production was below normal during the 1983 growing season and steadily declined from an average of 58.9 g/m^2 (oven-dry) in August 1983 to its disappearance in February 1984 in the four impoundments sampled. No measurements were taken on seed production during this study.

Alligator Observations

Observations of 502 alligators were made during the 19-month study period; 61.2% were small (< 1.5m) alligators. Overall, more alligators were counted on Cooperfield, the open marsh and unit 3 (Fig. 15.8). No alligator

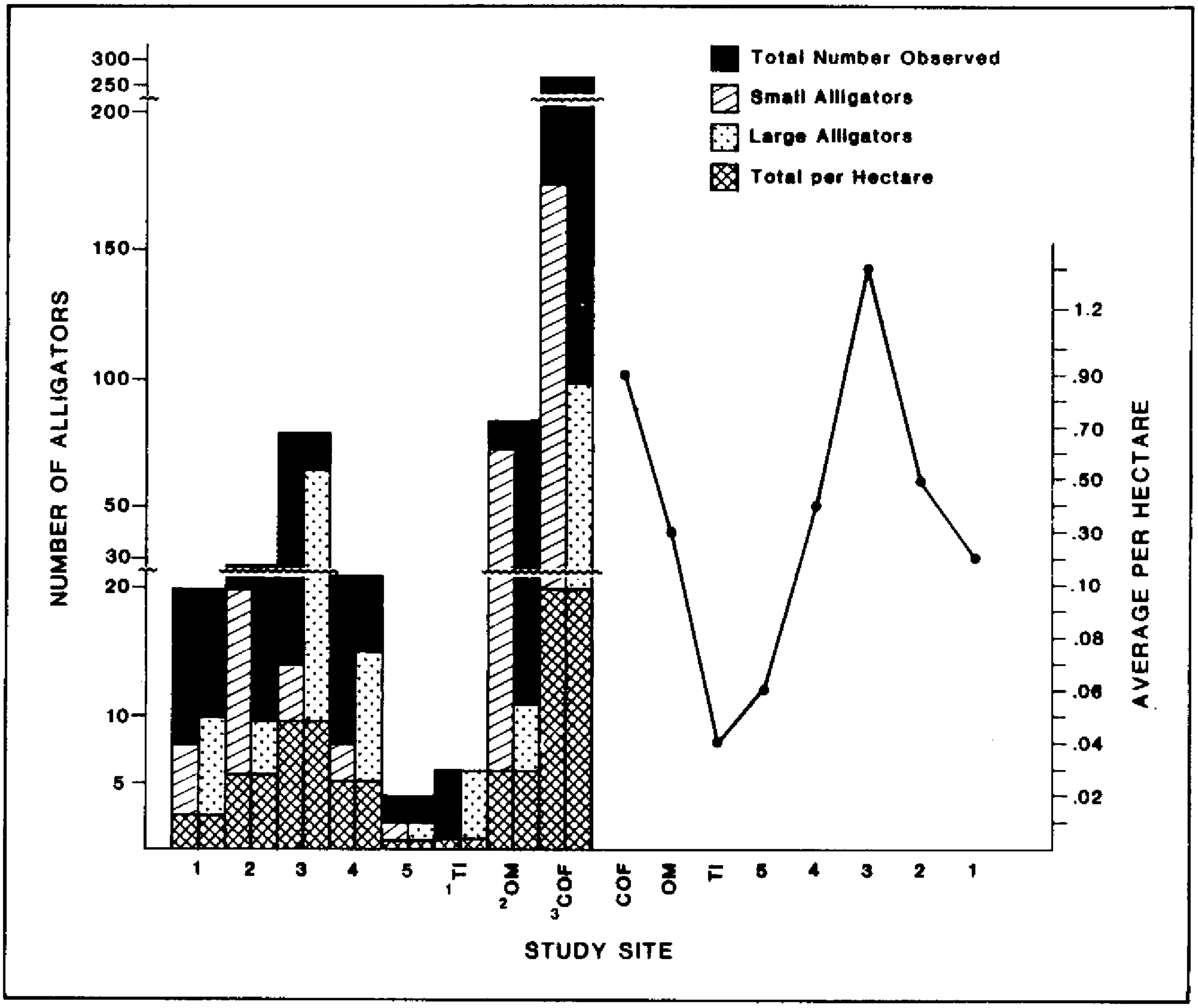

Figure 15.8 Total and average number of alligators counted by study site, 1983 to 1984.

nesting activity was observed during the study. Significantly more alligators/ha were observed on Cooperfield than the other sites. This may have been due to the proximity of Cooperfield to a freshwater pond. Units 2, 3, 4, and the open marsh had approximately the same numbers (per area). Units 1 and 5 and the tidal impoundment received the lowest utilization. As illustrated in Fig. 15.9, unit 3 had above-average alligator numbers that probably resulted from a short-term increase in prey fish and crab availability. Alligators were observed in all months except December, January, and February.

Table 15.12

Seasonal availability of *Ruppia maritima*, in measured biomass (g/m^{2}dry weight), by sample period and site, 1983-1984.

	Aug.[2]		Oct		Dec		Feb	
Site	In[1]	Out	In	Out	In	Out	In	Out
2	-	199.47	69.00	19.10	Trace	0.0	Trace	Trace
4	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	-	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CF[3]	-	0.0	36.27	14.40	18.00	0.0	0.0	0.0
Mean	-	58.93	20.85	9.25	0	0.0	0	0
± one SD		110.53	32.81	10.69	-	-	-	-

[1] In = inside exclosure; Out = outside exclosure.

[2] No sample taken inside exclosure; weights reflect the mean from one sample outside each of three exclosure in each unit for August.

[3] CF = cooperfield.

DISCUSSION

We identified 81 waterbird species using the study area during the 19-month study period. The species count included approximately 90% of the

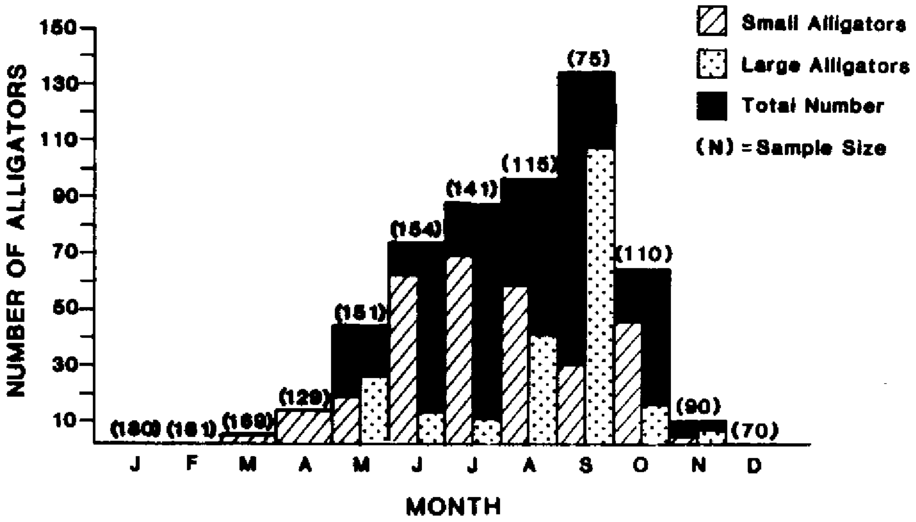

Figure 15.9 Seasonal distribution of numbers of alligators, 1983 to 1984.

waterbirds characteristic of the brackish intertidal coastal zone (Forsythe, 1978). Of 77 wetland birds (75 species plus peeps and dowitchers), 56 (72.7%) were counted using unmanaged sites and 76 (98.7%) using the managed sites. This contrasts to the 68 waterbird species previously reported for South Carolina impoundments (Sandifer et al., 1980) and the 94 bird species recorded using the high-salinity North Inlet estuarine marsh system (Christy et al., 1981; Bildstein et al., 1982a). The latter studies, however were conducted over a much larger area and recorded 15 bird species (e.g., Passeriformes and Strigiformes) not targeted in our study. Also, the sandy back beach portions of DeBordieu and North Islands were included in the North Inlet study, producing three sandpiper species (Arenaria interpres, Calidris canutus, Crocethia alba) not characteristic of salt-marsh habitats (B. Christy, personal communication). Thus removing nontarget species (including black vultures, Coragyps atratus, and turkey vulture, Catharetes aura) from their list resulted in fewer species (74) for the North Inlet marsh than observed during our study. Eleven other waterbirds observed using larger impoundments on the Tom Yawkey Wildlife Center and not recorded during this study were: fulvous whistling-duck, Dendrocygna bicolor; tundra swan Cygnus columbianus; white-fronted goose, Anser albifrons; snow goose, Chen caerulescens; canada goose, Branta canadensis; redhead, Aythya americana; greater scaup, A. marila; ruddy duck, Oxyura jamaicensis; black rail, Laterallus jamaocensis; whimbrel, Numbernius phaeopus; and black tern, Chlidonias niger. Adding these birds to the species count would increase species richness to 87 for managed units. However, average relative diversity (species richness/75 species plus peeps and dowitchers) was higher (0.74) for the six managed units (range,= 0.66 to 0.90) than the open marsh (0.69) or the tidal impoundment (0.43) (Table 15.2).

Water level was the most important abiotic variable during this study and was inversely correlated with bird use (Tables 15.4 and 15.5). The correlation of bird numbers with air temperature on both sites (Table 15.4) may have been confounded with season (Fig. 15.2, Table 15.8).

There was 77-cm mean difference in water level between unmanaged and managed sites during the spring; it was 59 cm overall. Tidal range varied from about 0 to 92 cm in the open marsh and 56 to 152 cm in the tidal creek twice daily. Impoundment water levels were more stable and seasonally predictable, ranging from 0 cm (spring) to about 73 cm (late summer), gradually reducing over the winter. There was no mean difference in salinity between Cooperfield and the open marsh during the spring; it was only 1.6 ppt difference overall. Again, seasonality may have confounded salinity.

Waterbird numbers significantly correlated with water level on both sites. Tidal, temporal, and weather-related factors such as percent cloud cover can influence the behavior and activity patterns of waterbirds (Burger, 1983). In particular, water level directly influences availability of prey and foraging habitat (Catts et al., 1963; Custer and Osborn, 1978; Chadbreck, 1979; Connors et al., 1981; Howard and Lowe, 1984). Gradual water-level reductions from fall through late winter allow waterfowl greater access to aquatic vegetation and deposited seeds. Other physical factors (e.g., extreme temperature or rainfall) may directly and indirectly influence resource use in birds (Kushlan, 1981), especially for birds foraging visually during periods of high water turbidity or ice.

Most units did not differ between morning and evening counts. Differences were observed in the tidal impoundment and units 3 and 5. Burger et al. (1977) found shorebird activity patterns to be a function of tide time rather than time of day. Although avian activity is usually higher in the morning (Robbins, 1981a), our sampling concentrated in the highest activity periods to maximize data collection.

Low dissolved oxygen increases prey availability at the surface, and probably is a factor associated with high morning use of managed units by fishing birds and alligators during stress periods (Kushland, 1976). Low dissolved oxygen was not a factor in the tidal impoundment, which had greater morning use by birds. Other important factors (i.e., feeding rhythm, wind, and water-surface conditions) probably increase morning activity periods.

Although annual variation in waterbird populations using tidal estuaries is not uncommon (Carnnell, 1983), only unit 5 had significantly fewer individual birds and species in 1983. Some variation is to be expected, depending on regional and local bird distribution, resource availability, and habitat manipulation among nearby resource managers. The majority of waterbirds sampled during this study are migratory; therefore, any particular bird species' or groups' importance may be a function of season (Figs. 15.4 and 15.5).

The number of individual birds and species differed between season; the most-used sites were the managed units except during the summer, when use of the open marsh increased and was similar to most managed units (Table 15.8). The least-used sites were unit 1, the tidal impoundment, and the open marsh (Table 15.10, Fig. 15.6).

The managed units had high foraging bird (waders, aerial divers, cormorants) activity during the fall. The regression model for Cooperfield indicated that bird numbers increased with decreasing air temperature. In contrast, fewer birds were counted with decreasing temperatures in the open marsh. The progressive increase in prey (fish, shrimp, crab) numbers and biomass through the summmer was concentrated in impoundments with immigration with maturation of larval forms. During summer, the open marsh had similar bird numbers but fewer bird species (per area). Prey become lethargic and easier to catch with cooler fall temperatures and were also influenced by high numbers of migratory birds. Feeding behavior dominated activities of birds using managed and unmanaged sites (Epstein and Joyner, unpublished data).

As noted by Reeves (1983), birds formed feeding aggregations during the fall season. Cormorants formed swimming groups (about 6 to 75 individuals) and, together while actively feeding, would maneuver abundant prey into sections of the impoundments. Subsequently, aggregations of aerial divers (including kingfishers) fed in front of the advancing cormorants, occasionally robbing prey. Similarly, very numerous wading birds were actively feeding on fleeing prey. Snowy egrets and tricolor herons ran along dike edges, just in front of the cormorants, catching prey attempting to escape. These observations (Table 15.8, Fig. 15.5) and other research (Kushlan, 1976; Howard and Lowe, 1983; Barlow and Bock, 1984) suggest that fishing birds and alligators can reduce the standing crop of prey in some situations.

Birds concentrate in managed units during certain periods. Hypothetically, this may cause a shift or transfer of prey mortality by feeding birds from the open marsh to the managed units, which temporarily would reduce prey mortality rates in the open marsh system. Birds were particularly active on managed units from late October to mid-November

1983. There was less use of impoundments by foraging birds as the abundance of prey slowly decreased, but more use by migratory waterfowl during the winter and shorebirds during the spring. Gradual water-level reductions from winter to spring to increase widgeon grass availability for waterfowl also increased prey and habitat availability for other waterbirds. This suggests that management of coastal brackish impoundments can be directed toward several wildlife groups, particularly during seasonal or critical periods, and supports the findings of Fredrickson and Taylor (1982) for freshwater areas. Overall, species richness for the open marsh was similar to the smaller units (Table 15.2), but the number of species and individual birds differed by season (Table 15.8 and 15.9).

The larger unit (Cooperfield) had greater numbers of individual birds and species per hectare than the other sites. Cooperfield also had greater waterbird use in winter (waterfowl) and spring (shorebird), and higher average annual use-days for some species such as bald eagle (54.7%), osprey (58.5%), american avocets (97%), and mottled ducks (56.1%). The ability of large wetlands to attract bird populations has been attributed to habitat diversity and large food supplies (Weller and Fredrickson, 1974; Swiderek, 1982).

Waterbird use of units 2 to 5 did not differ, but these units were used more than unit 1 and the open marsh. Fewer numbers and species of birds were counted on the tidal impoundment (unit 6). This may have been due to the elevation of the bed, dense emergent habitat, and no interspersion of open water (Baldwin, 1967). The importance of any one particular site varied with bird group and species; however, for example, northern harriers and clapper rails used sites having greater emergent cover (units 1, 5, and both unmanaged sites) (Table 15.10, Fig. 15.6). As noted by Shoemaker (1964), clapper rails occur primarily in areas similar to the unmanaged sites. Bildstein et al. (1982b) showed that clapper rails are a significant component of the open, salt-marsh community in South Carolina.

Apparently, unit 5 functioned separately from the other units, having varying but high levels of bird use. The water-control structure of unit 5 was very old and did not function to its full capacity during the study, allowing unwanted tidal exchange. This provided abundant sheet water on the bed of unit 5 during the drawdown of the second field season and may have increased habitat and resource availability for shorebirds (i.e., softer bottoms for probing birds). Moreover, overall shorebird use increased during the second field season, probably because the drawdown was extended during that season. As noted by Burger et al. (1977), shorebirds concentrate and feed in wetter mud-flat areas such as depressions and ditch edges of impoundments that retain 1 to 2 cm of water after drawdown. Shorebird use of the managed units was five times higher than that reported by Rundle and Fredrickson (1981) in Missouri.

Although waterfowl were the primary target species of management, shorebirds dominated (53%) the use of impoundments (2224 AUD/ha), and highest numbers occurred in the spring. Of the 21 shorebird species, 10 accounted for 97.5% of the group's average annual use of impoundments. Shorebird use was lowered when managed units were reflooded in late spring. Subsequently, shorebird use of open-marsh mud flats increased, but most shorebirds appeared to leave or move to other unflooded impoundments in the area.

Most managed units had greater shorebird use than unit 2, probably because of the lack of drawdown of unit 2 in 1984 (minimum of 20 cm water level) which prevented shorebird use of the mud-flat habitat. Nonetheless, some species (i.e., dowitchers, yellowlegs, common snipe) commonly used the higher emergent and emergent-edge habitats. Maintaining water circulation and a minimum of 20 cm of water over the impoundment bed in unit 2 during the 1984 drawdown period apparently benefited wader, waterfowl, and surface diver groups (Table 15.10).

Five species of waterfowl contributed 95.6% of the group's average annual use (59,484 AUD); 26.8% of all waterbird groups. Cooperfield, units 4 and 2, respectively, had the greatest (75.3%) waterfowl use per hectare and also had greater coverage of desirable food plants. In contrast, units 1, 3, and 5 had less-desirable habitats and lower waterfowl use. The open marsh and the tidal impoundment had much lower waterfowl use (1%). Chabreck et al. (1974) found that duck use of brackish impoundments was only slightly greater than the use of open brackish marshes in Louisiana. Natural food plants, such as widgeon grass and dwarf spike rush, were abundant in their control areas; however, this is not characteristic of the tidal marshes in South Carolina. Bildstein et al. (1982b) found that waterfowl comprised no more than 5% of all birds observed during winter in a nearby open salt marsh. Food-habit studies of wintering waterfowl in South Carolina indicate that ducks prefer foods found in managed impoundments to those found in open tidal marshes (Conrad, 1965; Landers et al., 1976). High waterfowl use of impounded marshes is directly related to management of desirable food plants and cover (Baldwin, 1967; Wilkinson, 1970). Mottled ducks and least bitterns were observed nesting in impoundments, and mottled duck broods were observed on the managed units. Black-necked stilts were observed nesting in larger Yawkey Center impoundments.

The larger number of waterfowl counted during the first field season probably resulted from greater availability of food plants, although there have been annual declines in waterfowl populations wintering in South Carolina (Strange, 1985). Widgeon grass production was erratic during this study and may have accounted for the lowered waterfowl numbers during the second field season. Studies on nearby impoundments, however, have shown that waterfowl can consume up to 89% of available widgeon grass during the fall season (Swiderek, 1982). Food availability (i.e., water level) is an important factor in impoundment use by ducks (Chabreck et al., 1974; Chabreck, 1979). Waterfowl use increased in the second field season during the period of low water level and drawdown (1984), when widgeon grass seed and dwarf spike rush were readily available (Table 15.6).

Drought conditions probably caused the decline of widgeon grass during 1983. Also, other factors (fish, crabs, turbidity) may have negatively influenced widegeon grass production (Joanen and Glasgow, 1965; Chabreck, 1967). Sampling procedures from other concurrent investigations may have artificially increased turbidity levels and lowered widgeon grass production.

Ordinarily, water would be channeled from Summer Duck pond or the adjacent freshwater reserve pond through spillways between impoundments to offset periods of high salinity and temperature. This was not done during the study so that each impoundment could be managed as an individual unit (see Chapter 4).

Some waterbirds form aggregations by attracting others to good feeding sites (Ward and Zahav, 1973; Kushlan, 1981). Proximity to food and water and isolation from human disturbance are important factors influencing roost site selection in birds (Eiserer, 1984). Eight species, primarily white ibis (45.9%) and great egret (42.3%), used the trees and snags adjacent to Cooperfield during the late summer and fall as a roosting site (Table 15.11). Similar areas occuring adjacent to or behind impoundments are commonly used as communal roosting sites for some wader species (Sandifer et al., 1980).

In the open marsh, fishing birds aggregate where prey become trapped in isolated depressions and salt pans during extreme conditions. However, predatory birds and alligators respond effectively to short-term availability of easily obtained prey in the managed units. For example, alligator density quickly reached 13/ha in unit 3 in September 1983. Early-morning low levels of dissolved oxygen, coupled with extended drought and high temperatures, apparently caused the high availability of prey fish and crab species in this unit. Above-average numbers of predatory birds and 3 small and 43 large alligators were counted actively feeding in open-water habitat. This one observation accounted for 59% of the total alligator sightings in unit 3 (Fig. 15.9). Normally, alligators are not as active in September (T. Murphy and P. Wilkinson, personal communication).

Fish kills are common in some estuaries (Copeland et al., 1984) and impoundments (Sandifer et al., 1980), although no fish kills (dead fish) were observed during this study. Apparently, stressed fish and crabs were preyed on by birds and alligators so greatly that prey populations are reduced before a large-scale die-off of fishes occurs. Although impoundment fish kills can sometimes be avoided with proper water circulation (M. Prevost, personal communication), a leading cause is the use of pesticides in nearby agricultural lands (Miglarese and Sandifer, 1982).

Impoundments, dikes, and remnant dikes provide optimum habitat for alligators in South Carolina (Sandifer et al., 1980) where most (73%) alligators nest in impoundments and 80.3% of these impoundments are managed for wintering waterfowl (Wilkinson, 1983). Some water-level drawdown manipulations may, however, temporarily reduce alligator nesting activity in impoundments (Wilkinson, 1983; Davidson and Chabreck, 1984).

CONCLUSIONS

The value of tidal estuarine wetlands as critical breeding, nesting, feeding, and wintering habitat for many species of wetland avifauna is well documented (Pitelka, 1979; Erwin and Korschgen, 1979). South Carolina's tidal wetlands provide relatively high wading bird guild richness because of good climate and abundant shallow marshes (Kushlan, 1981), and are vital to numerous migratory waterbirds as wintering and stopover areas (Sprunt and Chamberlain, 1970; Forsythe, 1978).

Of the total 58,427 ha of impounded marshland in South Carolina, approximately 49% are presently "working" impoundments that are managed under various levels of sophistication and environmental conditions, and another 51% are considered tidal or free flowing (Morgan et al., 1975; Tiner, 1977; Aichele, 1984).

The value of properly managed impoundments to wildlife in South Carolina and other states is well recognized (Provost, 1959; Chabreck, 1975; Miglarese and Sandifer, 1982; Fredrickson and Taylor, 1982; Davidson and Chabreck, 1984). Osprey, bald eagle, and alligator nesting activity has been linked with impoundments, both in South Carolina and throughout the United States, and highest activities are within or near impoundments managed for waterfowl (Henry and Notlemeier, 1975; Murphy and Coker, 1978; Griffin et al., 1982; Wilkinson, 1983). Impoundments in South Carolina have benefited tundra swans (Cely, 1979) and the endangered wood stork (T. Murphy, personal communication).

Brackish impoundments managed for widgeon grass provide higher and more diversified waterbird use than unmanaged marsh or tidal impoundments. The condition of dikes (i.e., number of breaks) and stage of vegetative succession (i.e., bed elevation) may be important factors in the overall value of similar sites to wildlife. On the basis of these results, we do not promote impounding of pristine salt marsh, but we do advocate better management of existing impoundments to optimize resource use by many wild species. The degree of water control and management sophistication can be critical factors to successful management. Impoundments in good "working" condition but under improper or poor management may not provide the necessary conditions for optimum wildlife utilization.

Most waterbirds are migratory, and the importance of any one particular site to certain bird groups is related to season and management. Predatory birds and alligators respond effectively to short-term periods of high availability of prey in managed units. High predation rates by birds and alligators may reduce the prey base in some situations.

Managed marsh impoundments have higher individual numbers of birds and species than unmanaged sites. Shorebirds, waterfowl, and waders provided 93.8% of the average annual use of the study area and dominated (93.1%) the use among impoundments. High waterbird use of impoundments appears directly related to season, management, unit area, and resource availability. The larger impoundment (Cooperfield) had significantly greater waterbird use overall and higher counts of alligators as well. Other managed units had significantly more waterbird use during certain seasons or management stages. Water-level manipulations to encourage both the growth of waterfowl food plants and waterfowl use provided favorable conditions to large influxes of other migrating birds.

In conclusion, coastal brackish impoundments managed for widgeon grass and other desirable waterfowl food plants in north central South Carolina provide water-level manipulations and water depths that benefit a variety of nongame species. These results have major implications for multi-species management of South Carolina's coastal impoundments. Slight alterations of water-level strategies to increase resource availability can enhance conditions for many wild species and still maintain high waterfowl utilization.

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SECTION IX

INTEGRATION

Chapter 16

Integration and Interpretation of CWIP Results

M. R. DeVoe, D. S. Baughman, and J. M. Whetstone

SUMMARIZATION OF CWIP RESULTS

The Coastal Wetland Impoundment Project (CWIP) was designed to determine ecological similarities and differences between the study impoundments and an adjacent tidal wetland system. This summary highlights the major findings of the study and offers a series of observations on the effects of the impoundment management strategy employed on-site on the ecological processes of the system.

Physical Setting

The substrate of the study impoundments consisted of a 10 to 40 cm surface layer of organic, brown clayey silt, overlying a gray silty-clay layer (Chapter 5). Piezometer measurements indicated a near-zero flow of water between the impoundment beds and the underlying shallow-water aquifer, suggesting that the impoundment beds were essentially impermeable. Interstitial water analyzed from impoundment core samples was saline, indicating that groundwater discharge was not acting to flush the impoundment system.

Similar analyses were conducted on the impoundment dike structure. Because the dikes were constructed by excavating marsh bottom from a perimeter area and depositing the material on the adjacent marsh surface, a potentially porous, fibrous organic layer was formed between the marsh substrate and the dike structure. Permeability determinations indicated that this organic layer was indeed a conduit for water exchange between systems; however, the magnitude of the observed flow (598 to 916 liters/day) was found to be insignificant compared to the total volume of water contained in the impoundments. These results strongly suggest that the exchange of water between and among the study impoundments and Chainey Creek occurred almost exclusively through the water-control structures (trunks), and argues against the possibility of a significant exchange of nutrients through the impoundment beds and dikes.

Tidal movements of major nutrient fractions in the Cat Island impoundments were considerably different from those observed in the adjacent tidal wetland (Chapter 6). On an annual basis, the tidal wetland showed a net export of ammonium (NH_4) and orthophosphate ($o\text{-}PO_4$) (400 mg m^{-2} yr^{-1} and 320 mg m^{-2} yr^{-1}, respectively) with higher export rates occurring during summer. There were periods of net monthly import of these fractions, particularly from March to May, but the high export rates in summer offset this pattern. The annual net export of NH_4 and $o\text{-}PO_4$ has been documented in other marsh systems (see Nixon, 1980 for a review), and has been proposed as a significant source of limiting nutrients for estuarine ecosystems during summer periods of high productivity. In comparison, the study impoundments generally showed opposite trends characterized by much lower rates of tidal exchange. Ammonium was exported at a rate of 92 ± 64 mg/m^2 on an annual basis, while $o\text{-}PO_4$ was imported into the impoundments at a net rate of 20 ± 10 mg m^{-2} yr^{-1}. However, during summer both constituents were imported into the impoundments.

In contrast to the trends observed for the inorganic nutrients, the tidal exchange of phytoplankton biomass was more comparable in magnitude between the study impoundments and the adjacent wetlands system. However, this biomass exchange differed considerably in direction of flow. The tidal wetlands imported phytoplankton biomass throughout the year at a rate of 210 mg m^{-2} yr^{-1} (chlorophyll-a). No significant seasonal differences were observed, except possibly for December and January, when the rate of flux was greatly reduced. On the other hand, the impoundments exported phytoplankton biomass (100 ± 40 mg m^{-2} yr^{-1}), except for two peaks of import in April and May.

Differences in mean concentration between ebb and flood tide were determined for total (TOC), dissolved (DOC), and particulate (POC) organic carbon (Chapter 6). The DOC fraction dominated total organic carbon in both the tidal marsh and impoundment systems. Peaks in concentration of 40 to 60 mg/liter were noted in June for both systems. DOC in the tidal marsh was consistently higher on ebb tides throughout the year, suggesting that DOC is exported from the marsh. In the impoundments, ebb tide and flood tide concentrations were similar during spring. However, DOC concentrations were as much as three times higher on ebb tide from late summer and throughout the fall, again suggesting that DOC was exported from the impoundments during this period.

POC exhibited similar seasonal trends in both the impoundments and tidal marsh. Highest values for POC concentrations were noted in spring and summer for both systems (5 to 50 mg/liter). Mean POC concentrations in the tidal marsh on ebb tide were consistently higher than mean flood tide values, suggesting some export of POC during the year. On the other hand, POC values for the impoundments were variable, and no obvious pattern of import or export was observed.

Collectively, the annual tidal exchange of DOC, POC, and phytoplankton biomass was comparable between the two systems. Nevertheless, the quality of the exchange of nutrients was observed to be clearly different. Some of these differences can be attributed to the quantities of water moving between the two systems. During summer months of restricted water flow, tidal nutrient exchange was reduced because of the maintenance of high water levels in the impoundments. This situation was quite the opposite in the tidal wetlands, where maximum rates of nutrient export occurred during the summer. In addition, dissimilarities in nutrient exchange at Cat Island may have been due to the biotic and geochemical characteristics of each of the two systems. Impoundments are dominated by submerged benthic plant communities that will affect the mechanisms governing nutrient processing when compared to intertidal systems. As yet, however, data have not been generated to evaluate these differences.

Dissolved oxygen (DO) concentrations in the study impoundments were measured to compute gross community productivity and assess the quality of the impoundment environment as habitat for macroinvertebrates and fishes.

Diurnal changes in dissolved oxygen levels were recorded during all seasons of the two-year field study; the greatest daily ranges occurred during the period May to September (ca 7.0 g O_2/m^3). Highest DO values were observed at dusk in March, May, and June, with lowest values recorded for dawn periods in July and August (18 to 19 g O_2/m^3 and 0.2 to 0.5 g O_2/m^3, respectively). The low values measured for the summer months apparently did not directly account for any decapod crustacean or fish mortality, but at times populations of these organisms were observed at the water surface where they experienced heavy predation from waterbirds. Sublethal oxygen stress may have been the cause of this surface swimming behavior.

Primary Productivity and Systems Metabolism

Gross community productivity, computed from diel changes in DO in the study impoundments, ranged from fall and winter levels below 2.0 g O_2 m^{-2} day^{-1} to spring and summer peaks of 4.0 to 6.0 g O_2 m^{-2} day^{-1} (Chapter 8). Mean annual gross production and aerobic community respiration for the Cat Island impoundments were 1027 ± 107 g O_2 m^{-2} yr^{-1} and 1608 ± 82 g $O_2 m^{-2} yr^{-1}$ respectively. Considerable net system productivity (P:R>1) occurred during spring and early summer as submerged macrophytes spread over the shallow flats of the impoundments. However, the annual P:R ratio of 0.64 indicates the importance of heterotrophic processes, which are stimulated by organic inputs from the emergent macrophytes within the impoundments.

The study impoundments also supported high phytoplankton production (664 g O_2 m^{-2} yr^{-1}) which probably dominated total aquatic production in these systems during late summer and fall. High phytoplankton production was responsible for the large daily variations in DO levels observed during summer and fall. In contrast, the relative importance of phytoplankton production is usually low in open intertidal wetlands (Pomeroy and Weigert, 1981). The presence of large areas of standing water with high nutrient concentrations and little water exchange appears to be the major factor supporting high phytoplankton productivity in the study impoundments under management. This condition is also important in controlling patterns of total nutrient exchange between the systems.

Data derived from preliminary studies on the benthic microalgae of the study area are not conclusive but do suggest several trends (Chapter 9). The magnitudes of biomass and primary production of the benthic microalgae in the study impoundments and the intertidal wetlands system generally agreed with literature values for various coastal environments (Colijn and DeJonge, 1984; Varela and Penas, 1985). Photosynthetic rates were significantly higher during the day; however, high respiration rates in the water column and in the benthic community appeared to offset the production.

Macrophyte assemblages were mapped and classified into communities in both the study impoundments and the adjacent tidal wetland (See Appendix Figs. 7.1 to 7.10). Seven communities were identified in the impoundments, with the *Ruppia maritima*-*Eleocharis parvula* community dominant in terms of percent cover (mean = 57%; range = 41 to 67%) (Chapter 7). In contrast, the tidal wetland was characterized by three macrophyte communities; *Spartina alterniflora* and *S. cynosuroides* were the dominant communities (50% and 46% cover, respectively). Macrophyte diversity was greater in the study impoundments than in the tidal wetland. The seven impoundment communities represented 19 species, whereas the three wetland communities represented five species. This difference in community structure can be attributed to the management scheme employed for widgeon grass (*R. maritima*) production.

To assess the contribution of macrophyte production to total primary productivity, net aerial primary productivity (NAPP) was estimated for each community in both wetland systems. NAPP estimates for the study impoundments (1331.0 ± 422.4 g m^{-2} yr^{-1}), and the tidal wetland (1968.0 ± 607.8 g m^{-2} yr^{-1}) were not significantly different, and are consistent with estimates found in the literature for species at southeastern latitutes. Similarly, NAPP values for impoundment and tidal *S. alterniflora* and *S. cynosuroides* were not significantly different. Conversely, the 1983 NAPP estimates for *Scirpus robustus* in the impoundments was significantly lower than that for *S. robustus* in the tidal wetland. This difference was apparently due to selective freeze damage to the *Scirpus* community in the impoundments during the 1983 spring drawdown.

The management strategy for the study impoundments is selective for *Ruppia*, so it was not surprising that this community dominated, in terms of percent cover, impoundment macrophytes (Chapter 7). The contribution for the *Ruppia-Eleocharis* community to total NAPP was intermediate compared to that of the other six impoundment macrophyte communities, but it was probably underestimated because the methods used did not account for losses due to grazing or mortality. It is interesting to note, however, that the standing crop of the *Ruppia-Eleocharis* community peaked in June in each year and was largely gone by the fall, when the migratory waterfowl arrived.

Overall, the data indicate that although estimates of total primary production in the impoundment and open wetland systems studied were similar, the relative contributions of phytoplankton, benthic algae, and macrophytes differed between systems. In the tidal wetland, primary production was dominated by emergent vegetation, whereas submerged macrophytes, benthic algae, and phytoplankton were the significant primary producers in the study impoundments (Chapter 10).

Planktonic Community

The annual standing stock of zooplankton was generally higher in the study impoundments than in Chainey Creek, with significant seasonal variability (Chapter 11). Impoundment zooplankton populations decreased to the low standing stock levels observed in Chainey Creek during periods of extensive impoundment flushing for the control of mosquito larvae (March to April) and during periods of low impoundment water levels when greater tidal exchange occurred with Chainey Creek. Conversely, the standing crop of zooplankton was highest in impoundments during periods of reduced water exchange with Chainey Creek, primarily in August and September. The peak period of impoundment zooplankton biomass also corresponded with the highest values measured for phytoplankton production.

Benthic Community

Harpacticoid copepods and nematodes dominated the meiofauna populations at all study sites (Chapter 12). The preliminary investigation of the meiofauna community indicated that tidal wetland sites (intertidal Spartina marsh and subtidal creek bottoms) harbored more species than analogous sites within the study impoundments. This was particularly true for the subtidal sites where 13 nematode and 11 copepod species were found in the creek, versus 9 and 7 species, respectively, in the five study impoundments. Among impoundments, no two were alike in terms of meiofauna abundance, and the meiofauna appeared to exhibit a patchy distribution that could not be explained by differences in abundance values between the impoundment ditches and flats.

Habitats within the study impoundments supported different and less-diverse assemblages of macrofaunal invertebrates than analogous habitats in Chainey Creek and the adjacent wetland (Chapter 12). Although vegetated sites in the open wetland accounted for 65 taxa, 39 taxa were collected at complementary sites in the study impoundments. Similarly, nonvegetated sites (i.e., perimeter ditches) in the impoundments contained 17 taxa of benthic macrofauna, whereas comparable sites in Chainey Creek contained 63 taxa. Faunal assemblages in impoundments primarily consisted of hydrobiid snails, insects, oligochaetes, and some polychaetes. In contrast, gammurus amphipods, isopods, and polychaetes were more common in the tidal wetland. Such physical factors as sediment composition, availability of organic matter, dissolved oxygen concentrations, hydrogen sulfide accumulation, and predation affect the spatial patterns of macrobenthos and may have accounted for the observed differences between the impoundment and adjacent wetland systems.

Nektonic Community

Utilization of the study impoundments by demersal and pelagic organisms (decapod crustaceans and estuarine fishes) was directly influenced by the nature and timing of water exchange between Chainey Creek and the impoundments. The degree to which a particular species was able to inhabit the impoundments depended on the timing of natural recruitment with periods of significant water exchange. Among penaeid shrimps, postlarval Penaeus aztecus recruited to the study area almost exclusively during the May to June period of maximum water exchange between the two systems and, therefore, were relatively adundant in collections at the impoundment water-control structures (N = 73.5; N/100

m^3= 4.52) (Chapter 13). Conversely, P. duorarum postlarvae recruited into the study area in late summer and early fall during periods of minimal water exchange. As a result, they were much more abundant in creek samples (N = 338.7; N/100 m^3 = 4.37) than in impoundment trunk samples(N = 27.5; N/100 m^3 = 1.69). Juvenile blue crabs were almost always more abundant at impoundment stations (N = 50.5 per station at impoundments; 38.3 per station in creek); however, megalopae were virtually precluded from entering the impoundments, because their recruitment coincided with the late summer-early fall period of low water exchange (362.7/station in creek; 44.5/station in impoundments).

Fishes that were abundant as larvae or juveniles in Chainey Creek during May, the period of maximum water exchange, were recruited into the impoundments (Chapter 14). This was particularly evident with fishes of the families Sciaenidae, Engraulidae, Sparidae, and Clupeidae. In June and July, larval Elops saurus, Megalops atlanticus, Bairdiella chrysoura, and Cynoscion regalis were recruited into impoundments during high tide events when waters flowed into the impoundments over the trunk spillways. Fishes that recruited into the study area during periods of little water exchange did not utilize the impoundments to any large extent. For example, spot, Leiostomus xanthurus, is recruited in late summer and early fall in estuarine areas but were able to make little use of impoundment habitats (of 29,452 individuals collected in the study, only 1418 were collected from the impoundments).

The data also suggest that those pelagic fishes and decapods recruited into the impoundments during periods of significant water exchange in late spring to early summer had restricted access to Chainey Creek during periods of natural emigration out of the study area. For example, only 7.6% as many penaeid shrimp were collected emigrating from impoundments as were collected immigrating into these systems. Although, while the larger shrimp in the creek apparently emigrated to deeper waters during summer and early fall (leaving mostly juveniles behind), shrimp in impoundments were unable to emigrate. This difference is reflected in the mean length of P. setiferus in the two habitats during this period: 12.7 cm in the impoundments, 8.9 cm in the creek. Similarly, the greater abundance of mature female blue crabs within impoundments during months when spawning migrations to high salinity waters typically occur suggested retention of crabs within impoundments (Chapter 13). Estuarine transient species of fish entering impoundments as larvae or juveniles during periods of maximum water exchange in spring were essentially prevented access to Chainey Creek during periods of natural migration out of the estuarine environment. This situation may have affected their ability to complete their respective life cycles.

Diversity and abundance of decapod crustaceans and fishes differed somewhat between the study impoundments and Chainey Creek. The composition and number of decapod crustacean species collected by seine and trawl in the creek and impoundments were similar. The most abundant decapod species (*Palaemonetes pugio*, *P. vulgaris*, *Penaeus aztecus*, *P. setiferus*, *P. duorarum*, and *Callinectes sapidus*) were essentially the same in both habitats. On the other hand, 16 more species of fishes were collected in the tidal creek system (N = 69) than inside impoundments (N = 53). The dominant fish species collected from the creek was *Fundulus heteroclitis*, whereas *Gambusia affinis* dominated the impoundment fish assemblage. Most of the impoundment fishes were adapted to utilize the oxygen-rich waters at the air-water interface, but these fishes were most vulnerable to predation by waterbirds. In addition, fishes that normally prey on benthic or planktonic organisms had a wider range of food items in the creek environment than similar feeders in the impoundments, because of the lower diversity of macrofauna found in the managed systems. The dominant impoundment fishes tended to be species noted to be opportunistic feeders.

Temporal patterns observed in the decapod crustacean and fish communities were influenced by hydrographic conditions and the life history patterns of individual species. For example, over the two-year field study, increased species richness and total number of decapod species in impoundments and Chainey Creek occurred in summer and early fall, largely because of ingress of stenohaline marine species into the study area during periods of high-salinity conditions. Abundance and biomass, however, were lowest in summer and early fall, coinciding with high temperatures, high salinity, and low dissolved oxygen concentrations in both systems.

Wildlife Community

The study impoundments served higher numbers of waterbirds and more-diversified waterbird assemblages than either the tidal wetland or the tidal impoundment (Chapter 15). The average annual use days for shorebirds (2224 versus 124), waterfowl (1141 versus 340) and waders (580 versus 186) in impoundments greatly exceeded the use of the unmanaged sites. In addition, of 77 wetland bird groups that utilized the study area, 76 were observed in the impoundments, but only 56 were observed in the unmanaged sites. Although the waterfowl bird group was the primary target of widgeon grass management, shorebirds dominated the average annual use of the study area (54.8%), followed by waterfowl (26.8%) and waders (12.2%). The remaining waterbird assemblages (surface divers, aerial divers, and raptors and rails) together comprised 6.2% of the average annual use of the study site.

Distinct seasonal patterns of waterbird use of the impoundments were observed. In summer and fall, waders dominated the waterbird assemblages (61.3% and 45.5%, respectively). By winter, waterfowl populations accounted for 61.5% of all waterbird utilization; in the spring, the shorebirds accounted for 78.9% of avian usage. The seasonal differences observed during the two-year field investigation were directly related to the natural feeding and resting behaviors of these waterbird groups and the water-level management practiced on the impoundments.

Alligators were observed in all months of the study except December, January, and February. Of the 502 alligators counted, 61.2% were less than 1.5 m in length. The greatest concentration of alligators was obseved on the larger, managed impoundment, Cooperfield, which was to a degree a function of that impoundment's proximity to a freshwater pond. In 1983, impoundment 3 was utilized by more alligators when compared to the other sites; this was due to a short-term increase in prey fish and crab availability.

Summary

Taken as a whole, the study area, with its managed impoundments, tidal creeks, open wetlands, and small parcels of high ground, was documented to be an integrated and productive ecological system. The impoundments were important habitat areas for many species of waterbirds, reptiles, and other wildlife, whereas the tidal creeks and wetlands served an equally important role in providing habitats for transient and resident species of crustaceans and fishes. The two systems were different in regard to the overall community structure of their respective major biological components, but the basic ecological processes occurring in each were similar. It became apparent early on in the study that the impoundment management strategy employed on-site played a significant role in the way the integrated system functioned. From our data it is clear that the major differences observed in the two systems are, in fact, a function of transfer effects. These effects are due primarily to tidal influences, water-level patterns, and the degree of water exchange between the two systems.

These general findings, although not novel in and of themselves, suggest that efforts to resolve the issues regarding impoundments in South Carolina should be focused on the techniques and technology of management. It may be possible to minimize impacts and maximize desirable conditions in impoundments through calculated and tested management strategy manipulations.

MANAGEMENT IMPLICATIONS

Impoundment management as presently practiced is both an art and a science. Management is based primarily on the experience of the manager and his or her knowledge of an area, secondarily on scientific data. The methods employed by most impoundment managers are similar and rely primarily on the manipulation of water-levels through the use of water-control structures (trunks). However, the actual water-manipulation regimes may vary considerably among impoundments and managers, depending on site characteristics (especially salinity), management goals, and the preferences of individual managers. Nevertheless, most actively managed impoundments in South Carolina are managed for waterfowl (Chapter 3).

Current waterfowl management practices employ some combination of salinity manipulation (usually through the introduction of fresh or brackish water), water-level manipulation (including periodic draining and flooding) and in the majority of cases, some disturbance of the impoundment bed by burning or cultivating of the vegetation. The goal of these practices is to deter the growth of undesirable emergent plants while simultaneously promoting the growth of aquatic plants more attractive to migrating waterfowl. There is an apparent trend toward more-intensive management over the last decade, with those areas under public management typically the most intensively managed.

The CWIP examined the ecological characteristics of a set of impoundments subjected to a single, but typical, management strategy targeted to the attraction of waterfowl in a brackish-water environment. Thus the data resulting from the ecological studies are specific to this system. The general patterns and trends observed during the field investigations and subsequent analyses should apply however, to many impoundment systems in South Carolina, because the primary driving force in impoundment systems is the method by which they are managed. Based on these observations, recommendations for improvements in impoundment management practices are presented below. These recommendations should be tested at the earliest opportunity.

Enhancement of Impoundment Management of Target Species

The most obvious finding of this project is that coastal brackish-water impoundments managed for widgeongrass production are highly effective in attracting waterfowl, along with large populations of other waterbird species. The managed impoundments attracted higher numbers of waterbirds and more diversified waterbird assemblages that the open-marsh area. Surprisingly, waterfowl comprised only 26.8% of the average annual use, but they dominated the usage of the managed areas during the winter season (61.3%). The production of widgeon grass was the primary objective of the management program during the CWIP study. The peak in the standing crop biomass of widgeon grass occurred in July 1983 and August 1984 (see Chapter 7). Because of above-average rainfall and extremely high tides, the reflood process was delayed a month in 1984, and this might have been responsible for the later peak in widgeon grass biomass. These observations suggests that by delaying the spring flooding process, it may be possible to time maximum widgeon grass production closer to the season when it would be utilized by migrating waterfowl. The peak in widgeon grass production in late summer may have been affected by the high temperatures and salinities that occurred during this period. Increased water circulation may minimize this effect.

The potential for managing impoundments for specific target species other than waterfowl has also been demonstrated (Olmi, et al., 1986). By delaying the time of maximum water exchange (usually during the drawdown-reflood process), it is possible to selectively recruit individual aquatic species into impoundments during periods of maximum population densities in the adjacent creek (see Chapters 13 and 14). A related project, sponsored by the S.C. Sea Grant Consortium, has demonstrated that coastal impoundments can be managed to selectively recruit naturally-occurring penaeid shrimp by initially flooding the impoundment during periods of maximum postlarval shrimp densities in an adjacent creek. Dissolved oxygen and temperatures were maintained above minimum requirements for shrimp survival by allowing for at least 10% water exchange per day. Shrimp yields ranged from 100 kg/ha in a small impoundment (1.5 ha) during a good commercial shrimp fishery season to 0.9 kg/ha in a larger impoundment (5 ha) during a poor commercial shrimp fishery season (lower shrimp yields in the larger impoundment may have resulted from a hole in the dike). During good years, coastal brackish impoundments may produce between 50 and 100 kg/ha of naturally-occurring penaeid shrimp if there is successful recruitment of postlarval shrimp and if adequate water exchange is maintained (Olmi, 1986).

Enhancement of Water-Quality Conditions

Water-quality conditions in the study impoundments in summer, when water circulation was minimal, affected the composition and community structure of the macrobenthic organisms and fishes (see Chapter 13 and 14). Low DO concentrations combined with high temperatures and salinities appeared to be the primary factors responsible for stressful conditions. Although these factors are primarily the result of atmospheric and climatic conditions (e.g., rainfall and air temperature), the study results suggest that by increasing water exchange through the trunks during periods of high temperature and salinity and low DO, adverse impacts on aquatic fauna may be reduced (see Olmi, et al., 1986). This may be accomplished by several means: (1) a quick, partial drawdown and reflood process; (2) an adjustment of the flashboard risers to permit daily tidal flushing over spillways; (3) an increase of bottom water circulation flow through the inside gate of the impoundment trunk structure; or (4) a combination of all of the above.

Enhancement of Non-Target Organism Migration

One of the primary concerns of marine biologists regarding impoundments is the barrier that impoundments pose to normal recruitment and emigration of transient marine species that utilize wetland areas for a portion of their life cycle. Organisms that are recruited into the impoundments are those species that are abundant in the water column during periods of maximum exchange. The converse is also true; that is, organisms whose peak recruitment times occur during periods of little or no water exchange are not recruited into the impoundments. However, based on the investigations of crustaceans and fishes (Chapters 13 and 14), those animals that do enter the impoundments are impeded in their normal emigration patterns by the water-control structure during times when the riser boards are set to maintain a specific water level. Improving bottom circulation, by allowing water exchange through the inside gate as opposed to the flashboard riser, would enhance both the emigration of marine organisms and the water-quality conditions. It may also be possible to schedule impoundment flooding so that selected animals are not recruited. This would require the monitoring of the feeder creek to determine when these organisms are or are not present. Such management manipulations need to be evaluated for their effectiveness and cost.

Based on the results of the CWIP, it may be possible to develop impoundment management strategies for waterfowl habitat that enhance the use of these areas by nontarget species. This is not to say that impoundment wetland areas would be as accessible as open, tidal wetlands, but with proper intensive water-level management these impounded areas may provide adequate habitat for both waterbirds and marine organisms.

Mosquito Production and Impoundment Management

Although the CWIP did not specifically address the issue of mosquito production in coastal impoundments, the S.C. Sea Grant Consortium did support a preliminary investigation (Tidwell, 1980) in conjunction with the S.C. Department of Health and Environmental Control and the Charleston

County Mosquito Abatement Program. Dr. Tidwell's study of salt marsh and impoundments in the Santee Delta region indicated high mosquito production in some impoundments managed for waterfowl.

Salt-marsh mosquitos, Aedes sollicitans and Aedes taeniorhynchus, lay their eggs on damp soil and then hatch into larvae when these areas are flooded. Therefore, when impoundments are flooded by either heavy rains or controlled flooding, the mosquitos begin their life cycle. Mosquito population densities vary greatly between sites, but in general, mosquitos survive in most substrates and salinities. Consequently, conditions in brackish-water impoundments make them very susceptible to the production of large populations of mosquitos.

Management of impoundments to minimize the production of mosquitos should include two key practices. First, the impoundments must be set up to allow the beds to drain adequately into the perimeter ditches or canals. By doing so, waters containing mosquito larvae can be removed from the impoundment beds, making the larvae more accessible to predatory fish. In smaller impoundments this may not be difficult; however, larger impoundments may require additional cross ditching and/or trunks to provide adequate drainage. Second, the management scheme should be designed to remove developing mosquito larvae during the reflood process. This procedure was followed during the CWIP and involved a second flushing-reflood event soon after the major reflooding process to further reduce mosquito production in impoundments.

RESEARCH NEEDS

The CWIP has provided the initial comprehensive information base on the ecology of a brackish-water impoundment complex; an analysis of the current status of impoundment ownership, management, and use throughout the state; and an overview of suggested improvements for impoundment management. Nevertheless, a number of questions require further exploration and study. The following suggestions for research were generated through dicussions with the CWIP investigators and technical advisors after thorough review of CWIP results, taking into account the issues that have surfaced subsequent to the initiation of the CWIP in 1982.

The CWIP was conducted on a series of small, intensively managed brackish-water impoundments at Cat Island, South Carolina. Although the physical and ecological characteristics of this impoundment complex were well-documented during the CWIP, the transferability of these data to impoundments of larger size, of different geographical regions, of different salinities, or subjected to other management schemes has not been assessed. For example, the results of this study underscore the importance of impoundment hydrography (water movement) as a significant driving force in the system. However, because the majority of impoundments in South Carolina are larger in size than those studied, additional work is needed on how large systems are influenced by water-circulation patterns. In addition, the effects of water exchange and periodic flushing and flooding events on water quality inside impoundments and in adjacent water bodies need to be determined for these larger systems. These studies should include an examination of the effects of periodic releases of large volumes of water from impoundments on water pH, nutrient levels, and DO concentrations.

Similarly, additional study should be directed at determining whether trends observed in the ecological characterization of the Cat Island impoundments are representative of other impoundment systems. For instance, NAPP for the five impoundments examined under the CWIP was not significantly different from that for the adjacent open wetland area. The relative contributions to total primary productivity by benthic algae, phytoplankton, and macrophytes in the two systems were significantly different, however. Examinations of NAPP should be made for other impoundment systems to determine if trends found are similar to the Cat Island system. Further studies of primary productivity might include the determination of underground biomass, turnover rates, and detritus export. Addressing these questions would provide a better measure of how representative the results of the CWIP are to impoundment systems throughout South Carolina.

Water-circulation patterns appear to be the most significant factor responsible for the differences observed between impoundments and open wetlands. Results of the CWIP suggest that improved water circulation between the two systems reduced the differences observed. Thus future research should focus on investigations of innovative methods for improving the amount and timing of water exchange. Additionally, assessments should be made to determine the optimal number and design of impoundment water-control structures necessary to maintain adequate circulation and water-quality conditions in impoundments, using DO as the indicator. This could be addressed through the use of laboratory models, and verified with field investigations. Further, enhancement of circulation and drainage in larger impoundments may require additional cross ditching and/or cross diking. The costs and benefits of such modifications should also be explored. In essence, the development of techniques to optimize the circulation and exchange of water between impoundment and open wetland systems may have significant implications for the management of coastal wetland impoundments.

The CWIP examined the ecological differences between open wetlands and brackish-water impoundments under one particular management scheme designed to attract waterfowl. Statewide, a variety of management schemes have been developed to attract waterfowl and, more recently, for aquaculture purposes. Impact analyses of the more-intensive schemes, especially those involving cultivation and/or burning, are lacking. The effects of these techniques on impoundment productivity and habitat utilization by aquatic species may be significantly different from those observed during the CWIP. Other management-related research should include studies to determine the feasibility of double-cropping widgeon grass or possibly employing a later drawdown-reflood process to produce a later crop of widgeongrass for waterfowl. The practicality of instituting management protocols (for example, multiple flushing, to reduce mosquito production) should be evaluated. Additional studies on the effects of management schemes implemented for the production of other target species such as shrimp or crawfish and multi-species management for both waterfowl and shrimp would also expand the base of knowledge that now exists.

Long-term research on managed wetlands should include an analysis of the ecological similarities and differences of breeched impoundments with actively managed impoundments and tidal wetlands. Other multi-year investigations should focus on (1) the trophic dynamics of impoundment communities, (2) the role of predation and mortality in shaping the community structure of faunal populations, (3) the nature of the carbon cycle in impoundments and how it influences secondary production, and (4) the degree to which waterbirds influence nutrient levels in, and through predation, remove fish and invertebrates from, impoundments.

Above all, the investigation of management techniques to increase water exchange, both in volume (to maintain adequate water quality) and timing (to provide for the immigration and emigration of marine/aquatic species), is critical for the development of management protocols and the wise use of this valuable wetland resource.

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Chapter 17

The Coastal Wetland Impoundment Project: Implications for Policy

M. E. Tompkins

South Carolina's settlers created important opportunities through the management of her coastal wetlands. Today, long after the demise of rice and cotton culture, new opportunities may be emerging in impounded fields that were cleared and prepared at such great cost. The transition away from the agricultural practices of the eighteenth and nineteenth centuries has been a long process, with results still unclear.

The most noteworthy aspect of the long process of change in these coastal wetlands involves the emergence of a significant interest in managing these areas for migrating waterfowl. It has become clear that wetlands can be managed to increase their attractiveness to waterfowl and, accordingly, to enhance their value as sites for waterfowl hunting. Work undertaken in this project (Chapter 15) demonstrates the success of a common management regime devoted to attracting waterfowl, and our survey of coastal property owners (reported in Chapter 3) shows that there is substantial interest in this use of currently impounded areas.

The work of many scientists, lasting over the four years of the Coastal Wetland Impoundment Project (CWIP), has helped to clarify the problems and opportunities associated with wetland impoundments in South Carolina. As is often the case with carefully controlled scientific studies, this study answered some old questions, improved our understanding of some others, and identified new issues and problems. The

CWIP confirms some common beliefs about the management of the fields, but it also raises new questions about current management practices.

A number of East and Gulf coast states are also faced with wetland management issues. For example, several Mid-Atlantic states (e.g. Delaware and New Jersey) manage wetlands for waterfowl habitat and mosquito control. Southeastern states, including North Carolina, South Carolina, and Georgia, control wetland water levels primarily to attact waterfowl. Florida's coastal wetlands continue to be managed to reduce mosquito production, while Louisiana and Texas are concerned with salt-marsh subsidence, along with the enhancement of waterfowl populations and control of the salt-marsh mosquito. In each case, similar major issues focusing on the impoundment and management of natural wetlands have emerged. Consequently, although the research carried out under the CWIP focuses on South Carolina impoundments, the implications of this research directly apply to management questions currently being delated in other states. Therefore, the State of South Carolina has a unique opportunity to develop an innovative wetland management policy; a policy which may serve as an example for natural resource decision-makers outside South Carolina.

TRANSFER EFFECTS

The most-important consequence of the impoundment of wetlands involves the impact of imposing a dike around a relatively uniform wetland field. These dikes create a variety of transfer effects, limiting exchange with the surrounding environment in several ways.

Dikes restrict significant water exchanges to the period when water-control structures are open. Restricted water exchange limits the ingress and egress of aquatic species to the cycles introduced by management regimes. It also produces pulse effects. Because we know from our survey (Chapter 3) that typical management schemes restrict the number of exchanges, it appears likely that these "pulses" may be rather strong. Additionally, dikes impede water circulation that may produce stressful water-quality conditions for many aquatic species within the impoundments.

Dikes also shape the impact an impoundment has on the surrounding system. Depending on the timing of water exchange, they may restrict the access of species seeking wetland nursery sites, or they may capture these transient species before they can move out to common property fisheries. This timing can also affect the spawning of undesireable species, such as mosquitoes, which are often associated with impoundments. Some of these effects may depend on such a seemingly simple consideration as the location of the opening in a water-control structure (as Chapter 16 has suggested). They may also differ based on the size of a particular managed system. However, we know too little about the impacts of very large impoundments even though extensive acreage is located in them.

The ecological consequences of diking have been discussed in detail in this treatise, but the transfer effects also have clear implications for shaping the state's policies toward impoundments. The results of this study, and the experience of the cooperating investigators, suggests that the impacts associated with impoundments may depend on the scheduling of periods of exchange within time frames of a week or two. This timing must be related to the spawning schedules of particular species (which vary from season to season); it must also be related to climatic events that influence salinities (through freshwater pulses and saline instrusions) and water temperatures. These environmental parameters are best determined through on-site monitoring and assessment, which suggests that intensive management is probably required to balance the various consequences of management regimes most effectively.

Our studies suggest that management strategies which permit additional exchange with the surrounding system would help minimize the adverse transfer effects of impoundments. This recommendation appears to be particularly important for a number of the sites along the coast where relatively simple management regimes are reportedly practiced. On the other hand, the variability and complexity of the transfer effects we have encountered suggests that they all will not necessarily be remedied by simple "cookbook" management schemes. Further, it will be difficult to devise simple regulatory schemes that can ensure the balance desired among competing objectives. As a result, it appears unlikely that a simple and unambigous statement of desirable management practices can be achieved at this time.

Therefore, it would be desirable for the State of South Carolina to encourage impoundment managers to increase water exchange with the surrounding ecosystem. This exchange would improve the availability to wetland-dependent species and improve the likelihood of enhanced water-quality conditions within impoundments, and thus reduce potential impacts on the surrounding ecosystem. State policy should focus on first, encouraging managers to adopt management regimes to facilitate this recommendation and, second, improving our understanding of the consequences of the transfer effect. It should not, however, concentrate on inflexible and detailed specification of management practices at this time.

THE PRACTICAL WORLD OF IMPOUNDMENTS

The CWIP has also improved our appreciation for the skills and interests of those managing and using these sites. State policies and private practices influence these sites and their use; this project has involved several types of inquiry that have improved our understanding of the relationship between the activities of both state and federal natural resource agencies and private impoundment managers.

It is clear that controversies over the rights of various interests in impoundments have not subsided. Our survey of impoundment owners and managers demonstrates that many assert strongly-felt claims to private ownership of these sites. In a number of cases, many report that they have undertaken substantial efforts to document their claims. At the same time, respondents report continuing problems with "trespassing" by individuals who apparently do not concede that these private owners can exclude the public from their fields.

Our survey of the status of impounded wetlands along the coast reveals that many sites are being actively managed and used by those who claim them. The State of South Carolina has not challenged the continuation of their current activities, nor does the state appear likely to do so in the near future. On the other hand, a number of other sites have fallen into disrepair and are now described by survey respondents as "formerly impounded." The costs of rediking, both economic and political, seem to rule out the reimpoundment of these sites any time soon. The number of sites where only "repairs" would be necessary to restore dikes and water-control structures appears to be relatively small. The interests of individuals claiming these sites and the concerns of groups worried about the significance of allowing re-impoundment have sparked many of the controversies we have seen in recent years.

We have found much evidence suggesting that controversies over the ownership and control of impounded fields are likely to continue; however, our survey suggests that opportunities may exist for compromise solutions to these disagreements.

The analysis of current management practices reveals an important opportunity for the State of South Carolina. Many of those responding to our inquiries reported that they managed their fields with relatively simple management techniques. Although we cannot confidently prescribe precise management schemes appropriate for each site, we have identified a number of principles that would dramatically improve these simple approaches. More-extensive and better-timed exchanges with the surrounding ecosystem will clearly help to minimize the problems associated with the transfer effects we have already discussed. Also, it appears likely that more-intensive management can reduce the contribution of impounded areas to mosquito production while improving the value of these wetland areas for the activities most desired by their managers or owners. Thus many impoundment managers have an important opportunity to improve their management practices, and these changes could have immediate benefits for both owners and the public at large.

Our survey of impoundment managers further documents a common belief that the primary emphasis of impoundment management is focused on enhancing plant growth to attract waterfowl. This has a number of consequences: it constrains efforts to ameliorate the transfer effects we have already discussed; it shapes conflicts over the use of impounded fields; but it also focuses our efforts to improve the use of these valuable wetlands. At the same time, our survey reveals the substantial diversity of current waterfowl management practices. It is clear that efforts to improve the understanding of current management and use of impoundments must focus primarily on the role of waterfowl management. As the dominant interest in the active management of impoundments, improvements in waterfowl management regimes (and their implementation on currently managed sites) will provide the greatest immediate benefit to the state and its citizens.

THE INFORMATION PROBLEM

The CWIP underscores an important problem that time and again faces the state and its citizens in formulating wise policies for the future: the need for information. Although the CWIP represents one of the most-comprehensive studies of its kind, we must recognize several important limitations on any attempt to extend its findings to impoundments throughout the state. There are several reasons for this. First, the field studies were confined to five small, similarly-sized impoundments, bordered by tidal creeks and open wetlands. We found important differences among the study impoundments we had expected to serve as replicate systems. We also found that conditions in the five fields varied dramatically on both a seasonal and an annual basis. Some of these changes were easy to predict, as was the case when high tempertures and low dissolved oxygen levels created stressful conditions for some aquatic species in the impoundments. It seems clear, too, that the size of an impounded field is important (although we do not fully understand all the factors that may be involved). The units we studied are clearly much smaller than many that are managed along the coast (see Chapter 3), which may have made them easier to control and manage. The experience of the participating investigators suggests that other sites along the coast will present new, sometimes distinctive problems. We conclude, accordingly, that "reconnaissance studies," relying on a few isolated observations of an otherwise unknown site, cannot provide adequate information about the ecological characteristics of a particular site, based on the information that is available today.

A second limitation is that the study focused on impoundments managed under a particular style of waterfowl management. Our data suggest that some improvements in the timing of water manipulations might enhance the availability of target plant species and that modifications in the management regime might ameliorate the adverse effects on other species and on other wetlands activity. The practical consequences of these suggestions could not be tested within the two yearly management cycles studied, but the suggestions have important implications for the success of management regimes and for their impact on other factors valued by the community. We conclude, accordingly, that additional study of impoundment management regimes and their consequences is required for development of wise policies for the state's wetlands.

Most actively managed wetlands in South Carolina are used to attract waterfowl to support hunting and associated activities for personal and commercial use. Although management regimes developed for this purpose are becoming increasingly sophisticated, and this study suggests some ways of improving them, far less is known about strategies that would enhance the prospects for multiple and competing uses of these sites. State policy-makers encounter increasing interest in using these sites for aquaculture (with particular interest emerging in crawfish culture on freshwater sites), but too little is known about the potential for successful management for both aquaculture and waterfowl, or about the prospects for management focused primarily on other uses of these sites. We conclude, accordingly, that additional studies are needed of multiple-objective management regimes, and those focused on objectives other than the attraction of waterfowl, for development of wise policies for the state's wetlands.

We have also found that our understanding of remnant impoundments is inadequate to provide any basis for making recommendations about relevant state policy. Understandably, those concerned with the impact diking has on water flow and exchange will want to know whether the structures associated with remnant impoundments may nonetheless restrict circulation and otherwise impede natural processes. Such concerns may lead to state policies focusing not only on rediking, but also on "dediking," the removal of these old structures. It should be noted that our current understanding does not reveal whether these old dikes and structures do, in fact, have significant negative impacts.

Decision-makers encounter pleas from scientists for more studies and more information with some impatience. Here such cynicism appears unwarranted, in our view. On the one hand, the state's stake is large, with more than 70,000 acres of scarce wetlands currently under management, and thousands of other acres subject to claims by parties interested in bringing them under more-intensive management. On the other hand, our study suggests that these sites function differently from other wetland environments in important ways and that we know too little about the differences.

THE POTENTIAL FOR CONTINUED CONFLICT AND THE VALUE OF A BALANCE APPROACH

Management regimes have proved controversial because of the transfer effects already discussed. Our analysis suggests, however, that some of the negative effects of these management regimes can be ameliorated through improvements in exchange with the surrounding system. Impoundment managers interested in attracting waterfowl may not need to sacrifice the quality of the vegetation they produce in order to eliminate mosquito production, improve the availability of the impoundment to juvenile species, and reduce the likelihood of stressful conditions for aquatic species. They may also have the opportunity to increase the productivity of their impoundment for other valued species without sacrificing their primary focus.

Our survey discloses continuing differences over the ownership of impoundment sites. The interests of those claiming ownership, based on historic patterns of use and legal transactions sanctioned by the state, are pitted against those arguing that often-ambiguous claims may have lapsed and that there is some residual public interest in these sites. The survey suggests that many private claimants are prepared to defend their claims, while the state continues to contest claims held to be unwarranted. This work also suggests, however, that in a relatively small number of sites, "repairs" are all that is necessary to restore an impounded field to more-intensive management. Economic feasibility and opposition from some groups is thus likely to focus controversies over re-impoundment on a relatively small number of sites.

This study has not resolved the divergent views on the question of what should be done with South Carolina's resource of coastal wetland impoundments. These views depend on the different values placed on the resources associated with wetlands. Some seek waterfowl for hunting; others cherish natural resources for their scenic and aesthetic role; still others value wetlands as nurseries for species caught elsewhere; and so on. These sites may well be viewed as promising for dredge-and-fill operations leading to coastal developments of other kinds. In some respects, these many interests are incommensurate, although we have found promising signs of opportunity to satisfy diverse views through the enhancement of management regimes applied to the impounded sites.

Conflicts nonetheless extend beyond these differences. Disagreements over the priorities placed on transient marine species and waterfowl are likely to persist; our studies suggests means of ameliorating some of the impacts associated with the dominant management regimes, but they also suggest that some tensions remain. Other adverse effects of impoundment management can apparently be reduced, but in the eyes of some, these reductions will still fall short of the desired character of natural wetlands. Although some elements of the controversies over ownership and title claims may be resolveable, other aspects are clearly going to persist. Apart from these controversies, we also see important areas requiring further research to address significant questions that have been raised in the course of this study.

Still, the study affords substantial opportunities for the state and its citizens. Management-strategy recommendations clearly have substantial promise. Several aspects of the political controversies which have characterized discussions of state policy toward impounded fields appear to be amenable to solution. Finally, our understanding of the ecological processes at work in impounded fields has been improved, and the limitations on our knowledge have been narrowed and focused. This report, then, should serve as a foundation for improving the use that the people in South Carolina make of their precious coastal wetland resources.