

TECHNICAL REPORT NO. 17

FINAL REPORT

A CONCEPTUAL MODEL OF SALT MARSH MANAGEMENT
ON
MERRITT ISLAND NATIONAL WILDLIFE REFUGE,
FLORIDA

Clay L. Montague*
Alexander V. Zale
H. Franklin Percival

Florida Cooperative Fish and Wildlife Research Unit
Newins-Ziegler Hall
School of Forest Resources and Conservation
Institute of Food and Agricultural Sciences
University of Florida, Gainesville, FL 32611

and

*Systems Ecology and Energy Analysis Program
Department of Environmental Engineering Sciences
A.P. Black Hall
University of Florida, Gainesville, FL 32611

Supported by:

The National Aeronautics and Space Administration

in cooperation with

U.S. Department of the Interior
Fish and Wildlife Service
Cooperative Agreement NO. 14-16-0009-1544
RWO #15

6 August 1985

TABLE OF CONTENTS

	<u>Page</u>
LIST OF TABLES	4
LIST OF FIGURES	5
ACKNOWLEDGMENTS	7
STATEMENT OF PURPOSE	8
INTRODUCTION	8
Values of Saltmarsh Impoundments	9
Values of Natural Salt Marsh	11
Concerns About Impoundments and the Value of Merritt Island Marshes	11
Focus of This Study	14
ECOLOGY OF MERRITT ISLAND SALT MARSHES	15
Theoretical Basis for Production	15
The Occurrence of Biota and Environmental Stress	16
Nutrient Supply	17
Non-energy Environmental Conditions	17
Notion of Automitigation	17
Determinants of Production and the Concept of Feedback	18
Ideas for Impoundment Management to Enhance Ecological Production	20
Diversity of Merritt Island Salt Marsh	20
The Concept of Diversity	21
Importance of Diversity in Natural Areas	21
Considerations in the Measurement of Diversity	22
Principal Determinants of Diversity	22
Characteristics of Disturbance and Temporal Variation That Affect Diversity	23
Characteristics of Biota That Affect Diversity	24
Summary of Diversity Concepts	24
Ideas for Impoundment Management to Enhance Ecological Diversity	25
Relationships Between Marshes and Estuaries	25
Energy, Carbon, and Biota	25
Nitrogen	27
Phosphorus and Sediments	28
Sulfur, Energy, and Acid Rain	28
A Scenario of a Southeast Florida Estuary Without Marshes ..	29
Summary of Relationships and Conclusion	29
Food and Cover for Estuarine Fish and Shellfish	30
Foods of Estuarine Fish and Shellfish	30
Food Value of Detritus	31
Vagile "Link" Organisms	33
Accessibility of Foods	34

	<u>Page</u>
Cover for Estuarine Fish and Shellfish	35
Egress of Vagile Fish and Shellfish from Marshes	36
FUNDAMENTALS OF MARSH MANAGEMENT FOR MOSQUITO CONTROL AND ATTRACTION OF WINTERING WATERFOWL	38
Mosquito Control	38
Waterfowl Attraction	38
ECOLOGY OF MERRITT ISLAND SALTMARSH IMPOUNDMENTS	41
Effects of Impoundment on Ecological Production	41
Primary Energy (Sunlight and Turbidity)	41
Water Circulation and Freshening of Water	42
Whole-system Stress (Low Oxygen, Hypersalinity)	47
Nutrient Supply	47
Effects of Impoundment on Overall Diversity	48
Effects of Impoundment on Estuarine Fish and Shellfish	49
Summary Diagrams of the Influence of Impoundment on Estuarine Fish and Shellfish	49
Cover	52
Ideas for Impoundment Management to Enhance Estuarine Fish and Shellfish	52
Analysis of Commercial Landings for the Inshore Fisheries of Brevard and Volusia Counties, 1951-1982	53
Spotted Seatrout	53
Blue Crab	55
Spot	59
Mullet	59
Florida Pompano	59
Summary	63
Effects of Impoundment on Waterfowl	63
MANAGEMENT OPTIONS FOR MARSHES ON MERRITT ISLAND NATIONAL WILDLIFE REFUGE	68
Options	68
Permanent Flooding	68
Impoundment Elimination	69
Vestigial Impoundments	69
Seasonal Flooding	69
Seasonal Flooding With Added Potholes	69
Leaky Impoundments	70
Intensive Management For Waterfowl Foods	70
Integrated Marsh Management	70
RESEARCH AND DATA NEEDS	72
LITERATURE CITED	73

LIST OF TABLES

	<u>Page</u>
Table 1. Water Level Data for a Restored March and from Three Impounded Marshes on Merritt Island National Wildlife Refuge (Data from W. Leenhouts). SD = Standard Deviation, N = Number of Observations between September 1977 and April 1980	12
Table 2. Salinity Data for a Restored March and from Three Impounded Marshes on Merritt Island National Wildlife Refuge (Data from W. Leenhouts). SD = Standard Deviation, N = Number of Observations between September 1977 and April 1980	42

LIST OF FIGURES

	<u>Page</u>
Figure 1. Features of impounded salt marsh. Note the positive feedback loop involving economic development.	10
Figure 2. Hypothetical influences on primary production in Merritt Island salt marshes. Major sources for production are underlined. Note the positive feedback loop between nitrogen fixation and primary production.	19
Figure 3. Conceptual model of relationships of salt marshes to estuaries. Complex possible exchanges of elements between salt marshes and estuarine water leads to temporal variation and uncertainty concerning the of salt overall influence marshes (natural or impounded) on and biogeochemistry energetics in estuaries.	26
Figure 4. Conceptual model of factors influencing egress from natural or impounded salt marsh. Note that more access necessitates more pumping.	37
Figure 5. Conceptual model of salt marsh management to control mosquitos and attract wintering waterfowl.	39
Figure 6. Salinity and Water Level Data from the Restored Marsh, T-10-K, from September 1977 through April 1980 (data courtesy of W. Leenhouts, MINWR).....	43
Figure 7. Salinity and Water Level Data from Black Point Impoundment, T-10-J, from September 1977 through April 1980 (data courtesy of W. Leenhouts, MINWR).....	44

	<u>Page</u>
Figure 8. Salinity and Water Level Data from the Roach Hole Impoundment, T-10-D, from September 1977 through April 1980 (data courtesy of W. Leenhouts, MINWR).....	45
Figure 9. Salinity and Water Level Data from the Fresh Impoundment, T-24-D, from September 1977 through 1980 (data courtesy of W. Leenhouts, April MINWR).....	46
Figure 10. Conceptual model of major influences on food for estuarine fish and shellfish. Note the importance of accessibility of food.	50
Figure 11. Conceptual model of major influences on cover for estuarine fish and shellfish. Note the importance of accessibility of cover.	51

	<u>Page</u>
Figure 12. Numbers of vessels registered for commercial use in Brevard and Volusia counties, 1963 to 1978. Data courtesy of Florida Department of Natural Resources.	54
Figure 13. Commercial landings (pounds) of spotted seatrout in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982.	56
Figure 14. Numbers of vessels registered for recreational use in Brevard and Volusia counties, 1963 to 1983. Data courtesy of Florida Department of Natural Resources.	57
Figure 15. Commercial landings (pounds) of blue crabs (hard) in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982. From 1958 to 1962, landings data for the two counties were not reported separately.	58
Figure 16. Commercial landings (pounds) of spot in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982. Note the substantial increase in landings in Brevard County in the 1980's.	60
Figure 17. Commercial landings (pounds) of mullet (both white and striped combined) in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982.	61
Figure 18. Commercial landings (pounds) of Florida pompano in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982.	62

ACKNOWLEDGMENTS

This document was produced at the expense of the National Aeronautics and Space Administration through the U.S. Fish and Wildlife Service. We acknowledge the assistance of K. Key and M. Busacca, NASA, and S. Vehrs and W. Leenhouts, USFWS, in pursuing the issue and securing the funds for this investigation.

Special recognition is given to W. Leenhouts, Merritt Island National Wildlife Refuge, and J. Salmela, Brevard County Mosquito Control District. These individuals have provided time, encouragement and enthusiasm. Above all they provided valuable insight into the ecology and management of the Merritt Island salt marshes owing to their collective years of experience on the site.

A number of other individuals have been instrumental in the technical aspects of this task and have provided literature, citations and discussion: we acknowledge W. Knott, M. Koller, and J. Ryan, NASA; F. Montalbano, Florida Game and Fresh Water Fish Commission; R. Hinkle and his staff, Biometrics Corp.; G. Gilmore, Harbor Branch Foundation Inc.

R. Gregory ably administered and Cooperative Fish and Wildlife Research Unit throughout most of the study period and has provided technical discussion. T. Hingtgen initially screened the coastal impoundment and salt marsh literature making our work infinitely easier. E. Tuggle made many trips to University of Florida libraries, drafted figures, and made many photocopies related to this effort.

Drafts of this report were reviewed by

M. Busacca,
J. Carroll, Jr.,
F. Johnson,
K. Key,
W. Leenhouts,
F. Montalbano,
S. Vehrs.

STATEMENT OF PURPOSE

Diking and holding water on salt marshes ("impounding" the marsh) is a management technique used on Merritt Island National Wildlife Refuge (MINWR) and elsewhere in the Southeast to: a) prevent the reproduction of saltmarsh mosquitos, and b) attract wintering waterfowl and other marsh, shore, and wading birds. Because of concern that diking and holding water may interfere with the production of estuarine fish and shellfish, impoundment managers are being asked to consider altering management protocol to reduce or eliminate any such negative influence. How to change protocol and preserve effective mosquito control and wildlife management is a decision of great complexity because: a) the relationships between estuarine organisms and the fringing salt marshes at the land-water interface are complex, and b) impounded marshes are currently good habitat for a variety of species of fish and wildlife. Most data collection by scientists and managers in the area has not been focused on this particular problem. Furthermore, collection of needed data may not be possible before changes in protocol are demanded. Therefore, the purpose of this document is two-fold: 1) to suggest management alternatives, given existing information, and 2) to help identify research needs that have a high probability of leading to improved simultaneous management of mosquitos, waterfowl, other wildlife, freshwater fish, and estuarine fish and shellfish on the marshland of the Merritt Island National Wildlife Refuge.

INTRODUCTION

As an alternative to spraying DDT and other insecticides, nearly all of the salt marsh in the vicinity of Merritt Island, Florida, was diked between 1959 and 1966 (Leenhouts 1983) in order to hold water on marshland to prevent the production of saltmarsh mosquitos. This technique works because females of the saltmarsh mosquitos Aedes sollicitans and A. taeniorhynchus lay eggs on the soil surface (where they hatch following inundation by tides or rain) but not on standing water (Provost 1968, 1973b; Nielsen and Nielsen 1953). Species of mosquitos that are able to live in the resulting standing water are not nearly as productive, so the nuisance is considered sufficiently controlled by this method (Clements and Rogers 1964; Provost 1968).

Early efforts to control mosquitos by impounding were effective, but often resulted in the death of saltmarsh vegetation (e.g., black mangroves, grasses, and succulents) because of "overflowing" (Clements and Rogers 1964; Provost 1968; Bidlingmayer 1982). Overflowing occurred primarily because: 1) the minimum flood level and duration for effective mosquito control were not well known, and 2) water sufficient to last the entire season of mosquito production had to be stored early in the season as insurance against drought (J. Salmela, pers. comm.). Concern over the loss of vegetation was expressed notably by Dr. Maurice Provost of the Florida Medical Entomology Laboratory in Vero Beach, who worked with the Brevard County Mosquito Control District to develop less destructive, but effective water level control of mosquitos (Provost 1968, 1973b, 1977). With present knowledge and pumping capabilities, saltmarsh mosquitos can be controlled by flooding in the vicinity of Merritt Island with far less loss of saltmarsh and mangrove vegetation (Clements and Rogers 1964; Provost 1968, 1973b).

Values of Saltmarsh Impoundments

A purported benefit of the continuously high water on marshes noted by Provost (1959, 1968, 1969a, 1969b) and Trost (undated) was increased use of marshes by waterfowl and wading birds. Waterfowl are now managed on MINWR by holding water on the marshes at levels believed beneficial to the birds while allowing sufficient mosquito control (W.P. Leenhouts, personal communication), but the inundation period and water depths that are now used for waterbirds are often in excess of that required for control of saltmarsh mosquitos. Water level control can be terminated in fall if mosquito control is the only objective, but on the Merritt Island National Wildlife Refuge (MINWR) water is retained on the marsh until after wintering waterfowl leave in about March.

Because salinity in impounded marshes often is lower than the salinity of estuarine water (Bidlingmayer 1982; W. Leenhouts, unpubl. data) and because water is held on the marsh longer than it would be under natural conditions, impounded salt marsh provides habitat for a variety of fish (especially freshwater species) and wildlife not usually found in natural salt marshes (Provost 1968; Miglarese and Sandifer 1982; Snelson 1983). Many of these organisms are more common to freshwater marshes of Florida (e.g., alligators, kingfishers, centrarchids). These accumulations are readily measurable. Not readily measurable is the effect of impoundments on estuarine fish and shellfish populations. However, it is clear that impoundment management strategies that preclude ingress and egress of estuarine fish and shellfish have excluded these organisms from large expanses of marsh which they formerly occupied (see Lewis et al. in press for a review of this phenomenon).

Although impoundment undoubtedly results in reduced production of some species (notably mosquitos, and perhaps other organisms as well), a variety of values of impoundments can accrue in addition to mosquito control and waterfowl accumulation, owing to the controllability of water levels and salinities in separate subdivisions of marsh. Some of these values are indicated in a conceptual model of impoundment features illustrated in Figure 1.

At the top of Figure 1 is impounded salt marsh, which negatively influences mosquito production and use of insecticides for mosquito control. This enhances living and working conditions in the vicinity of Merritt Island. Such enhancement of the human environment inevitably leads to more economic development, more by-products of development, and more pressure to develop, to utilize, and to preserve natural areas by respective advocates of each.

Impoundment also positively influences accumulations of: 1) certain species of waterfowl (Trost undated; Provost undated; Heitzman 1978; Wicker et al. 1983); 2) certain wading birds (Trost undated; Provost undated, 1968, 1969a); 3) certain fish (Snelson 1983; Wicker et al. 1983); 4) alligators (Wilkinson 1983); and 5) upland mammals that use dikes as habitat (Migliarese and Sandifer 1982). The density and diversity of vertebrates using these areas is undoubtedly higher than is found in

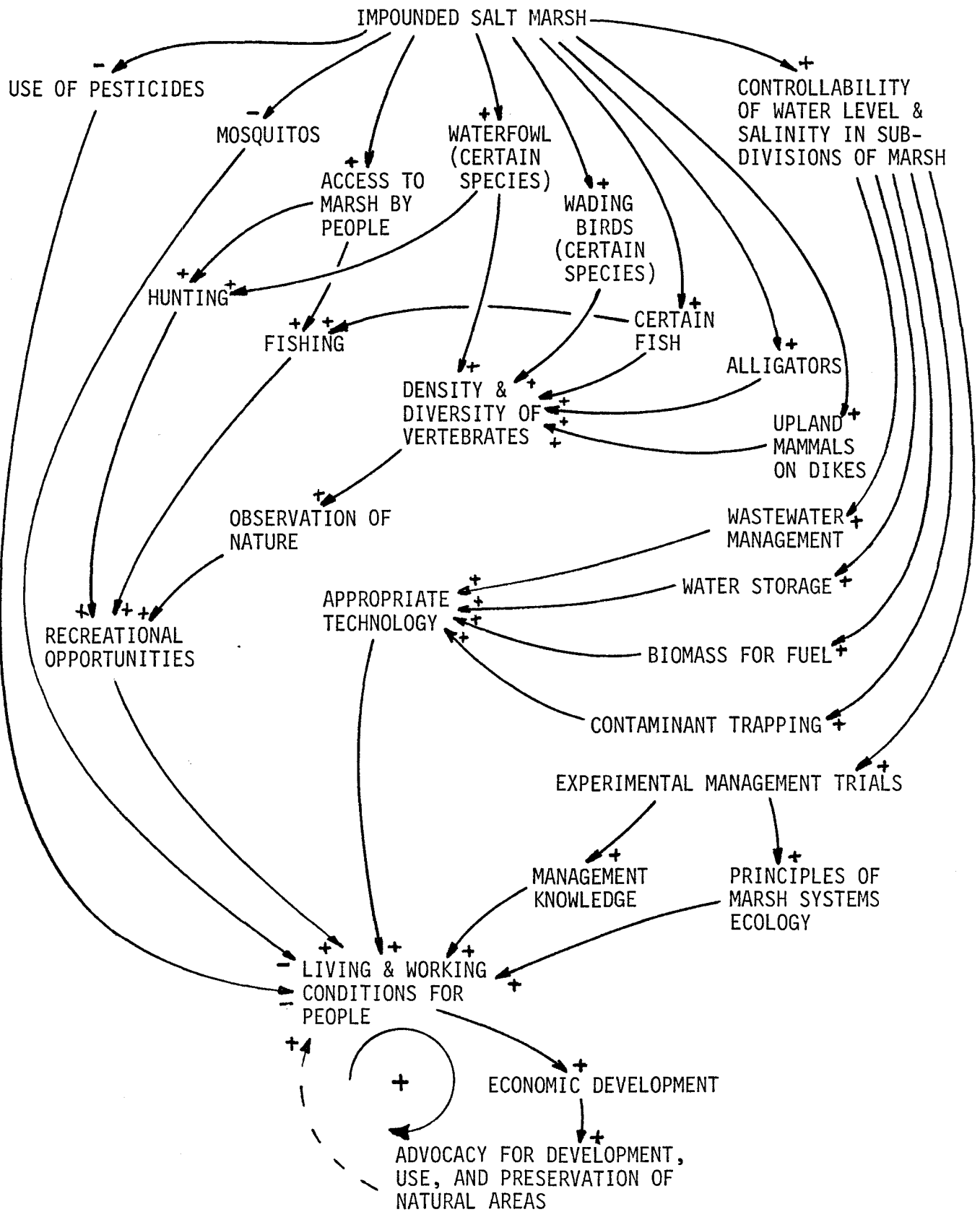


Figure 1. Features of Impounded Salt Marsh. Note the positive feedback loop involving economic development.

natural salt marsh. In addition, the dikes and access roads that accompany impoundment enhance access by people to these marsh areas for fishing, hunting, and observation of nature. These activities considerably enhance the recreational opportunities in the vicinity of Merritt Island, which also improve living conditions for people.

The controllability of water levels and salinities in separate subdivisions allows a multitude of other uses of these areas to meet particular needs. Such needs include use of some impounded marshes for wastewater management (tertiary treatment), for biomass fuel production, for water storage, and for contaminant trapping. When alternative methods for meeting these needs are even more destructive to our environment, use of impoundments will be appropriate technology for human survival. Regardless of the method, however, meeting these needs will result in preservation or enhancement of living conditions for people and hence allow even more development.

Finally, and perhaps most pertinent to management of a wildlife refuge, the controllability and subdivision of marshes allows a variety of experimental management regimes to be tried. As long as adequate data are recorded to preserve continuity from manager to manager (so that what is learned by one is adequately transferred to the next), management experiments will have a high likelihood of producing a greater diversity of desired species, including those of the estuarine fishery. In addition, careful monitoring of the effects of a variety of management experiments can advance the field of systems ecology, so that general principles useful for solving a variety of environmental problems can be discovered and validated.

Values of Natural Salt Marsh

Natural salt marshes are said to perform a variety of functions of value to humans (OTA 1984). These include: 1) food and cover for estuarine fish and shellfish of economic value; 2) sediment trapping and stabilization; 3) reduction of storm surge and waves; and 4) removal of nutrients that can produce blooms of unwanted algae in estuaries. The quality of these functions of marshes is adequate enough to have been recognized in numerous articles (Nixon 1980), but may not be as good as can be engineered. The cost, however, of these functions is the cost of protection of these areas, which has been relatively low in the past. As pressures of development increase, however, the cost of natural marsh preservation increases. State and federal agencies (e.g., USFWS Div. of Ecological Services, U.S. EPA, Florida DNR) spend considerable effort in such habitat preservation.

Concerns About Impoundments and the Value of Merritt Island Marshes

Of primary concern is whether natural functions of MINWR salt marsh have been precluded by impoundment. Of particular concern is the issue of food and cover for estuarine fish and shellfish. Elucidation of this problem is exacerbated by differences between the natural cycle of flooding and draining of MINWR marshes and those of tidal marshes where many of the purported values have received the greatest study such as those of Georgia

(see Pomeroy and Wiegert 1981), Massachusetts (see Valiela and Teal 1979 a,b), and Louisiana (see Gosselink 1984). The well-studied marshes of Georgia for example are flooded and drained twice per day, with short periods (two or three days) of drought during neap tides without rains. The average tidal range is up to 8 feet in Georgia depending on proximity to the ocean. This tidal energy provides water motion and circulation through these marshes as well as almost daily access of estuarine fauna to the marsh surface. In the vicinity of Merritt Island, however, marshes are typically dry (except for rainfall) from January to October when a general rise in water level causes frequent and almost continuous inundation for the remainder of the year (Provost 1973a), but wind energy rather than tides is the primary power for water movement (Dubbelday 1975).

An important determination to be made on Merritt Island is the amount of time unimpounded marshes are inundated. This is likely to be highly variable not only from year to year, but also from place to place around Merritt Island. Because topographical relief is so low in these marshes, slight differences in elevation can affect the time of inundation of large expanses of both impounded and unimpounded marsh. An additional consideration is the presence of several causeways in the vicinity of Merritt Island. These impede the flow of water and hence can create locally higher and lower water levels for a given wind speed and direction.

Water levels have been recorded by MINWR by observing a tide-stick approximately once per month in many Merritt Island impoundments as well as in the restored marsh T-10-K. Data from this marsh as well as from three of the impounded marshes are presented in Table 1. Much of the marsh area is believed by Leenhouts (personal communication) to be inundated only when water levels exceed one foot above mean sea level. Vegetatively, such areas tend to consist of quantities of *Spartina bakerii* (Leenhouts, personal communication). In the restored marsh, during the period from September 1977 to April 1980, water level exceeded 1.0 ft on only 4 of 29 observations. In the adjacent Black Point impoundment (T-10-J), water level exceeded 1.0 ft on 16 of 29 observations.

Particular effort has been spent determining inundation time of a marsh in the southeast part of Merritt Island near the Bennett Causeway (not part of MINWR) by the U.S. Fish and Wildlife Service, Ecological

Table 1. Water Level Data for a Restored Marsh and from Three Impounded Marshes on Merritt Island National Wildlife Refuge (Data from W. Leenhouts). SD = Standard Deviation, N = Number of Observations between September 1977 and April 1980.

MARSH	LOW	HIGH	MEAN	SD	N
T-10-K (Restored Marsh)	0	1.25	0.51	0.32	29
T-10-J (Black Point Imp.)	0.20	1.55	0.95	0.43	29
T-10-D (Roach Hole Imp.)	0.55	2.55	1.70	0.39	28
T-24-D (Fresh Imp.)	1.40	2.80	2.03	0.38	29

Services office in Vero Beach, Florida. Some of this marsh (exact acreage unspecified) is believed to have been inundated for perhaps 150 or more days per year in 1981 and 1982 (A. Banner, unp. data).

Despite the uncertainty about the time of inundation, the frequency and duration of water level fluctuation in the vicinity of MINWR is considerably different than in the tidal marshes of Georgia, Massachusetts, and Louisiana, where most of the functional relationships of marshes to estuaries have been studied. Prior to impoundment, much of the acreage of Merritt Island marshes was inundated nearly continuously for perhaps 100 days per year (judged from unp. data of Ned Smith), with wind and rain, but no tidal energy available to create water movement. Tidal salt marshes elsewhere (e.g. Georgia) are inundated perhaps 300 days per year for 12 hours per day (NOAA tide tables). Water movement through tidally-flooded marshes should be much greater and more predictable than the wind-driven circulation of Merritt Island. Wind does not circulate shallow water very effectively because turbulent eddies cannot usually form (H.T. Odum 1967). Marsh vegetation will create additional resistance to wind and water movement.

Merritt Island marshes are perhaps so different from the marshes of greatest scientific study that results and conclusions from the majority of the salt marsh literature have little applicability. Water movement and inundation period, seasonal temperature fluctuations, and sediment supply and type are considerably different from those of the major study sites of salt marsh ecology (see Introduction of Montague et al. 1984a). The filtering capabilities of the Merritt Island marshes are probably much less than those of tidal marshes, because estuarine water covers the former marshes during the winter when vegetation there is relatively senescent or not as actively growing as at other times of year (Chynoweth 1975). Although of the same genus, Spartina alterniflora (the principal component of the majority of salt marsh studies) does not closely approximate Spartina bakerii (a common plant in Merritt Island impoundments) in habitat or presumably in physiological requirements. Vegetation of much of the Merritt Island salt marsh includes species typical of "high marsh" (marsh near to dry land) of the Atlantic and Gulf coasts (e.g. Salicornia spp., Batis maritima, Distichlis spicata, Paspalum vaginatum; see Sweet 1976; Leenhouts and Baker 1982; Montague et al. 1984b). Differences in sediment may result in different limiting nutrients and different effects of marsh on chemical constituents of estuarine water (see section entitled "Relationships Between Marshes and Estuaries"). Hence, values of Merritt Island marshes largely remain to be determined.

Relationships between high marshes and estuaries elsewhere have not been well-established (Nixon 1982). The studies of Byron (1968) on a North Carolina marsh dominated by Juncus roemerianus, Blum (1969) on a Massachusetts marsh dominated by Spartina patens, and particularly Borey et al. (1983) on a Texas marsh co-dominated by Spartina patens and Distichlis spicata are perhaps indicative of the relationships between infrequently flooded high marsh and estuarine water. Neither Byron nor Blum could demonstrate a net export of organic matter to the estuary. Byron demonstrated a net uptake of nitrogen on his study sites, and Blum demonstrated a net uptake of manganese. Borey et al. demonstrated an export of only 2.4 to 5.5% of net aerial primary production, which

consisted of refractory dissolved organics. They attributed this low value both to the lack of twice-daily tides of a high amplitude and to the indirect methods of measurement of export used in some of the published studies that show considerably more export, to which they compare their results. Their paper is a concise review of current thinking about export of organic matter from marshes to estuaries.

Focus of This Study

A large number of issues presently occur in scientific study of salt marshes, and also a large number of issues have been raised by a variety of interests with regard to the potential values and damage caused by impoundment of salt marshes on Merritt Island and elsewhere. These issues include not only the potential for damage to stocks of estuarine fish and shellfish, but also the potential for storage of contaminants from pesticides formerly used in agriculture and mosquito control, the effects on a variety of other wildlife including the disappearance of the dusky seaside sparrow, wastewater application and water storage in impounded marshes, and seagrass development in nearby estuarine waters. Our focus is primarily on the salt marshes of Merritt Island National Wildlife Refuge and the effects of impoundment and their management for mosquito control and waterfowl on ecological production and diversity in general and on estuarine fish and shellfish in particular. We will also consider briefly effects on other wildlife. With appropriate modification, the information in these sections should provide a general conceptual framework for considering a variety of other concerns and problems.

ECOLOGY OF MERRITT ISLAND SALT MARSHES

Salt marshes are some of the most biologically productive lands on earth (E.P. Odum 1971; Turner 1976; Teal 1980) and Merritt Island salt marshes are apparently no exception, though only one study is known to us. Chynoweth (1975) found an annual production of certain marsh plants in the breached impoundment T-10-K to be approximately $2100 \text{ g(dw)} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, about half of which is carbon. These are comparable to production values of salt marshes elsewhere (Wiegert 1979, Teal 1980, Costanza et al. 1983). Unfortunately, Chynoweth reported production from only three plant types, Spartina bakerii, Distichlis spicata, and Sesuvium portulacastrum. Batis maritima, several species of Salicornia, Paspalum vaginatum, and black and white mangroves are dominant plants in many marshes in the vicinity of Merritt Island. Production of these on Merritt Island have not been determined.

Plant production in ecosystems is responsible for animal production. Plants are either consumed directly by grazing insects that then become prey for insectivorous animals, or they die and are decomposed by a variety of bacteria, fungi, microfauna, and meiofauna. This decomposer community then becomes food for "detritivorous" macrofauna which are food for commercially or recreationally important fish and wildlife.

Theoretical Basis for Production

To understand why salt marshes are so productive and how to manage this production, theory of ecological production can be helpful. Ecological production is dependent upon the availability of: 1) biota; 2) essential nutrients; and 3) energy available to be converted into new biota using essential nutrients. A shortage of any of these can limit production. These three requirements are somewhat interdependent, and in non-extreme environments (see Occurrence of Biota and Environmental Stress below), where a variety of organisms can survive (see Principle Determinants of Diversity, which follows), the magnitude of ecological production should be proportional to the sum of primary environmental energies and environmental energy subsidies converging on an ecosystem (see H.T. Odum 1984 for related discussion).

Primary energies are defined here as those that are directly converted to chemical energy of organic compounds by biota. World-wide, these include not only sunlight, but also geothermal energy, as has been recently demonstrated most explicitly in the case of the very rich biotic community of the Galapagos Rift thermal vents (Ballard 1977; Levinton 1982). The processes of photosynthesis and chemosynthesis are responsible for conversion of these primary energies into food energy, which is utilized by a web of consumers, including fish and wildlife of direct value to people.

Energy subsidies are flows of energy in the environment that are not directly assimilated by plants, decomposer microbes, or animals, but are exploited by organisms in such a way that more of the energy that they do

assimilate (from sunlight in the case of plants, or from food in the case of animals) can be allocated to production of more organisms (E.P. Odum et al. 1979). That more productive organisms will occur in the presence of energy subsidies in non-extreme environments (defined as above) is a fundamental tenet of the theory of natural selection (Lotka 1922a, 1922b).

A subsidy in excess can become a stress, its value as a subsidy can saturate (law of diminishing returns), or a perceived energy release may not, in fact, be a subsidy. Therefore, subsidy mechanisms must be identified and their effects on production measured before any ranking of effectiveness of particular subsidies is possible.

Wind is an example of an environmental energy subsidy in Merritt Island saltmarsh impoundments. It influences water circulation and wave action, which in turn facilitate the encounter of organisms with nutrients or foods (E.P. Odum 1974). Circulation also facilitates the separation of organisms from their metabolic wastes (standing water does not enhance production). Because less of an organism's directly assimilated energy need be utilized for these functions, a natural selection occurs for organisms that both utilize these subsidies and redirect assimilated energy to production. Therefore, in environments where energy subsidies exist, ecological production should be greater.

Water circulation caused by the ebb and flow of the tides has been said to account for the very much higher aerial production of Spartina alterniflora along the edges of tidal creeks of the southeastern United States (E.P. Odum et al. 1983 refer to this as "tidal subsidy"; see also Wiegert et al. 1983). In the only published study to date comparing primary production in a natural and an adjacent impounded marsh, E.P. Odum et al. (1983) reported 31% higher annual aboveground net production of giant cutgrass (Zizaniopsis miliacea) in the natural marsh than in the impounded marsh, although standing crops were almost identical (see also the data of Morantz in Whitman 1976). The authors attributed the difference in production to twice-daily tides in the natural marsh. On Merritt Island, little daily tide occurs, and it seems unlikely that impoundment would have as large a negative effect on production as in the cutgrass marshes. Water circulation occurring for any reason, including pumping, should provide energy subsidies with corresponding enhancement of production.

The Occurrence of Biota and Environmental Stress

Environmental stress occurs for a species when it is exposed to an environment that is so different from that within which its ancestors were naturally selected that it has little or no adaptation for contending with the stress (see also E.P. Odum et al. 1979). What is stressful for one species, however, may not cause a change in overall ecological production in an impoundment, though changes in species composition may result. However, environmental conditions occasionally occur that are extreme enough to be suboptimal for the production of any species on earth. A few species may exist under such conditions, but overall ecological production would be expected to be reduced. In impoundments, sustained extremely high salinity (perhaps greater than 60 ppt) should be a sufficient stress to greatly reduce overall ecological production, though subtle changes in production may occur at lower salinities.

Nutrient Supply

For ecological production to be proportional to available energy input, sufficient nutrients must be available for building new organisms. Nutrients (primarily nitrogen and phosphorus) arrive at Merritt Island from a variety of external sources. Stream flows, non-point source discharges, sewage outfalls, groundwater flows, dustfall, and rainfall all contain nutrients for ecological production. Nutrients such as nitrogen and carbon can be fixed from atmospheric pools of nitrogen gas and carbon dioxide. Carbon fixation requires the energy of sunlight (and is proportional to ecological production). Nitrogen fixation requires energy of organic compounds (fixed via photosynthesis or imported; Hanson 1977a, 1977b).

Recycling of nutrients occurs as organisms feed, egest and excrete, or die and decompose (Johannes 1964, 1968; Pomeroy 1970). The presence of organisms available for these processes, however, should be proportional to available energy inputs except in extreme environments.

In all of these cases, energy supply is important in generating a supply of nutrients as well as recycling nutrients, which themselves are essential for ecological production, so the concept of the magnitude of ecological production as proportional to the sum of primary environmental energies and environmental energy subsidies converging on an ecosystem may hold if a number of species can occur and if sufficient time has elapsed for exploitation of available energy sources and subsidies.

Non-energy Environmental Conditions

Some environmental conditions may change without causing a significant change in energy or nutrient supply. Nonresponsiveness to change within some intermediate range of environmental conditions is common in both engineered and self-organized (e.g., ecological, social, economic) systems. This phenomenon, known as "dead zone" in systems engineering (Dransfield 1968), is a characteristic of systems with several components that have similar function, but have slightly different environmental requirements for maximal function. Several species of phytoplankton, for example, each with different temperature optima for maximum photosynthesis, may cause total photosynthesis of the water column to remain stable over small changes in temperature. This particular phenomenon has been termed "congeneric homotaxis" by Hill and Durham (1978). An impoundment of 5 cm water depth may have identical ecological production to one of 25 cm depth if energy and nutrient supplies are identical. The species comprising the community in these two impoundments may be radically different, but a predictable change in overall production seems impossible to rationalize.

Notion of Automitigation

If the above arguments about the causes of ecological production are true (and the development of production theory is continually evolving), any activity of humans that does not reduce the supply of energy and nutrients or create environmental stress should not affect ecological production even if non-energy conditions are changed in the environment. When water depth is increased in an impoundment to the level of an "overflowed" condition, emergent vegetation often disappears (Voigts 1976), but

overall ecological production of the area may not have been reduced. Perhaps only a shift in the types of animals and plants has occurred. As the water level increases, abundance of emergent vegetation may decline, while habitat for submerged vegetation is formed. With greater water level increases, light for benthic algae may be reduced, but more habitat for phytoplankton is produced. Since phytoplankton may further reduce light to both benthic algae and submerged vegetation, phytoplankton may in the end be the dominant converter of available energy and nutrient supplies to ecological products. However, the total production of the new community may be exactly the same as before water level was increased due to cybernetic feedback mechanisms (Rapport et al. 1985). We refer to this phenomenon as "automitigation" of ecological production. Of course, production of specific species that are favored by humans may be enhanced or reduced by any given change, whether whole-system production is affected or not (Rapport et al. 1985).

Determinants of Production and the Concept of Feedback

A conceptual model illustrated in Figure 2 summarizes major endogenous influences on primary production in salt marshes. Primary production in the marsh is influenced by: 1) available light; 2) supply of plant nutrients (nitrogen, phosphorus, etc.); 3) salinity; and 4) circulation of water. A positive influence (depicted by "+") is defined as one in which an increase of the stimulus produces an increase in response and decreased stimulus produces decreased response. Examples are available light, nutrient supply, and water circulation below some threshold amount. A negative influence (depicted by "-") is defined as one in which the direction of the response is opposite that of the stimulus. Salinity, for example, is shown as a negative influence on primary production.

Water circulation and available light are positive only when not in excess. Excessive water circulation may lead to erosion, and too much light may cause photoinhibition (Ryther 1956). The diagram as depicted is applicable when these factors are not excessive.

Available light is influenced both by the turbidity of water when it covers the marsh and by the amount of incident sunlight. Turbidity is influenced by available sediments and water turbulence (water circulation), which in the vicinity of Merritt Island is a function of wind and rain. Water circulation, therefore, simultaneously has a positive influence on production by subsidizing the supply of nutrients and removing wastes, and a negative influence by increasing turbidity. Thus the overall, or net, influence of water circulation on production can vary over a wide range of possibilities.

Supply of plant nutrients is influenced by nutrients in land drainage (dissolved, suspended, and bedload transport), quantity of sewage effluent, and nitrogen fixation. The quantity of nutrients in land drainage is influenced by agricultural and urban development and rain. The quantity of sewage effluent is also influenced by urban development.

Nitrogen fixation is an energy-using process that is often limited by organic matter (Delwiche 1970; Hanson 1977a, 1977b). Because primary production of organic matter in salt marshes is often limited by nitrogen (Gallagher 1975; Darley et al. 1981), a reciprocal relationship, or feed-

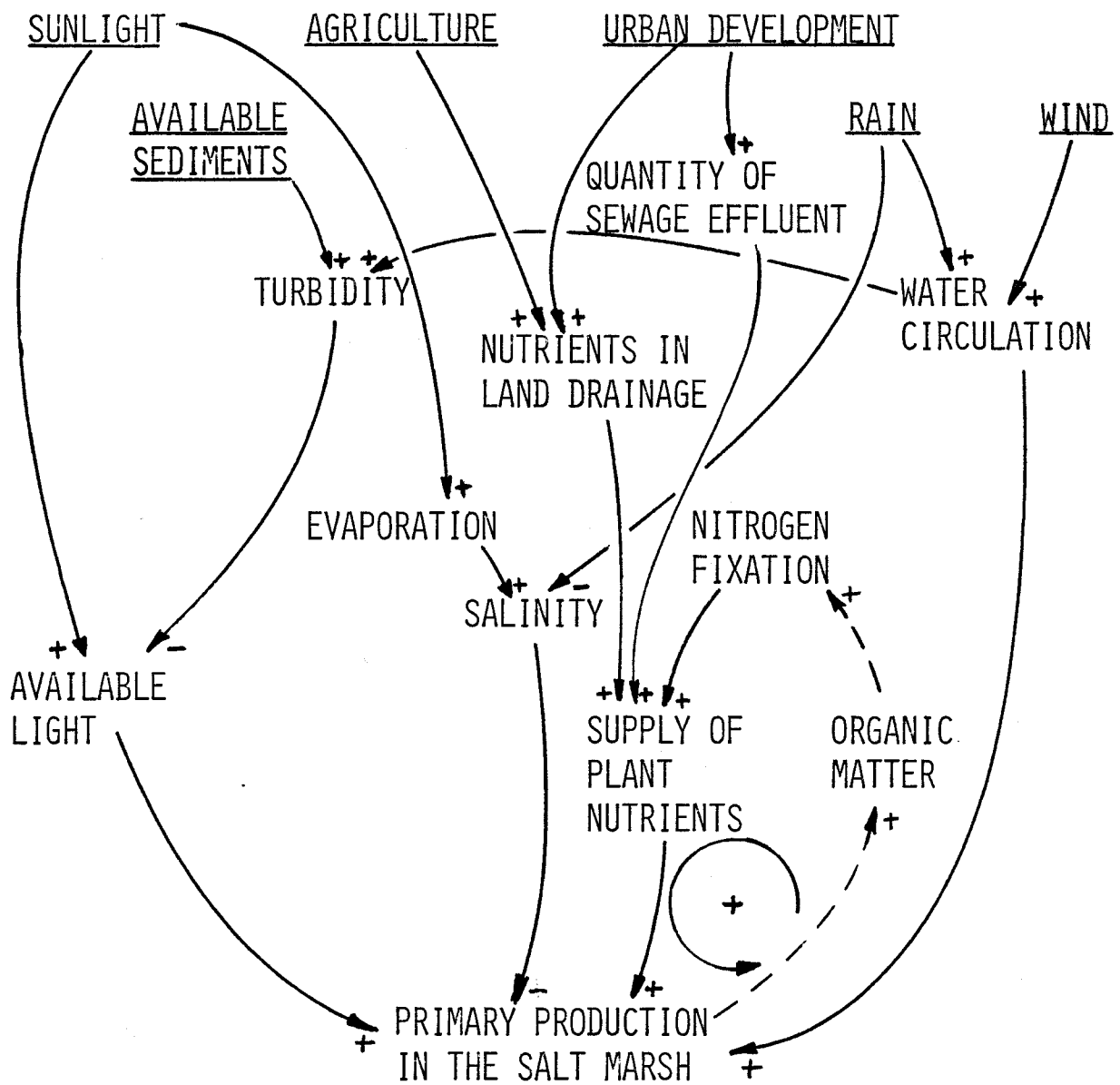


Figure 2. Hypothetical Influences on Primary Production in Merritt Island Salt Marshes. Major sources for production are underlined. Note the positive feedback loop between nitrogen fixation and primary production.

back loop, is formed. Such loops can be positive or negative. The loop shared by nitrogen fixation and primary production is positive. If a change occurs in a component of a positive loop, the direction of change is reinforced on every cycle of the loop. If the loop were negative, the change would be opposed on each successive cycle and either an oscillation or a smooth approach to a constant or steady-state would occur. Awareness of significant loops is important because they can produce unexpected results when changes are instituted in the environment.

Salinity of the marsh surface and interstitial (pore) waters is influenced by the supply of fresh water, the supply of salt water, and by evaporation. Freshwater supply is influenced by rain and saltwater supply is influenced by flooding. Evaporation is influenced principally by available sunlight (both through its direct excitation of water molecules and its influence on environmental temperature). Thus, the influence of sunlight on marsh primary production can be both positive (photosynthesis is a function of available light) and negative (evaporation raises salinity). The positive effect of sunlight should outweigh the negative effect except at very high salinities. Because of these simultaneous positive and negative effects of light, its overall effect on photosynthesis is non-linear in shallow marine systems (see also H.T. Odum 1967).

Ideas for Impoundment Management to Enhance Ecological Production

Control of some of the determinants of ecological production outlined in the previous sections is possible using structures and equipment already in place in Merritt Island saltmarsh impoundments. Management to enhance overall ecological production might include the following interdependent schemes: 1) maintenance of salinity in the range of brackish water; 2) preventing anaerobic conditions; 3) circulating water through the impoundments as much as possible without causing erosion and turbidity (and perhaps increases in BOD); 4) keeping non-phytoplankton turbidity low; and 5) addition of nutrients (e.g. sewage) if nutrients are limiting. One way to keep non-phytoplankton turbidity low is to establish submerged aquatic vegetation. Establishment of submerged vegetation can produce a positive feedback loop; production of submerged vegetation increases sediment trapping which lowers turbidity and increases available light for the production of submerged vegetation. This loop can reinforce the establishment of submerged vegetation, or if started the other direction, can quickly eliminate it. Establishing submerged vegetation requires keeping phytoplankton low because of turbidity and competition for nutrients. It may require wind breaks in some impoundments because of the possibility of uprooting vegetation.

Determination of factors limiting ecological production in impoundments would make for more effective management of ecological production, should this be a desired goal of management in some or all impoundments. A number of experimental and correlational studies (with respect to the parameters discussed above) could be devised.

Diversity of Merritt Island Salt Marsh

Natural salt marshes typically do not contain very diverse macroflora or macrofauna. Natural marshes in the vicinity of Merritt Island apparently

contained few species of vascular plants (Leenhouts and Baker 1982; Montague et al 1984b). To the north and west, marshes probably consisted largely of four to six plant species (though other species undoubtedly occurred in smaller quantities): Distichlis spicata, Paspalum vaginatum, Batis maritima, and one to three species of Salicornia. This assemblage is sometimes referred to as "grassy" marsh and it is typical of marsh known as "high" marsh that borders the upland fringe of salt marshes dominated by Spartina alterniflora elsewhere in the southeastern United States.

Higher elevations on Merritt Island perhaps contained Spartina bakeri and Juncus roemerianus as can presently be seen in the unimpounded area adjacent to Turnbull Creek. A transect toward the south and east included increasing frequency of black mangrove, Avicennia germinans and white mangrove, Laguncularia racemosa. The denser the mangrove, the lower the light penetration to the marsh surface, so the lower the frequency of the grassy marsh species (and perhaps the lower the diversity as the number of dominant species would concurrently drop from six or eight to two).

To understand why natural salt marshes are not very diverse, and to better manage ecological diversity in marshland both require careful consideration of the meaning, measurement and theory of diversity.

The Concept of Diversity

Species diversity is a measure of the variety of species in a given area as indicated both by the number of different species found in the area (called species "richness") and by the equivalence of the number of individuals in each species (called "evenness"). Thus an area is said to be diverse if it contains many species each represented by nearly the same number of individuals. The relative effect of a lack of either evenness or richness on diversity depends on how these two factors are combined into one index of diversity. Thus, the utility of a particular index must be evaluated with respect to the desired application.

Importance of Diversity in Natural Areas

Diversity is important both theoretically and in practice. Theoretically, following a disturbance, an area with a greater variety of plants, animals, and protists should stand a better chance of continuing life-processes such as photosynthesis, animal production, nutrient recycling, and decomposition at levels more similar to those before the disturbance. Genetic variety is believed to be the key to the survival of life during major worldwide shifts in climate. Monocultures of an inflexible species would be susceptible to eradication.

Pragmatically, diversity in natural areas is important in the same sense as a diversity of crops is to the survival of a small family farm. A diversity of commercially important fishery species allows economic stability for fishermen. A diversity of habitats allows management for a diversity of desired wildlife and enhances opportunity for, and may reduce the expense of, multiple-objective biological resource management. Appropriate evaluation of diversity in this sense should incorporate not only the variety of species within an area, but also the variety of species among areas.

Considerations in the Measurement of Diversity

Several methods of measuring evenness and richness and combining these into one index of diversity exist (Fisher et al. 1943; Emlen 1973). Others may be developed for special purposes. None, however, should be used without an evaluation of their suitability to a particular objective. Diversity of habitats may be more valuable than plant diversity within a particular habitat, for example. Maximizing the diversity of endangered species may or may not involve maximizing overall diversity.

Any given measure of diversity may be influenced by both the area covered in the sample and by the time required to complete the sample. A large area covered may include a variety of species, but subdivisions of the area may be very low in diversity. An impounded area on Merritt Island, for example, may have a large total number of plant species, each represented by nearly the same number of individuals (or biomass), but these species may be segregated into low diversity zones according to elevation. On Merritt Island National Wildlife Refuge, diversity is much higher among all impoundments than is indicated by the average diversity within impoundments (Leenhouts, pers. comm.) presumably because of differences in physical/chemical conditions among impoundments.

The time required for completing a sampling effort for determining diversity will influence the measurement relative to the rate of change of species composition in the sample area. If changes occur much faster than the sample can be collected, then the resulting number of species included in the sample may be higher than if a snap-shot of the area had been analyzed. It is an open question whether an area that supports 120 species in a year, but with only an average of 20 present at any one time is more valuable for its diversity than a system that supports only 60 species in a year with an average of 40 present at any one time. Considerable thought must be given both to the area sampled and the time interval of importance before judgement about changes in diversity can be fairly evaluated. Inconsistency in these aspects of diversity measurement promote inconclusiveness. There is considerable potential for error or manipulation of sampling to achieve a particular result.

Principal Determinants of Diversity

Theorists attribute a high diversity both to biotic specialization and to environmental variation. Given enough time for speciation, biotic specialization can occur in environments with relatively constant physical conditions and resource supplies such as the deep sea and the bottoms of deep lakes (Sanders 1968, Valentine 1973, Levinton 1982; Valiela 1984). Extreme environments, however, such as those with very high salinity (greater than 150 ppt), have low diversity no matter how constant the environment.

The highest species diversity seems to occur in areas that have considerable constancy in some environmental conditions, but also contain certain disturbances. A tropical coral reef, for example, occurs in an area where temperature and light vary little from month to month. These areas, however are subject to periodic storms that can topple branching reef corals. Disturbance of the reef communities by coral-eating fishes is

also common. Such disturbances overlay a patchwork of successional stages of the reef, thereby enhancing the overall richness and evenness of species (Strong et al. 1984).

Whether or not a disturbance enhances diversity depends on characteristics of the disturbance, on characteristics of affected biota, and on the time and area over which diversity is monitored. If the disturbance produces spatial heterogeneity within the sampled area, and sufficient time is allowed for new niches to be occupied, the disturbance may enhance overall diversity of the area.

Characteristics of Disturbance and Temporal Variation That Affect Diversity

If disturbance occurs in patches, the opportunity for enhanced diversity is present if the area sampled includes the patches. If the disturbance is area-wide, a general reduction in diversity might be expected at least temporarily. The time required for initial diversity to be restored should relate to the intensity (severity, amplitude, extremeness) of the disturbance. If the original richness and evenness of species recurs, the composition of species may be different, depending on characteristics of the species, and on the rigor of the environment. In rigorous environments such as alpine tundras, few species can live, so recovery after disturbance usually includes those same species. In the tropics, however, many alternative species are available during post-disturbance recovery, so resulting successional stages may not yield the same species from place to place or time to time.

If the change that occurs produces an environment that is foreign to available organisms, diversity may remain low for a very long time. If the environment produced is so foreign or extreme that it severely interferes with fundamental physiological processes, diversity may always be low (Rapport et al. 1985). This may occur if the disturbance supplies hazardous, non-biodegradable materials or produces extremes of pH, or very high temperatures or salinities.

Periodic disturbances or temporal variation may also reduce or enhance diversity relative to the period over which diversity is evaluated (Vogel 1980). The frequency, regularity, and abruptness of change are important. If the change is cyclic, stimulates a cyclic change in species composition, and a cycle of change is completed during the measurement period, then more species will be found than under lower frequency variation. Many ecosystems and organisms are dependent on such repetitive events which become anticipated through selection (Vogel 1980). If the rate of environmental change exceeds the rate that species composition can change, a lower diversity might be expected. If the rate of change is very low, changes in species composition may not be detected during the sampling period.

For example, periodic fire is now recognized to be an essential component of a healthy boreal forest (Heinselman 1971; Rapport et al. 1985). The same may well hold true for salt marshes on Merritt Island. Certain species are dependent upon fire for effective seed release and may possess adaptations to survive conflagrations. Periodic burns release minerals stored in soils and plant biomass, create space, and reduce

competition for water, nutrients, and light. Although fire may be important in maintaining a natural system, this natural system may be neither as productive nor as diverse as one that would replace it without periodic fire.

Diversity may be lower under irregular than under regular periodic change because a survival option is eliminated; survival is not possible by regular adjustment timed to coincide with regular events. Presumably, fewer organisms exist that can tolerate or avoid random change. Also presumably, fewer organisms exist that can withstand abrupt change as opposed to slower changes. If these notions are true, diversity should be lower in an environment of random and abrupt changes of intermediate frequency. However, in some settings, temporal variation may allow several species to coexist, each living most of the time at suboptimal conditions, but each occasionally receiving optimal conditions.

Characteristics of Biota That Affect Diversity

Availability of biota for recruitment into a habitat altered by some disturbance in time or space is an important consideration for diversity. If the surrounding area is inhabited by a large number of species, or if a diversity of organisms can be imported, then altered habitat may develop higher diversity faster than would occur otherwise.

Ability to tolerate or avoid change is an important consideration in evaluating change in diversity. Sedentary organisms must tolerate change, whereas vagile organisms can move if altered habitat is unsuitable. By avoidance, vagile organisms should be able to withstand more irregular and abrupt changes than sedentary organisms.

Another characteristic of importance is genetic variability amongst individuals of a species in a habitat undergoing change. If this variability is high, if the number of individuals is large, and if the production rate of individuals is high, then selection for individuals resistant to the change may occur (e.g., insecticide-resistant strains of mosquitos).

Thus, a given environmental change should be expected to have a greater affect on sedentary, slowly-reproducing species represented by low numbers of individuals of little genetic variability. If these species compete with species of the opposite characteristics, and if such species are available for recruitment following a change, then the effect of the change on overall diversity may be little if any, or diversity may even increase.

Summary of Diversity Concepts

Species diversity is a measure of the variety of species in a given area. The notion includes the number of species found (richness) and the relative representation of each species as compared to the others (evenness). Measures of diversity are sensitive both to the amount of area considered and the amount of time allowed for a measurement. Except after an unusually intense disturbance, diversity should appear higher with greater area and time considered.

Regular spatial and temporal variation and even some random disturbances can enhance species diversity. Evaluation of the potential effects of temporal variation and disturbance requires consideration of characteristics of both the change and the affected biota. Characteristics of the change of importance include: 1) area covered; 2) intensity; 3) foreignness; 4) frequency; 5) regularity; and 6) abruptness. Characteristics of biota of importance include: 1) ability to tolerate or avoid change either by their physiological characteristics, mobility, or genetic flexibility; and 2) availability for recolonization after a change.

Ideas for Impoundment Management to Enhance Ecological Diversity

The theoretical determinants and other considerations concerning diversity are many, but are not contradictory and therefore may be useful in ecosystem management. For example, to enhance diversity of any given subgroup of animals or plants, the following may be done: 1) provide a diversity of habitats in the area; 2) provide some patches of alternative habitat within an area; 3) provide open access to vagile species; 4) perhaps provide some temporal variation that is smooth, of low intensity and foreignness, and regular; 5) avoid temporal changes that are area-wide, abrupt, and irregular, though if these changes are highly localized (not area-wide), they may enhance habitat variety; and 6) avoid large areas of sustained conditions that interfere with fundamental life-processes and thereby interfere with both production and diversity (e.g. extremely high salinities, or temperatures, or extremes of pH, or very low dissolved oxygen).

Relationships Between Marshes and Estuaries

Recently, the values of marshes as improvers of estuarine water quality and exporters of organic detritus of great food value to estuarine fish and shellfish as initially purported (Teal 1962; Gosselink et al. 1973) have been called into question (see Haines 1979b; W.E. Odum et al. 1979; Onuf et al. 1979; Nixon 1980; Borey et al. 1983; Boesch and Turner 1984; Dame and Stilwell 1984; Dankers et al. 1984). Therefore, the overall influence of Merritt Island salt marshes on estuarine waters is unknown, and a variety of possibilities exist. Figure 3 illustrates some principal exchanges that occur between marshes and estuarine waters that are relevant to energy flow in estuaries from initial conversion by photosynthetic organisms, to the production of estuarine fish and shellfish. Principles for determining the net influence of salt marsh on surrounding estuarine water have not been developed and validated; the net effect of salt marsh on estuarine water must be determined by measurement on a marsh by marsh and estuary by estuary basis. No such studies have been conducted on Merritt Island marshes.

Energy, Carbon, and Biota

Salt marshes convert solar energy and inorganic carbon dioxide and carbonate into chemical energy of organic compounds, but they also harbor a variety of organisms that utilize this chemical energy and hence return inorganic carbon dioxide to the atmosphere and water (Figure 3). Therefore, the net influence of the salt marsh on estuarine water may either be to add to the organic carbon of the estuarine water (export), to

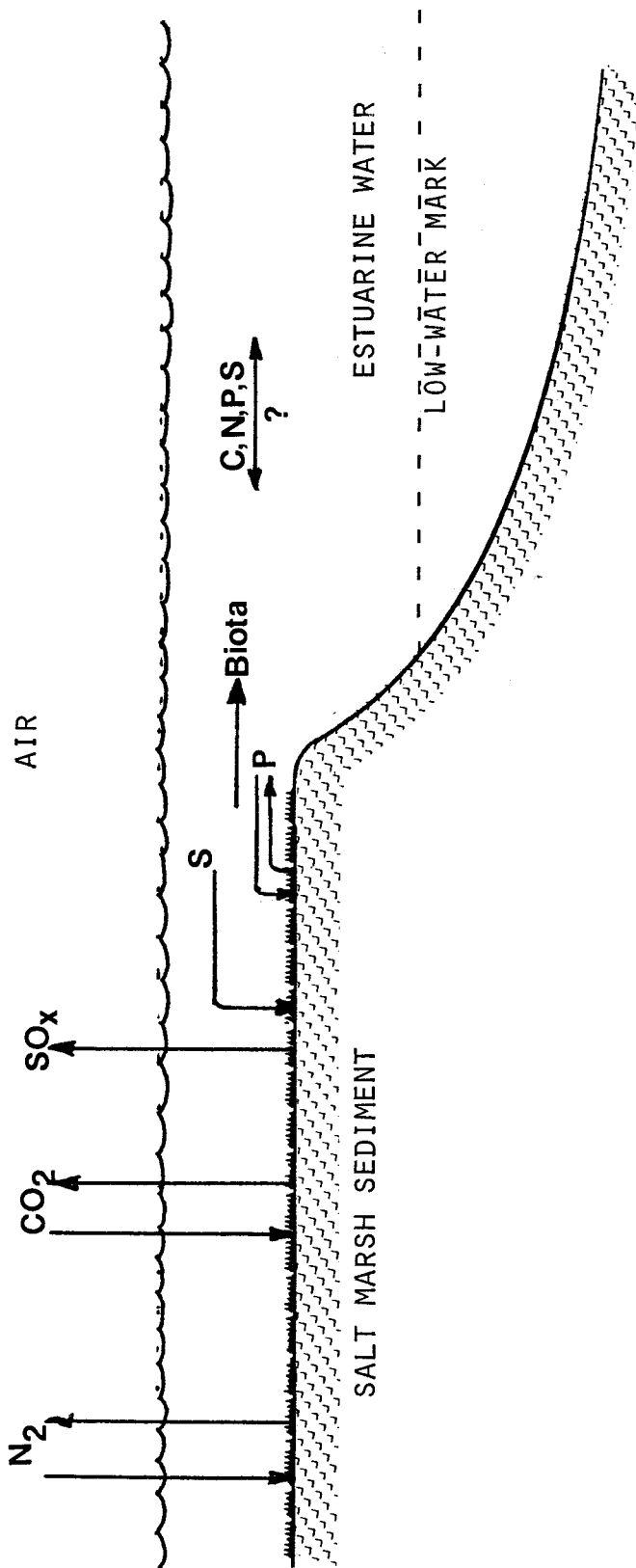


Figure 3. Conceptual Model of Relationships of Salt Marshes to Estuaries. Complex possible exchanges of elements between salt marshes and estuarine water leads to temporal variation and uncertainty concerning the overall influence of salt marshes (natural or impounded) on biogeochemistry and energetics in estuaries.

remove organic carbon from estuarine water (import), or to simply exchange organic carbon atom for atom with estuarine water. In any case, biota are produced from these processes, some of which may be estuarine biota of economic value, or the foods of such biota (Herke and Rogers 1984).

Both production and decomposition of organic matter occur in salt marshes, resulting in either net, import net export, or no net transport of detritus. Marshes of each net effect have been reported in the literature, and no consistent determinants of import or export have yet been agreed upon, though marshes with restricted access (as through a culvert), low tidal amplitude, and little freshwater, or groundwater inflow appear to be unlikely exporters of significant amounts of detritus (Valiela et al. 1978; W.E. Odum et al. 1979; Nixon 1980; Borey et al. 1983). Other determinants of export to be considered include: 1) the resistance to decomposition of vegetation produced in the marsh (rapid decomposition perhaps yields more food, but with less remaining for export); 2) the density of creeks (up to a point, more creeks per marsh area would allow better water movement); and 3) the ease with which a mass of water that comes from the marsh can exchange with the estuary (Imberger et al. 1983). The current view is that early estimates of export were inflated and the value of exported materials (especially vascular plant detritus) was exaggerated (Nixon 1980; Boesch and Turner 1984, Herke and Rogers 1984).

On the other hand, marshes on the fringes of estuaries do provide food and cover to growing estuarine biota that live in or temporarily visit these marshes and therefore may be very valuable as nursery grounds for estuarine fish and shellfish. The export of biota (including commercially important fish and shellfish) from these marshes may be their greatest value (Haines 1979b; Montague 1980; Boesch and Turner 1984).

Nitrogen

Nitrogen is a major nutrient of plants that is in relatively short supply in many salt marshes (Gallagher 1975; Patrick and DeLaune 1976; Valiela et al. 1976; Valiela and Teal 1979a, 1979b; Buresh et al. 1980; DeLaune and Patrick 1980; Darley et al. 1981) and estuarine waters (Ryther and Dunstan 1971; Thayer 1974; Parker et al. 1975), especially those in which phosphorus (another major plant nutrient) is in very great supply. Phosphorus supply is great especially in turbid estuaries that have accumulated iron-rich clays from erosion of uplands (Pomeroy et al. 1965, 1969, 1972; Aston 1980; Postma 1980; Meade et al. 1979). Iron in these clays forms a complex with phosphate that can be released to slightly acidic, anaerobic water, such as the interstitial water of salt marsh sediments (Patrick and Khalid 1974).

Amongst the multitude of microbes in the sediments of salt marshes, are those capable of fixing nitrogen gas as well as those capable of denitrification. Nitrogen fixation uses organic matter (Delwiche 1970; Hanson 1977a, 1977b). If this microbial community fixes more nitrogen than it removes, estuarine water may receive a net input of nitrogen available for uptake by plants and bacteria. On the other hand, nitrogen may be removed from water more than it is supplied, or these two processes may be in balance (Haines et al. 1977). If nitrogen supply limits production and decomposition, as so often has been measured (numerous references indicated

above), then the net effect of this microbial community is of great importance in evaluating the function of salt marshes in estuarine production.

Phosphorus and Sediments

Because fine sediments such as clays tend to accumulate in quiet waters, because salt marshes develop in quiet waters, and because these clays have a great sorptive capacity (Rae and Bader 1960; Pomeroy et al. 1965, 1969, 1972) salt marshes are sites of phosphorus deposition. Georgia salt marshes receive abundant iron-rich (red) clays from upland land drainage (Meade et al. 1975; Postma 1980). The present accumulation of phosphorus in the sediments of these marshes is sufficient to continue existing primary production for several hundred years, even if all inputs of phosphorus were discontinued (Pomeroy et al. 1972; Whitney et al. 1981).

Salt marshes are also sites of phosphate resupply to estuarine water. Excess phosphorus in the foods of animals (especially microfauna) is released in their metabolic wastes (Johannes 1964, 1968; Pomeroy 1970). In addition, several workers have demonstrated a flux of phosphate from saltmarsh cordgrass (*Spartina alterniflora*) to surrounding waters (Reimold and Daiber 1970; Reimold 1972; Gardner 1975). Thus mechanisms exist for both the removal of phosphorus from, and supply of phosphorus to, estuarine water. Unlike the cases of carbon and nitrogen, large reservoirs of gaseous forms of phosphorus are not available to be actively "pumped" by organisms into marshes from the atmosphere. Hence, the overall effect of marshes on the phosphorus content of surrounding waters is limited to net removal or balance. In turbid estuaries such as in Georgia, the overall effect of salt marshes on phosphorus is generally believed to be removal (Whitney et al. 1981).

Sulfur, Energy, and Acid Rain

Aspects of the sulfur cycle are also important in energy transformations in the salt marsh that lead to estuarine fish and shellfish (Howarth 1984). Sulfate reducing bacteria are apparently very active in salt marshes owing to both the supply of simple organic compounds (that result from decomposition of detritus) and the abundance of sulfate (the third most common ion in seawater) (Howarth and Teal 1979). Sulfate reducers grow by oxidizing these simple organic compounds with sulfate when oxygen is not available (as in the case of anaerobic sediments just beneath the sediment surface). This energy conversion process is not as efficient as it is with oxygen (Howarth and Teal 1980). By-products include sulfide and elemental sulfur, both of which contain energy that can be utilized by sulfur oxidizing bacteria if these products become juxtaposed to oxygen in the presence of bacteria (Howarth and Teal 1980; Howarth 1984).

Some of the energy-containing by-products of sulfate reduction are gaseous, such as hydrogen sulfide, dimethyl sulfide, and dimethyl disulfide (Brock 1979). These gases are partially responsible for the characteristic odor of salt marshes. The odor is indicative of both an energy and a sulfur loss from the salt marsh. Upon entering the atmosphere the energy is rapidly dissipated by photochemical oxidation reactions (Cadle and Allen 1970). Thus if sulfur oxidizing bacteria do not utilize these compounds before they escape, this energy will be eliminated from any

food chain, and the resulting atmospheric sulfur compounds will eventually return to earth combined with water in the form of acid precipitation.

Iron-rich clays, however, are important in trapping sulfide ions at the aerobic-anaerobic interface in sediments (Howarth 1979; Howarth and Teal 1979; Howarth and Hobbie 1982). If sulfur oxidizing bacteria do not convert the sulfide, and if free metal ions such as iron or manganese (Hatton et al. 1982) ions are present (which will occur if pH is low enough to allow any phosphate held on metals to be released), then the metal and the sulfide will combine to make metal sulfide (Howarth 1979). The black color of anaerobic mud in marshes is usually caused by iron sulfide. Salt marshes with a low metal content, perhaps those in Southeast Florida (Hoffmeister 1974), should emanate much greater quantities of sulfide to the atmosphere. The magnitudes of sulfur emissions from salt marshes and their possible contribution to acid precipitation is currently under study through the consulting firm of Environmental Sciences & Engineering, Inc., Gainesville, Florida.

A Scenario of a Southeast Florida Estuary Without Marshes

In some estuaries, especially those without inputs of phosphate-rich clays, phosphate supply may limit growth of estuarine seagrasses and phytoplankton. If fringing marshes are principally removers of phosphate (Whitney et al. 1981), then photosynthesis in estuarine water may be lower than would occur without marshes. If this difference in photosynthesis is not mitigated by the photosynthesis of the marshes, then it is possible that without salt marshes, overall estuarine photosynthesis would actually be higher (as discussed in the section on foods of estuarine fish and shellfish, the nutritional quality of phytoplankton and benthic algae as food may be greater than that of detritus from marsh vegetation).

The effect of this on estuarine fish and shellfish is not clear, because, although quality food supply may be greater in such a case, the cover afforded by marshes would be gone. Cover afforded by seagrasses (Orth et al. 1984) may decline too, if the higher levels of phosphorus in this scenario without marshes are utilized by phytoplankton, which increase turbidity of the water to the point that light limits seagrass growth (Livingston 1984).

Summary of Relationships and Conclusion

The possible net flows of energy and elements between marshes and estuaries are many. Pathways of both production and loss of converted energy and materials are possible. Each of the processes indicated in Figure 3 and most if not all other biogeochemical processes in salt marshes will respond to changes in temperature, salinity, water level, oxygen level, and pH (Presley and Trefry 1980; Patrick and Khalid 1974). Unless the overall effect of a marsh on estuarine water is very one-sided, considerable variation of this relationship from day to day or week to week may be expected. Assumptions about these relationships should be accompanied by long-term data from the marsh in question until valid principles for predicting these effects are established. Presently, insufficient data are available for Merritt Island marshes to allow determination of their relationships to adjacent estuarine waters.

Food and Cover for Estuarine Fish and Shellfish

Production of estuarine fish and shellfish depends on availability of both organisms and habitat. Salient features of habitat include: available nonstressful physiological environment (e.g. salinity, temperature, pH, oxygen), available food, and available cover. Good habitat does not guarantee use by organisms. Organisms may simply be unavailable because of disruptive conditions either elsewhere, or prior to the formation of new habitat (e.g. an unusually cold winter, widespread disease, loss of habitat for other life-history stages in the case of migratory animals).

Attraction and concentration of organisms does not guarantee enhanced production of organisms (elaboration of tissue per unit area per unit time), as concentration may limit growth, enhance disease transmission, or allow over-harvest. We will be discussing habitat with the production of the organisms in mind.

Foods of Estuarine Fish and Shellfish

Because salt, brackish, and freshwater marshes are very productive of emergent vegetation (W.E. Odum 1970a; Teal 1980), they are often thought of as necessarily productive of animals of commercial or recreational importance. The value of marshes to such animals depends not only on the food value and accessibility of foods, but also on what are currently considered species of commercial or recreational importance. The following discussion will be limited to the food value and accessibility of foods in marshes and the effects of impoundments on these.

Foods of estuarine fish and shellfish vary from species to species and from stage to stage in the life cycle of each species. Most if not all of the commercially important animals in estuaries have planktonic larvae that survive well on a phytoplankton-based food chain consisting not only of phytoplankton, but also of bacteria, protozoans, copepods, and other mero- and holo-plankton. Adult filter-feeders such as clams, mussels, and oysters also survive well on a phytoplankton-based food chain. Larval and early juvenile fish feed almost exclusively on zooplankton, which in turn feed on phytoplankton (W.E. Odum 1970a).

Potential foods of estuarine fish and shellfish that are found in marshes include: 1) detritus and its accompanying community of bacteria, fungi, microfauna, and meiofauna, 2) benthic microalgae and its accompanying community of microfauna and meiofauna, 3) phytoplankton and zooplankton, 4) dissolved organic compounds emanating from all organisms and accompanying bacteria, 5) sulfur- and sulfide-oxidizing bacteria (Howarth 1984), and 6) vagile and sedentary macro-organisms that consume the above foods and each other. At the base of this web of foods are the photosynthetic organisms, the primary producers that initially convert sunlight into chemical energy (i.e. food) (W.E. Odum 1970a). These include: 1) phytoplankton and benthic microalgae, which are consumed directly and which excrete dissolved organics; and 2) submerged and emergent vegetation, which are primarily food as detritus after death but which also leak dissolved organics and are eaten directly in small quantity (Teal 1962; E.P. Odum and de la Cruz 1967; Pomeroy et al. 1977; Wiegert 1979; Gallagher et al. 1980).

Food Value of Detritus

Vascular plant detritus, although commonly ingested by many species of estuarine fish and shellfish (Darnell 1958, 1961; E.P. Odum and Smalley 1959; W.E. Odum 1966, 1969; W.E. Odum and Heald 1972, 1975; Gilmore 1983), is less valuable as food than the more easily digested and nutritional benthic and planktonic algae. It has a lower % organic matter and calorific value than algae (W.E. Odum 1970b). Furthermore, energy from detritus is obtained by "detritivores" only after a community of bacteria, fungi, and microfauna has developed on the detritus (Haines and Hanson 1979); these organisms are the actual food being assimilated rather than the dead plant material itself (W.E. Odum 1970b; Montague et al. 1981; Marinucci 1982; Tenore et al. 1982). Striped mullet (Mugil cephalus) actively select small (and therefore older and more microorganism-rich) detrital particles (W.E. Odum 1968).

The lignin and cellulose of vascular plant detritus is difficult to decompose without special enzymes occurring in some bacteria. These materials comprise the majority of the dry weight of vascular plants and nearly all of the dry weight of the non-living portion of the detritus-microbe complex (R.L. Wetzel 1975). This is important in a comparison with algae as food because in each step of a decomposition process (detritus to bacteria to microfauna to meiofauna to ...; Odum and Heald 1975) an estimated 90% of the energy value of the food is dissipated as heat (Lindeman 1942) and is therefore unavailable to organisms in the food chain. Because detritivores simultaneously feed on several of these levels, the loss is usually less than 99.99%. Thus, if a detritivore feeds at an average of one step removed from the primary producer (i.e. detritus to bacteria to detritivore) 99% of the energy content of the detritus would be lost (see also Pomeroy 1980; Boesch and Turner 1984). However, most phytoplankton and benthic microalgae do not have to be broken down by a community of microbes before their energy content can be assimilated by the estuarine food web (see R.L. Wetzel 1977). Therefore, for microalgae only 90% is lost in the transfer to detritivores. Thus, 10 times the detritus must be produced to equal the energy value of algae to estuarine fish and shellfish.

This energetic difference can influence forage selection in facultative detritivores; in a situation where both detritus and algae were abundant, mullet fed almost exclusively on algae (W.E. Odum 1970b). Also, most detritivores probably cannot grow and reproduce on a diet solely composed of vascular plant detritus (W.E. Odum 1970a). Diets of detritivores invariably include at least 10-20% fresh algal cells (W.E. Odum 1969). Perhaps one of the most economically important food chains, that ending with larval and early juvenile fishes, is based primarily on production by phytoplankton (W.E. Odum 1970a); survival of these life history stages (which is a primary determinant of year-class strength) is largely a function of food supply.

Recent experiments by Lewis and Peters (1984) apparently demonstrated that juvenile Atlantic menhaden (Brevoortia tyrannus), a facultative detritivore, can assimilate detrital material of vascular plant origin, at high rates of efficiency (about 75%). However, they did not demonstrate the mechanism by which such efficiencies are achieved. As it is likely

that intestinal microbes play a part in this process, the detritus to microbes to detritivores chain, and its attendant losses of energy as described above, may be involved here also. Therefore, although the assimilation efficiency of vascular plant material by the "menhaden-microbe complex" is about 75%, assimilation by the fish itself, which they did not report, is probably much less. Nevertheless, the efficiency of this mechanism is probably greatly enhanced over that of organisms lacking an intestinal microflora (but still much less efficient than direct consumption of algae).

Nitrogen is important in the nutrition of detritivorous fish and shellfish because it is a fundamental building block of protein. Vascular plant detritus by itself is lower than most microalgae in nitrogen per unit carbon (Burkholder and Bornside 1957; Gosselink and Kirby 1974). As the decomposer community of bacteria and other organisms develops on detritus, the relative proportion of nitrogen increases in the detritus-microbe complex as a whole (Burkholder and Bornside 1957; E.P. Odum and de la Cruz 1967). Thus the nutritional value of the complex increases with time (Hanson 1982). The increase in nitrogen implies that the detritus-microbe complex collects nitrogen from the environment. Sources of nitrogen for this complex are the same as those of microalgae. Therefore, the bacteria of the detritus-microbe complex are competitors with microalgae for available nitrogen (Gosselink and Kirby 1974; Thayer 1974; Parker et al. 1975), which is a major limiting nutrient in many salt marshes and coastal zones. Actively decomposing organic detritus should not be considered the best possible food for estuarine fish and shellfish, but rather simply one of many utilizable foods in the estuary (Haines 1977). Stable isotope tracer analyses show that estuarine organisms perhaps rely more heavily on phytoplankton and benthic microalgae than on vascular plant detritus as the ultimate source of their food (Haines 1977; Haines and Montague 1979; Thayer et al. 1978), but location within an estuary can influence this relationship (Fry 1981; Peterson et al. 1985). Similar analyses may provide insight into the trophic relationships influencing estuarine fish and shellfish in the vicinity of Merritt Island.

The reader should not infer from this discussion that vascular plant detritus with accompanying microbes is not a valuable source of food for estuarine organisms; it most certainly is. Although the detritus food chain is less efficient than that of microalgae, detritus is always present (because of its refractory nature) and may therefore serve as an important buffer of the food supply if and when microalgal production is low (Kalber 1959). Furthermore, vascular plant detritus from present-day Merritt Island marshes may be a better source of energy than detritus in typical salt marshes. Because many Merritt Island marshes are now less saline than prior to impoundment, vegetation more typical of freshwater marshes has encroached in many areas. The detrital value of these plants is probably greater than that of the plants they replaced because there exist indications that freshwater marsh plants are less refractory, more nutritious, more readily attacked by detritivores, and more easily macerated than the saltmarsh species (W.E. Odum and Heywood 1978).

The conclusion to be drawn from all of the above is that both vascular plant detritus and microalgae produced in marshes are important ultimate sources of food for estuarine fish and shellfish; the relative importance

of each probably varies from marsh to marsh and estuary to estuary (and species to species). Thus, estuarine food chains should not be considered solely detritus-based, as has often been purported, but rather should be considered detritus/algae-based (W.E. Odum 1970b). Because it is likely that little if any of the detrital/algal production of Merritt Island marshes was ever, or now is, exported to the estuary (due to low tidal amplitude, relatively low freshwater inflow, and, especially since impoundment, restricted access; W.E. Odum et al. 1979) the critical management tactic to enhance estuarine fishery production would appear to be to enhance access by these organisms to the marshes such that they can feed on the foods (detritus, microalgae, and organisms that feed on these) produced and present there.

Vagile "Link" Organisms

If most of the production is decomposed in place in the marsh, and decomposing detritus is good food for many marsh residents, then unless transient organisms venture into the marsh, much of this food will simply decompose in place to the benefit of a multitude of microbes. Of course, nitrogen and sulfur transformations of importance to the global atmosphere occur because of these coastal microbes (MacIntyre 1970; Lovelock 1979), so the decomposing material is important where it is. However, when this material is utilized by transient organisms that venture into the marsh to eat the detritus-microbe complex, benthic microalgae, meiofauna, or larger organisms that eat these things (e.g. fiddler crabs, periwinkles), and if these organisms are themselves eaten by estuarine fish and shellfish of commercial or sports value, then the marsh can be said to be linked to this economic value (see Sikora and Sikora 1982).

Although a few of the economically important species will venture into the emergent vegetation of tidal marshes on occasion (e.g. redfish, blue crabs), a far more common place to find them is in the marsh creeks. This is especially true for juvenile estuarine fish (Zilberberg 1966; Dahlberg 1972; Burns 1974; Fritz et al. 1975; Subrahmanyam and Drake 1975; Cain and Dean 1976; Reis 1977; Shenker and Dean 1979; Weinstein 1979; Bozeman and Dean 1980; Reis and Dean 1981; Weinstein and Walters 1981; Crabtree and Dean 1982; Beckman and Dean 1984; Currin et al. 1984; Rozas and Hackney 1984; Weinstein et al. 1984). They may venture into the edge occasionally, but probably feeding is more efficient by cruising up and down the creeks. Also many sedentary organisms of economic value (clams, oysters) are found at the edge of the marsh in the marsh creeks much more commonly than in the vegetation (Dame 1976, 1979; Bahr 1976; Bahr and Lanier 1981; Walker and Tenore 1984; Mulholland 1984). However, some organisms such as grass shrimp and killifishes (W.E. Odum and Heald 1972; Welsh 1975; Vince et al. 1976; Talbot and Able 1984) move into the marsh at high tide, where they consume marsh organisms, and then return to the creek edge at low tide, where they are susceptible to consumption by predatory fishes. Such "link" organisms are important conduits between the marsh production and economically important vagile species of estuarine fish and shellfish. Other link organisms may occur and these should also be very important in making marsh production available to the estuarine fishery.

The situation on Merritt Island may be somewhat different, however. Because the marshes there are inundated for several months without daily draining, use of the vegetated marsh surface by juvenile estuarine fish may

be greater than in tidal marshes (where fish must return to the creeks regularly to avoid stranding during ebb tides). Lewis et al. (in press) note that ladyfish, snook, tarpon, mullet, and Irish pompano reside on the marsh surface during the seasonal inundations in areas south of Merritt Island. However, it is unclear whether these species actually prefer this habitat to marsh creeks and ditches or only enter it relatively infrequently; the risks of predation by wading birds on the marsh are probably relatively high.

Accessibility of Foods

The access to the foods of the salt marsh is as important as the presence of foods. The creek system in the marsh is a most important part of such access. Estuarine fish and shellfish move to the edges of marsh by these creeks to feed on link organisms. Resident sedentary shellfish such as clams and oysters are often found at the edges of marshes on muddy sand either in flats or in the sediments of marsh creeks. The edges of marsh creeks are more productive of microbes, animals, and plants than are interior areas (Smalley 1959; Odum and Fanning 1973; Gallagher et al. 1980; Sikora and Sikora 1982) and these edges are undoubtedly more accessible to estuarine organisms. Thus accessibility of the foods of estuarine fish and shellfish is enhanced near the edges of marsh creeks and ditches, as compared with the interior. Up to a (as yet undetermined) point, marshes with more creeks and ditches (if spoil is disposed of appropriately) per unit of interior probably support greater production of estuarine fish and shellfish (Browder et al., unpublished manuscript; but see Daiber 1974).

Access to marsh creeks at the marsh-estuary boundary is also important. Natural levees and man-made dikes prevent access, but natural marsh creeks and open water-control structures allow access. Marsh utilization by estuarine fish and shellfish should be greater with greater submerged cross-sectional area of open access at the marsh-estuary boundary. However, Gilmore et al. (1982) and Gilmore (1983) found intensive use of impoundments by estuarine fishes even though access was limited to single culverts. Unfortunately, it is impossible to reliably assess the relative effectiveness of culverts as access structures because quantitative estimates of fish use of unmodified control marshes do not exist. However, it is clear from Gilmore's research that even very limited access can result in substantial use of impoundments by estuarine organisms, perhaps equivalent to that of natural marshes. Whether this would also be true at Merritt Island, where tidal amplitude is much less than at Gilmore's sites, is unclear. Daily circulation of water through culverts may attract vagile fish and shellfish and enhance their passage.

The location and dispersion of access sites may influence accessibility. Fish use of culverts appears to be variable, perhaps as a result of their location relative to historic sites of marsh creeks (R.G. Gilmore, pers. comm.), and data presented in Gilmore (1983) suggest (albeit tenuously) that fish abundances in impoundments decrease with distance from culverts. More recent evidence demonstrates that abundances of fishes are enhanced in the vicinity of culverts (R.G. Gilmore, pers. comm.). These factors suggest that a positive correlation may exist between fish use of impoundments and number of access sites.

Exchange of marsh water with the estuary is important to the access of planktonic stages of estuarine fish and shellfish to the foods of the marsh. Exchange of water is not only a function of the access at the marsh-estuary boundary, but also a function of forces capable of moving water through the marsh. For coastal marshes, such forces include the ebb and flood of tides, the work of the wind, and mechanical pumping. The latter two are the most important on Merritt Island (Dubbelday 1975).

Access by vagile organisms that venture onto the marsh surface is possible only when the water covers the marsh. Natural salt marsh on Merritt Island is not regularly flooded by twice-daily tides, but rather remains dry for extended periods from perhaps January through September. It then may remain submerged for extended periods from October through December. If the water depth were higher more of the time, access by vagile fish and shellfish (including "link" organisms) to the foods on the marsh would be greater, though there is perhaps a limit to this effect also.

Cover for Estuarine Fish and Shellfish

Salt marshes contain not only foods for estuarine fish and shellfish, but also cover. The concept that the marsh is not only a good place to hide, but also a good place to eat (and be eaten) may seem contradictory. However, several lines of reasoning support these two simultaneous functions of marshes. First, some organisms clearly benefit perhaps at the expense of others. Deposit feeding organisms, for example, that consume organisms in deposits amongst the grasses, both eat their foods and are protected from their predators, though neither the predators nor the deposit-dwelling foods may benefit. Juvenile fishes may hide from predators in the edge of marshes, but may venture into the creeks to feed on zooplankton. Predators may sense the presence of an accumulation of prey and so spend more time and gain more prey per unit effort in marsh creeks. It is entirely likely that cover allows a build-up of prey in such a way that the area is a good place for a predator to feed, but also that the risk for an individual prey organism is reduced. This may apply to predatory fish as well as to wading birds. An area could not continuously be attractive to predators without a sustained supply of accessible prey. The simultaneous presence of food and cover can explain such a sustained supply. Prey organisms accumulate because of food and cover to the point where their sheer density increases the frequency of some individuals becoming exposed to predators. Increases in food for prey organisms may attract more prey than can be protected by existing cover, so more prey would be exposed to predators. If food was too low, however, this phenomenon might not be as likely to happen; prey organisms would accumulate perhaps only as a function of the cover afforded, so the benefit to a predator may not be as great. If, however, the only prey were those in the areas with cover, those areas would be good places to feed simply by being the only places to feed.

Both emergent and submerged vegetation can provide the dual functions of food and cover. Although some plants that become established on moist soil can tolerate extended submergence (e.g., Eleocharis parvula: F. Montalbano, pers. comm.), most submerged vegetation will not occur unless water of appropriate salinity and temperature nearly continuously covers

the sediment, and unless water circulation and light penetration are sufficient (Zieman 1982; Thayer et al. 1984). Light penetration is reduced by phytoplankton which may grow if an excess of nutrients occurs. Excess nutrients may arise from large accumulations of decomposing proteinaceous matter such as dead fish, from guano and excreta from large accumulations of birds or fish, from agricultural runoff, and from sewage outfall.

Emergent vegetation will occur if water levels are low enough to allow aeration of roots through aerenchyma tissue (Voigts 1976; Provost 1968) and if salinity is not too high. The cover afforded to estuarine fish and shellfish by emergent vegetation is limited to times of sufficient water coverage. As with the case of food, accessibility to cover should be enhanced by: 1) creek density, 2) open mouths of creeks, 3) circulation and exchange of marsh water with the estuary, and 4) depth and duration of inundation.

Egress of Vagile Fish and Shellfish From Marshes

A special problem of access for estuarine fish and shellfish is the potential for egress should conditions become stressful (e.g., low dissolved oxygen, extremes in temperature, salinity, or pH). Organisms may be able to enter a marsh when exchange occurs, or access points are open, but if exits are not available when stress occurs, trapped organisms may become lethargic or die. Stressed estuarine fish and shellfish may be quickly eaten by unstressed fish, shellfish, and wading birds. Those that are not eaten may recover, or may die and support the everpresent community of microbes in the marsh, whose activities may reduce the dissolved oxygen in the water to a point where that becomes stressful to previously unstressed organisms. This positive feedback loop can be avoided with flushing.

Egress is also important at times of year when fish and shellfish routinely leave the marsh to complete another phase of their life-cycle (Provost 1968). Historically on Merritt Island, water levels were high in October through December. At the end of this time, aquatic estuarine organisms routinely left the marsh (Harrington and Harrington 1961).

Reproduction of historical regimes of flooding and draining may not be essential to obtain good yields of estuarine fish and shellfish. Changed water regimes may simply result in a selection for members of each species that withstand the change, if the change is not outside the realm of survival for the species, and if the species has enough genetic variability, biotic potential, and individuals available for selection. However, egress from marsh areas in winter is essential for cold-intolerant species (e.g. snook, ladyfish, tarpon, shrimp).

Creek density, submerged cross-sectional area and duration of open access at the marsh-estuary boundary, and exchange of water with the estuary are all important for egress of vagile estuarine fish and shellfish although greater access at the marsh/estuary boundary may necessitate more pumping to achieve desired water levels (see Figure 4). In addition, harvest of species and consumption by waterbirds may be thought of as alternative egress. Commercial and sport fishing within marshes or marsh creeks that have limited egress directs these resources into humans rather than into wading birds, or decomposer microbes.

EGRESS OF FISH AND SHELLFISH

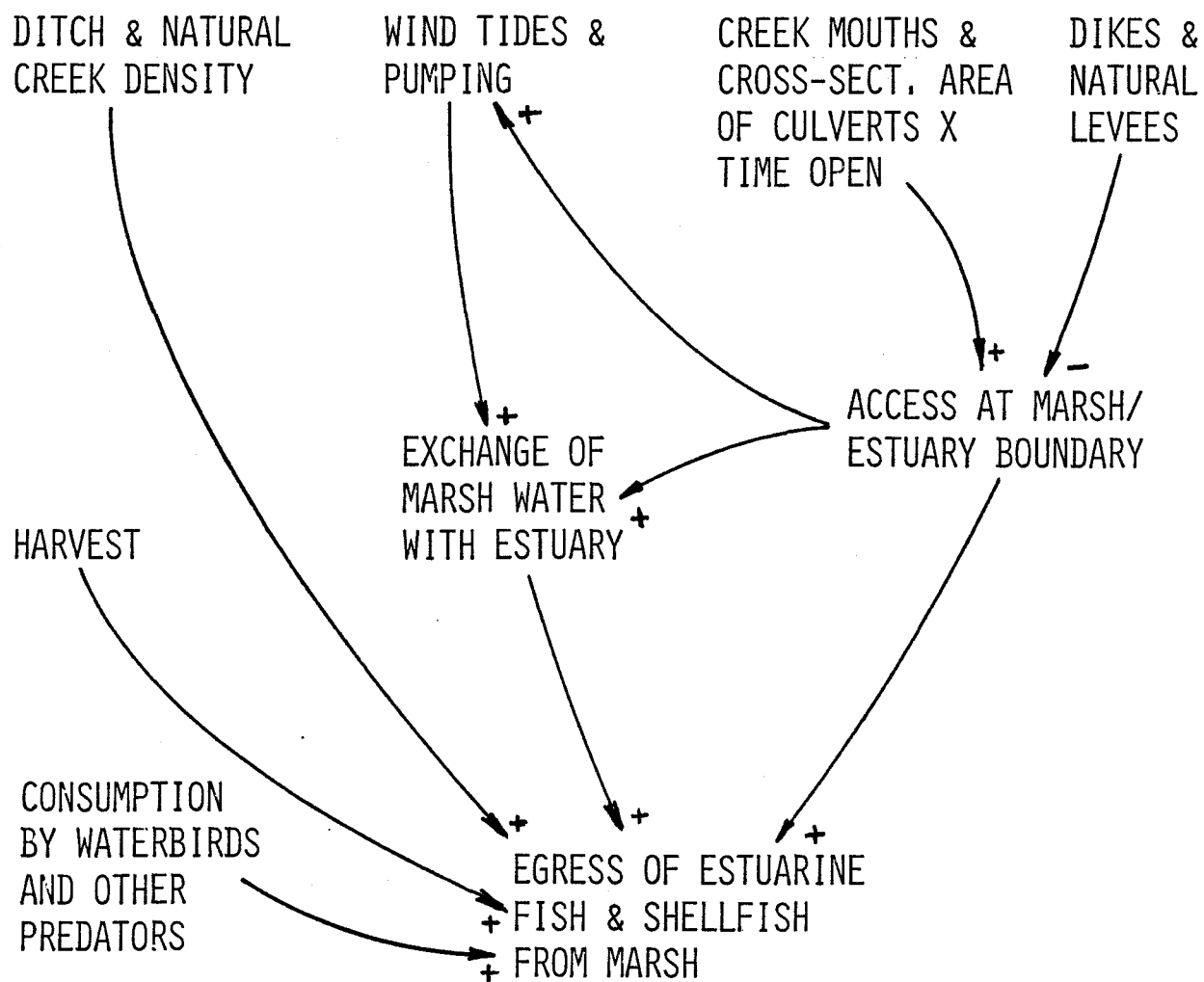


Figure 4. Conceptual Model of Factors Influencing Egress from Natural or Impounded Salt Marsh. Note that more access necessitates more pumping.

FUNDAMENTALS OF MARSH MANAGEMENT FOR MOSQUITO CONTROL AND ATTRACTION OF WINTERING WATERFOWL

Figure 5 illustrates the relationship between various structures in impoundments and their utilization for mosquito control and attraction of waterfowl. Only basic concepts are presented here. A multitude of problems may arise that supercede this conceptual model from time to time. The information in these subsections is derived from personal interviews and site visits with impoundment managers throughout the southeastern United States.

Mosquito Control

Controlling mosquito breeding in salt marshes is conceptually much simpler than attracting wintering waterfowl. Management of impoundments now principally involves maintaining water levels of a few inches on the surface of the marsh throughout the breeding season (March to May through August to October; Provost 1959, 1968, 1973b; Clements and Rogers 1964); female saltmarsh mosquitos cannot oviposit on standing water, but rather require soil substrates (Nielsen and Nielsen 1953; Provost 1968, 1973b). Mosquitos that replace these species are much less abundant (Clements and Rogers 1964) and do not cause nearly the biting nuisance of saltmarsh mosquitos. Because larvae must develop in standing water, saltmarsh mosquitos must exist in habitats with fluctuating water levels. The frequency of drawdown and reflooding then relates directly to the production of saltmarsh mosquitos, although excessive fluctuation (i.e. daily tides) will also reduce production if water does not remain on the marsh long enough for larvae to develop. By reducing the frequency of drawdown and reflooding, production of saltmarsh mosquitos is also reduced.

Other methods for mosquito control have been tried. Low density parallel ditching of the marsh during the 1930's was purported to help drain the marsh of pools of standing water where larvae could develop. This had little effect in the vicinity of Merritt Island, however, presumably because the larvae of these mosquitos are capable of growing and emerging very rapidly in very small depressions or cracks in marsh sediment, and low density parallel ditches did not intersect or drain all of the breeding sites.

Many "potholes" are present in Merritt Island salt marshes. When these are connected by ditch to the estuary, free access is established for feeding on mosquito larvae by larvivorous fishes. In some areas this technique ("open marsh water management", Ferrigno 1970; Ferrigno and Jobbins 1968; Ferrigno et al. 1969) may be suitable, in which case water would not need to be impounded for mosquito control (the presence of dikes and water control structures can enhance the effectiveness of OMWM, however). Wading birds and other piscivores may also be attracted to the fishes in these potholes.

Waterfowl Attraction

Management for waterfowl in salt marshes can involve more steps and difficulties because the objectives are to enhance specific plants that provide good food and cover for waterfowl, and to discourage undesirable

MARSH MANAGEMENT

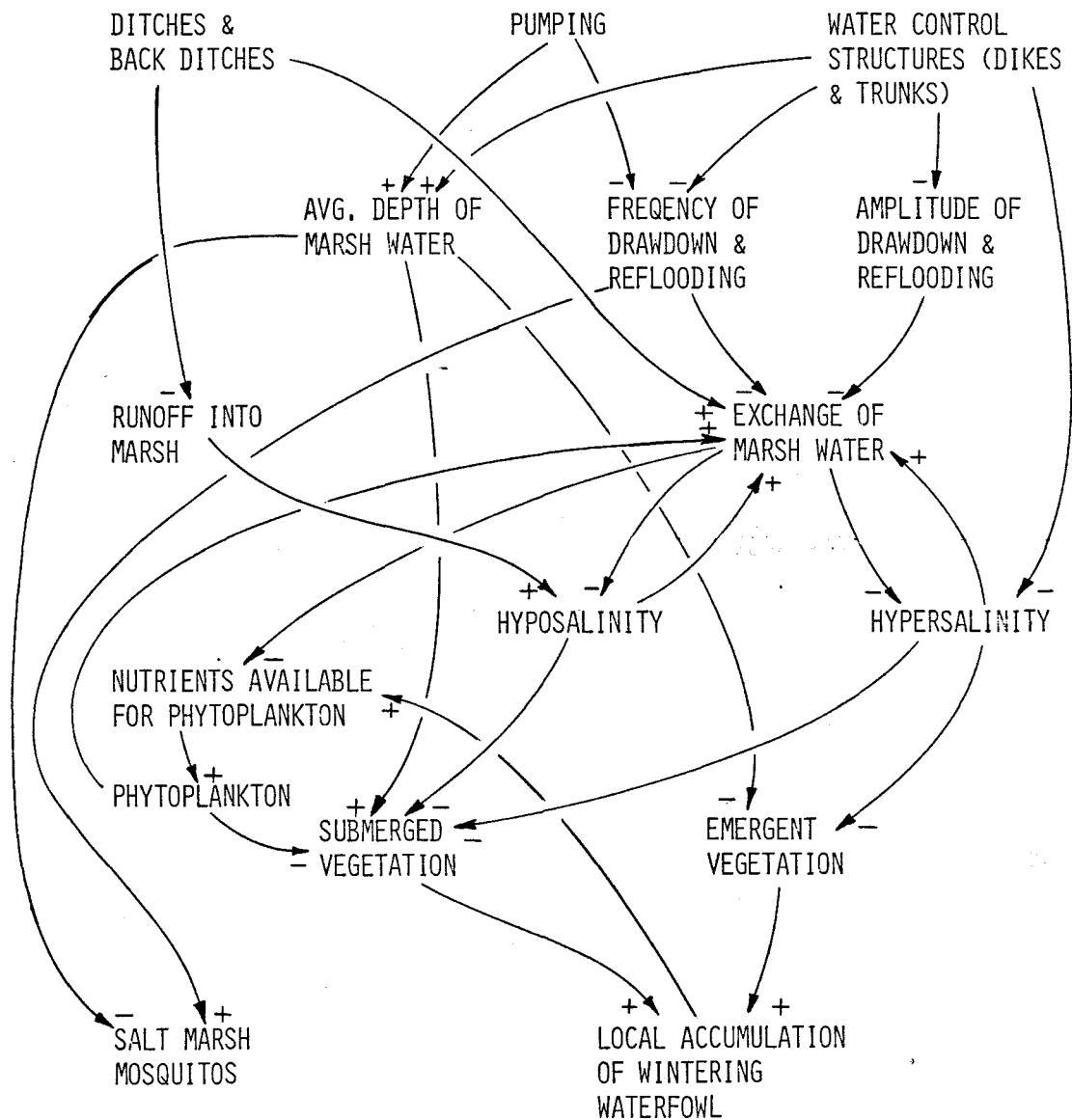


Figure 5. Conceptual Model of Salt Marsh Management to Control Mosquitos and Attract Wintering Waterfowl.

plants. Desirable plants include both emergent and submerged species. Success in production of desired vegetation appears to be dependent upon the degree of control one has over water level and the ability to circulate water in the impoundment. A corollary to that rule is that water salinity determines the species present.

The management of impounded coastal wetlands to attract waterfowl has been variously discussed (e.g., Chabreck 1960; Neely 1960, 1968; Yancey 1964; Baldwin 1967; Joanen and Glasgow 1965; Morgan 1974; Morgan et al. 1975; Heitzman 1978; Prevost et al. 1978; Miglarese and Sandifer 1982; Wicker et al. 1983). Waterfowl food management is a complex issue and elucidation of particular nuances associated with management of each species is beyond the scope of this report; such information can be found in the reports cited both above and in Montague et al. (1984a). The following synthesis is a theoretical treatment of the management principles involved. It is based on the literature and personal communication with a number of impoundment managers and waterfowl biologists (W. Conrad, J. Hiers, R. Joyner, W. Leenhouts, F. Montalbano, R. Perry, J. Salmela, T. Strange, P. Wilkinson, K. Williams) whose individual and collective experiences are invaluable. At this point, we also venture to add the explicit recommendation that anyone interested in investing in the management of such impoundments should study the available literature, but the real, current, and most valuable information is embodied in these (and similarly experienced) individuals. Site visits with them will provide the detail needed to help avoid years and many dollars of error in engineering and water management.

Desired emergent vegetation (primarily bullrushes, such as Scirpus robustus in brackish to estuarine salinities, but a large variety of plants as salinity approaches zero) will occur only if salinity and water depth do not get too high. In addition, water must be drawn down to bed level in early spring so seeds can germinate and seedlings become established prior to reflooding. Reflooding can sometimes result in a brood of mosquitos hatching, but if the larvae can be flushed into the estuary, consumption by estuarine fish can prevent a serious biting nuisance. If successful, emergent vegetation will cover much of the area. Because waterfowl require open areas, dense stands of emergent vegetation should be burned just prior to the arrival of wintering waterfowl. Wilkinson (pers. comm.) suggests that the ideal ratio of open to vegetated area is about 50:50.

Establishment of extensive growth of quality submerged vegetation is unlikely if left to chance. Both hypersaline and hyposaline water will inhibit establishment or growth of these plants (e.g., see Heald 1970). If water of estuarine or brackish salinity can be flushed through when appropriate salinities are available, the risk of poor development is greatly reduced. If the only water available is more estuarine than brackish in salinity (i.e., more saline), then growth of appropriate emergent vegetation seems less likely, so water levels are usually kept deep enough to prevent undesirable emergents from establishing, and all effort is put into submerged species that are good foods for waterfowl at these salinities (e.g., Ruppia and Chara). As in the case for emergent vegetation, water levels must be drawn down to achieve seed germination and seedling establishment for Ruppia. Chara, an alga, grows best on Merritt Island if impoundments are not drawn down, however (Leenhouts, pers. comm.).

Additional problems occur with the growth of submerged vegetation, however. For example, guano from accumulations of waterbirds in impoundments can stimulate phytoplankton which reduce light available for submerged vegetation. Once again, water circulation can alleviate this problem.

Thus, intensive management of waterfowl food plants requires frequent exchange of impounded water with the estuary. Such exchange, if practiced frequently, mitigates considerably a major possible negative influence of impoundments on estuarine fish and shellfish (see section on Estuarine Fish and Shellfish). Unfortunately, on Merritt Island, frequent exchange is possible only by operating expensive mechanical pumps (which pump estuarine water only), unless some impoundments can be set aside for water storage that could capture runoff and gravity-feed areas of need. Elevation and water level changes are probably insufficient on Merritt Island to allow storage of enough head to accomplish either frequent or substantial exchange unless the proportion of water storage area to waterfowl management area is large. A study of surface water hydrology in impoundments is beginning summer of 1985, funded by Florida Sea Grant College, J.P. Heaney, W.C. Huber, and C.L. Montague, principal investigators.

ECOLOGY OF MERRITT ISLAND SALTMARSH IMPOUNDMENTS

Effects of Impoundment on Ecological Production

On Merritt Island, energy inputs that should be considered in a hypothesis of impoundment effects on ecological production include: 1) sunlight, which is converted to chemical energy of organic compounds by photosynthesis; 2) wind, which enhances both air and water circulation and in turn subsidizes the encounter of organisms with their gaseous and aquatic nutrients and foods, and subsidizes the separation of waste products from organisms; 3) rain, which enhances water circulation (directly and by runoff), and which decreases salinity, which by itself may enhance community production (perhaps at the expense of certain species); and 4) human work, which results in water circulation at times of year when salt marshes do not otherwise receive circulation.

Primary Energy (Sunlight and Turbidity)

Light penetrating to the sediment surface may be greater if overflooding has removed dense grassy or mangrove vegetation, or may be less if vegetation prior to impoundment was more open and now the impoundment is more turbid. The net effect on biota is probably a substitution of species to more microphytes and less macrophytes (Voigts 1976), or if macrophytes, then these would be submerged vegetation such as Ruppia or Chara. In areas that have lost emergent vegetation, the work of the wind may be sufficient to uproot existing submerged vegetation and prevent establishment of submerged vegetation via turbidity and sediment destabilization.

Initial flooding of a marsh may reduce sunlight (compared to a periodically-dry marsh) because of light reflection (R.G. Wetzel 1975), though once a water level is established, increases in level may not have much further effect on overall ecological production due to automitigation.

Water Circulation and Freshening of Water

It is unclear how impoundment affects any energy subsidy from water circulation through Merritt Island salt marshes. For impoundment to reduce such a subsidy, the overall movement of water through impounded ecosystems would have to be lowered. Historically, water did not cover large areas of marsh for much of the year (perhaps 100 days of inundation), and during this time, water motion was probably determined by wind (Dubbelday 1975), as the daily tides on Merritt Island are very low (data from Ned Smith). Impoundments may capture and hold rainwater that would go to the estuary and dikes may also serve as wind breaks; however, if water level increases are sufficient to eliminate emergent vegetation, wind-baffling structure will be reduced in the impoundment thereby increasing the effective work of the wind, which could result in enhanced overall production at least at times of submergence.

Salinity of water impounded on Merritt Island salt marshes is highly variable owing primarily to variability in rainfall. Salinity and water level data from the restored marsh T-10-K and from three impounded marshes are plotted in Figures 6 through 9. Salinity data are summarized in Table 2. Impounded water, because it includes captured rainfall, is often presumed to be fresher than water on natural marshland, though water from unimpounded marsh also fluctuates with rainfall and drought. Salinity in the restored marsh T-10-K, for example, fluctuates between 6 and 39 ppt in the period from September 1977 and April 1980 (Table 2, Figure 6). During the same period, salinity in the adjacent Black Point impoundment (T-10-J) fluctuates between 5 and 39 ppt in a similar pattern (Figure 7).

Salinity in impoundments in which water levels are maintained by pumping with salt water can be high if evaporation occurs and rainfall is low (Bidlingmayer 1982). Impoundments that are pumped with salt water include T-10-A, B, C, D, and F, T-10-L and M, and the impoundments on Jack Davis Island. In the same period of reporting as above, the Jack Davis impoundments fluctuated between 16 and 53 ppt. Impoundment T-10-D (Figure 8) fluctuated between 12 and 57 ppt, the highest salinity recorded during this period in any of the impoundments reported.

Conversely, some impoundments have water of very low salinity. The "fresh" impoundment T-24-D (Figure 9) holds water very well and is always low in salinity. The ability of this marsh to retain water of low salinity is suggestive of a groundwater flow to T-24-D.

Table 2. Salinity Data for a Restored Marsh and from Three Impounded Marshes on Merritt Island National Wildlife Refuge (Data from W. Leenhouts). SD = Standard Deviation, N = Number of Observations between September 1977 and April 1980.

MARSH	LOW	HIGH	MEAN	SD	N
T-10-K (Restored Marsh)	6	39	23	10	29
T-10-J (Black Point Imp.)	5	39	20	9	29
T-10-D (Roach Hole Imp.)	12	57	37	11	29
T-24-D (Fresh Imp.)	0	22	6	5	29

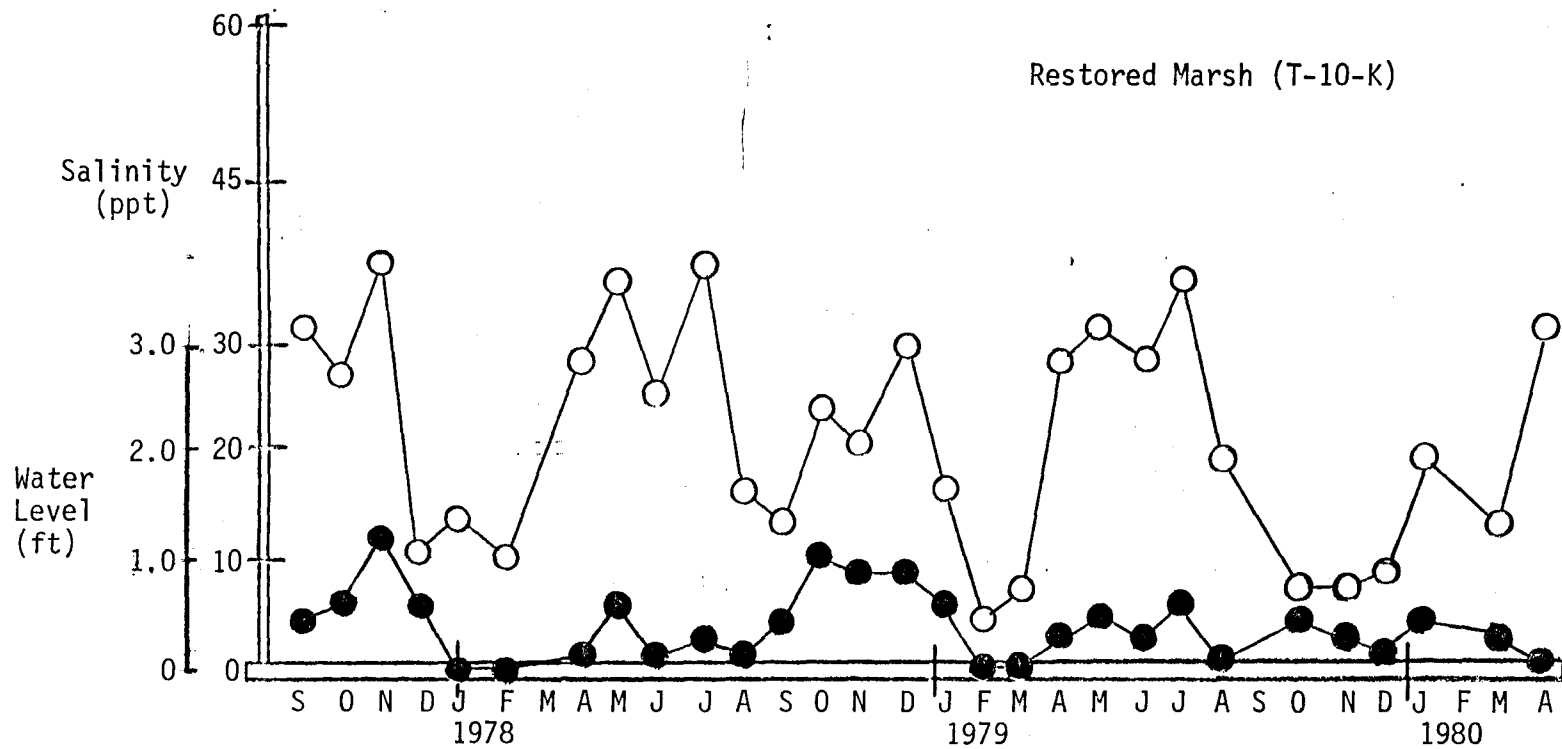


Figure 6. Salinity and Water Level Data from the Restored Marsh, T-10-K, from September 1977 through April 1980 (data courtesy of W. Leenhouts, MINWR). Salinity: open circles, Water Level: closed circles.

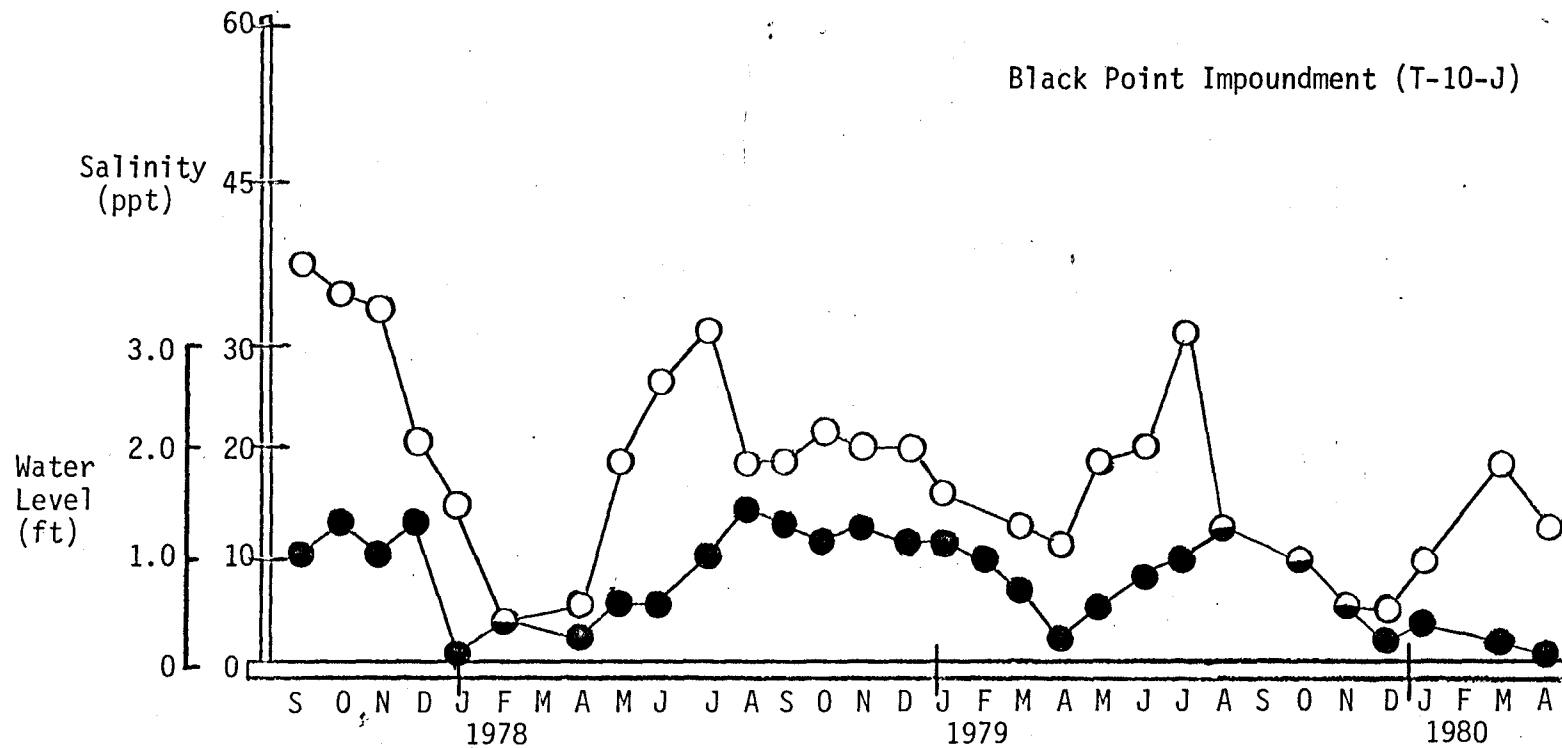


Figure 7. Salinity and Water Level Data from Black Point Impoundment, T-10-J, from September 1977 through April 1980 (data courtesy of (W. Leenhouts, MINWR). Salinity: open circles; Water Level: closed circles.

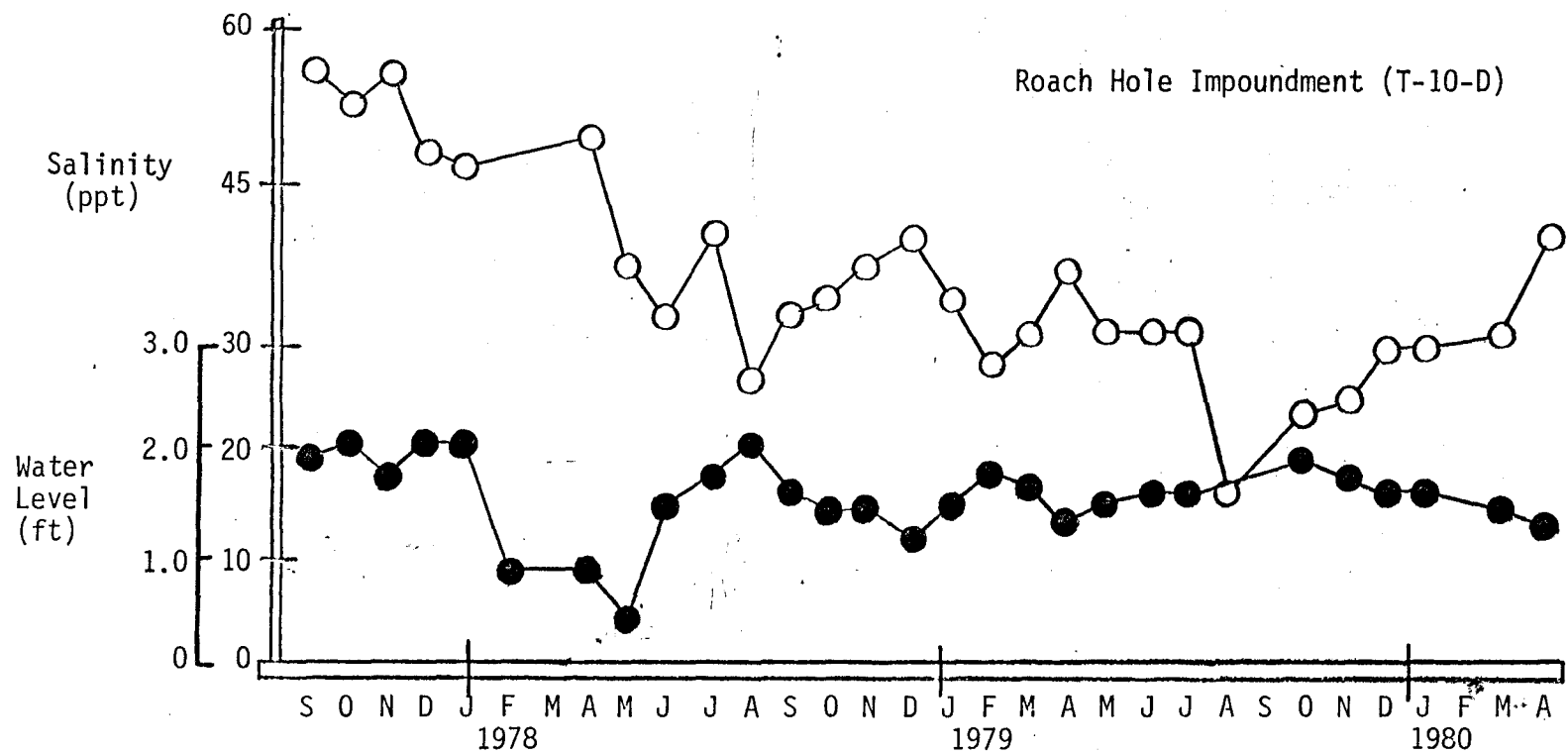


Figure 8. Salinity and Water Level Data from the Roach Hole Impoundment, T-10-D, from September 1977 through April 1980 (data courtesy of W. Leenhouts, MINWR). Salinity: open circles; Water Level: closed circles.

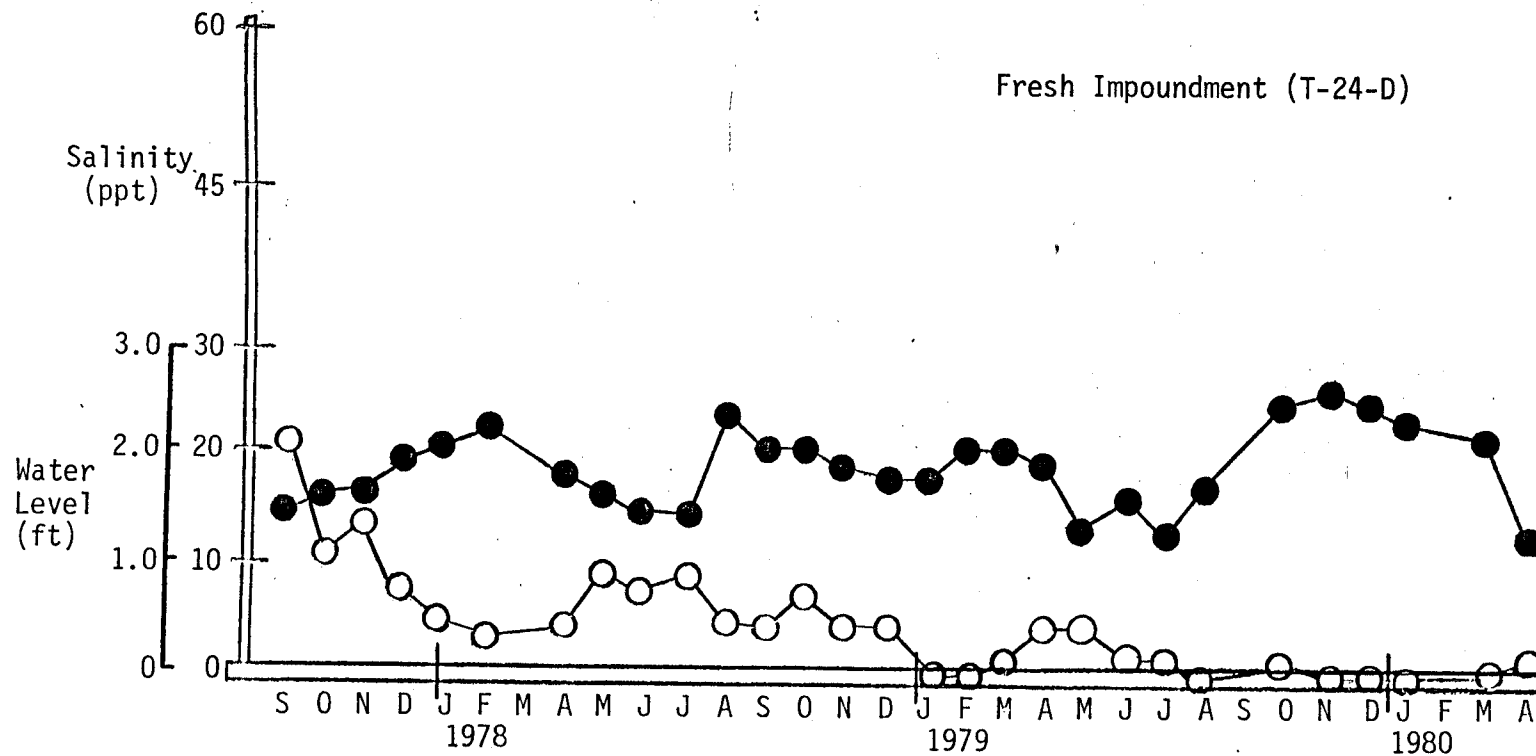


Figure 9. Salinity and Water Level Data from the Fresh Impoundment, T-24-D, from September 1977 through April 1980 (data courtesy of W. Leenhouts, MINWR). Salinity: open circles; Water Level: closed circles.

Thus, some impoundments on Merritt Island are fresher on average than surrounding estuarine water (see Lasater 1975), and some are saltier; the same impoundment may be fresher during the wet season and saltier during the dry season. Probably all capture rainwater that would otherwise go to the estuary, but we can find no evidence that the estuarine water has increased in salinity due to impoundment. An optimal salinity for overall production may occur in nature. Because many land and aquatic organisms maintain a body fluid salinity of around 9 ppt (Wilson 1972, p. 574), a salinity optimum for overall production may be somewhere in the neighborhood of 9 ppt. Above 9 ppt many organisms may allocate energy to excrete or exclude salts; below 9 ppt organisms may have to allocate energy to retain salt. The variation in ecological production that can be explained by variation in salinity in the range of 0 to 35 ppt (full strength seawater) is unknown as is the magnitude of such an effect, but it is subtle compared to the effects of very high salinity (e.g., greater than 60 ppt).

Whole-system Stress (Low Oxygen, Hypersalinity)

Despite the notion of a brackish salinity optimum for ecological production, environmental extremes do not presently seem sufficient to cause vastly lower ecological production, though clearly, species compositions have radically changed in overflowed or very saline impoundments due to a variety of stresses on individual species. It is possible that salinities in some impoundments on Merritt Island (e.g., T-10-D) are on occasion sufficiently high to lower whole-system production somewhat, but no experiments have been conducted to evaluate this possibility. Oxygen readings with time of measurement, salinity, and temperature recordings are needed, but at a frequency not possible without a dedicated researcher or expensive equipment.

Oxygen is probably not low enough to affect overall ecological production, despite chronic deleterious effects on certain species that may occur. Marshes are typically eutrophic because of their high productivity and resultant high rates of respiration (W.E. Odum 1970a); dissolved oxygen levels in marshes are therefore often low and it is unclear how impoundment affects this parameter (see Estuarine Fish and Shellfish section).

Nutrient Supply

Nutrient supply to impounded salt marsh may not be affected greatly unless trapped runoff (in those impoundments that are not back-ditched) is exceptionally rich in nutrients, in which case nutrient supply to the impounded marsh may be enhanced at the expense of the estuary. The estuary, however, continues to receive ever-increasing supplies of anthropogenic nutrients (East Central Florida Regional Planning Council 1975a, 1975b). In fact, addition of wastewater to an impounded marsh may enhance ecological production within the marsh (Haines 1979a; Hardisky et al. 1983; H.T. Odum, in press) and improve water quality in the estuary (as the wastes would no longer be pumped directly into the estuary). The feasibility of using wetlands for sewage treatment has been examined extensively (see references in E.P. Odum et al. 1983 and Haines 1979a) and is currently under study at Merritt Island by Ronnie Best (Mion et al. 1985). E.P. Odum et al. (1983) note that impounded marshes possess advantages over natural

marshes for sewage treatment because control over waste retention times, water levels, and harvest parameters are possible. Furthermore, wastewater management can be integrated effectively with mosquito control (Carlson 1983).

Note, however, that sewage effluent can produce subtle alterations of considerable detriment. For example, in the Great South Bay duck farm incident (Ryther 1954) duck-farm effluents enhanced production of microalgae, but the forms that prospered (Nanochloris and Stichococcus) were unsuitable for secondary consumers. Accordingly, fish and shellfish production declined. Marshes and estuaries are normally eutrophic, and additional inputs of nutrients may lower dissolved oxygen concentrations to levels deleterious to aquatic animals that cannot use atmospheric air (H.T. Odum, in press). Enhanced ecological production generally results in greater production of desirable organisms, but not necessarily; management for enhanced production should therefore be considered with this caveat in mind.

Effects of Impoundment on Overall Diversity

An evaluation of the influence of impoundment on diversity can be made by observation, but at present, few comparative data are available (but see Leenhouts and Baker 1982). An understanding of relevant theory of the causes of diversity may lead to 1) a hypothesis of the effects of impoundment on ecological diversity, which can be tested, and 2) guidelines for managing Merritt Island for enhanced ecological diversity (which, if implemented, will also serve as tests of the theory).

Although the diversity of certain subgroups of interest may have decreased, overall diversity of the area of Merritt Island that was formerly salt marsh has undoubtedly increased (Leenhouts, pers. comm.; personal observations). Both richness and evenness of species should now be greater because the diversity of salinity and water level among impoundments is greater. Vegetation, for example, formerly included typical salt marsh and mangrove species of this region of Florida, but now included are all of these, as well as species common to brackish and freshwater marshes. In addition, species of submerged marine/brackish vegetation that could only have been found in potholes prior to impoundment are abundant in many impoundments (e.g. Chara) and upland species inhabit dikes. Although it is possible that some of these additional species occurred in small areas of what is now impounded marsh, their relative prevalence has increased. It is doubtful that the current prevalence of salt marsh species is as low as the former prevalence of freshwater species, but even if such were the case, diversity should be higher because diversity of salt marshes is typically much lower than the diversity of fresher marshes.

Because vegetation is the foundation of food and cover for animals, a diversity of vegetation should foster a diversity of animals, though this diversity may not include all desired species. Desired species may include organisms that occurred in greater abundance prior to the change, whether or not the change accounts for their decline (e.g., dusky seaside sparrow). Despite this, however, the overall diversity of the area formerly called salt marsh has increased, and it has been replaced by a mosaic of produc-

tive brackish and freshwater marshes, and in a few cases, hypersaline areas of perhaps lower production.

Effects of Impoundment on Estuarine Fish and Shellfish

Closed water control structures and dikes without control structures do not allow ingress or egress of estuarine fish (Gilmore et al. 1982; Harrington and Harrington 1982). Control structures are not closed all of the time in most impoundments, however. When the water is held on the marsh, access to foods by estuarine fish and shellfish is possible if water control structures are open to allow ingress, or if fish entered while the structures were open (Provost 1973b). Merritt Island impoundments hold water on the marsh for much more of the year than occurred prior to impoundment. Perimeter ditches dug during the construction of dikes may enhance the production of estuarine fish by increasing marsh edge (Provost 1959, 1968), which is habitat for a variety of estuarine organisms (e.g., young snook; Gilmore et al. 1983) and is of fundamental importance to accessibility of foods and cover, and detrital export (a consideration of less direct importance to fish survival). Perimeter ditches, because of their depth, also provide refuge from predation by wading birds. Wading birds forage poorly in such habitats (Britton and Moser 1982). However, access to these ditches by fish is essential. Pumps can enhance the circulation of water through marshes. Such circulation could occur naturally only during the 100 or so days that the marshes were covered with estuarine water prior to impoundment, and then only if sufficient wind energy was available to actually move the water through the marsh. Impoundments that are open enough of the time to allow some ingress of estuarine fish may not be open at times when egress is essential either for completing life cycles or for more immediate survival.

Summary Diagrams of the Influence of Impoundment on Estuarine Fish and Shellfish

Figures 10 and 11 summarize the relationships between impoundment activities and production of estuarine fish with respect to food and cover, respectively. Production of estuarine fish is at the bottom of each diagram. In Figure 10, production of estuarine fish and shellfish is positively related to the presence and accessibility of foods. Foods for various species and life history stages of estuarine fish and shellfish include: 1) vagile link organisms; 2) zooplankton; 3) resident marsh organisms and detritus on the marsh surface; 4) phytoplankton; and 5) detritus and its accompanying community of decomposers exported to adjacent waters. Vagile link organisms occur, by definition, in proximity to the edges of marsh creeks, and themselves are consumers of the resident marsh organisms and detritus. Zooplankton feed on phytoplankton which occur if sufficient water is available.

Resident marsh organisms and detritus are a function of the quantity of submerged and emergent vegetation produced in the marsh. Emergent vegetation grows better near the edges of marsh creeks, though the causes of this phenomenon are complex (Haines and Dunn 1976). Hypersalinity will reduce both types of vegetation but will be prevented or alleviated by exchange of marsh or impoundment water with the estuary. Water level can be controlled sufficiently for both types of vegetation to coexist, but

FOOD FOR FISH AND SHELLFISH

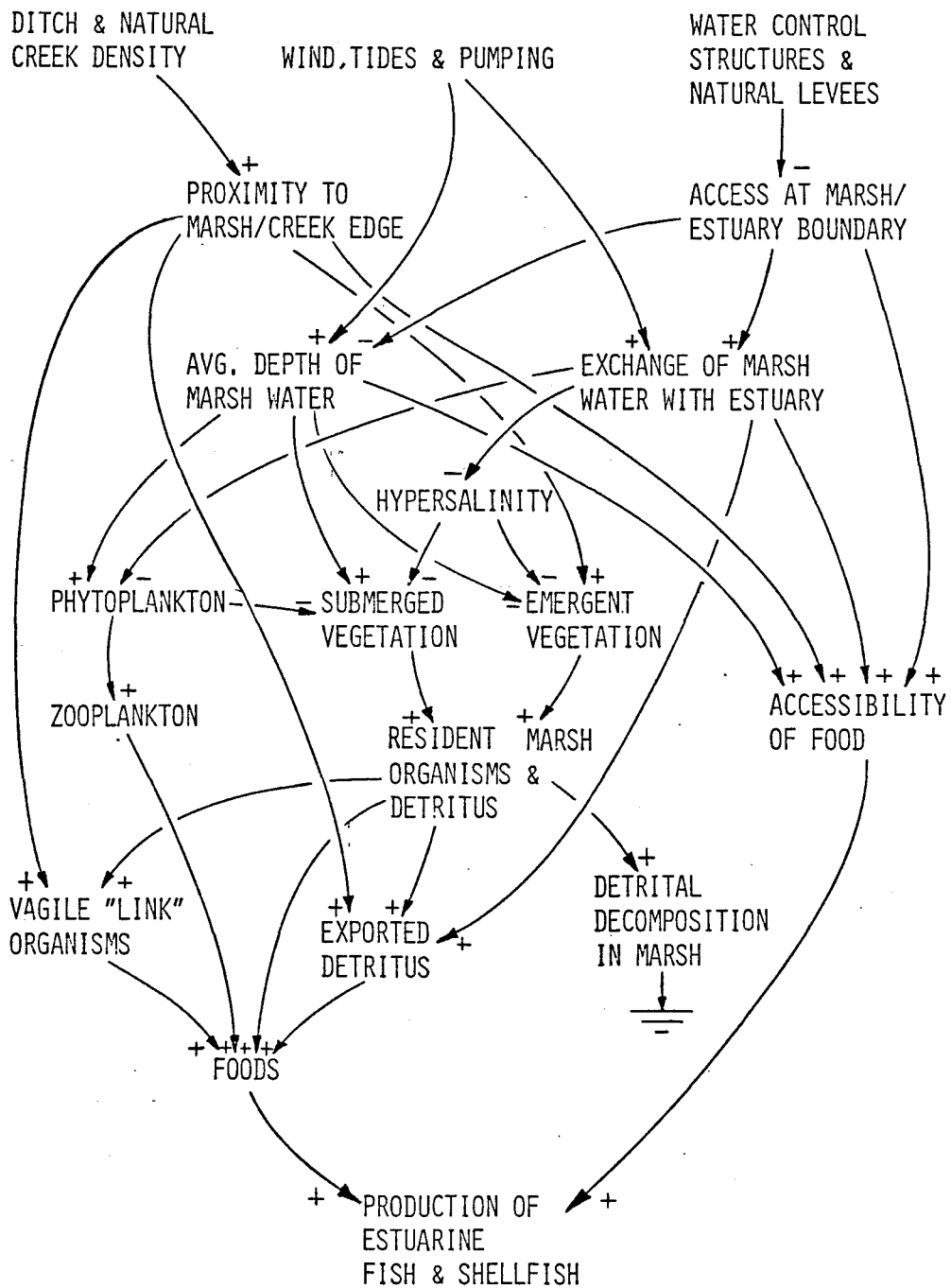


Figure 10. Conceptual Model of Major Influences on Food for Estuarine Fish and Shellfish. Note the importance of accessibility of food.

COVER FOR FISH AND SHELLFISH

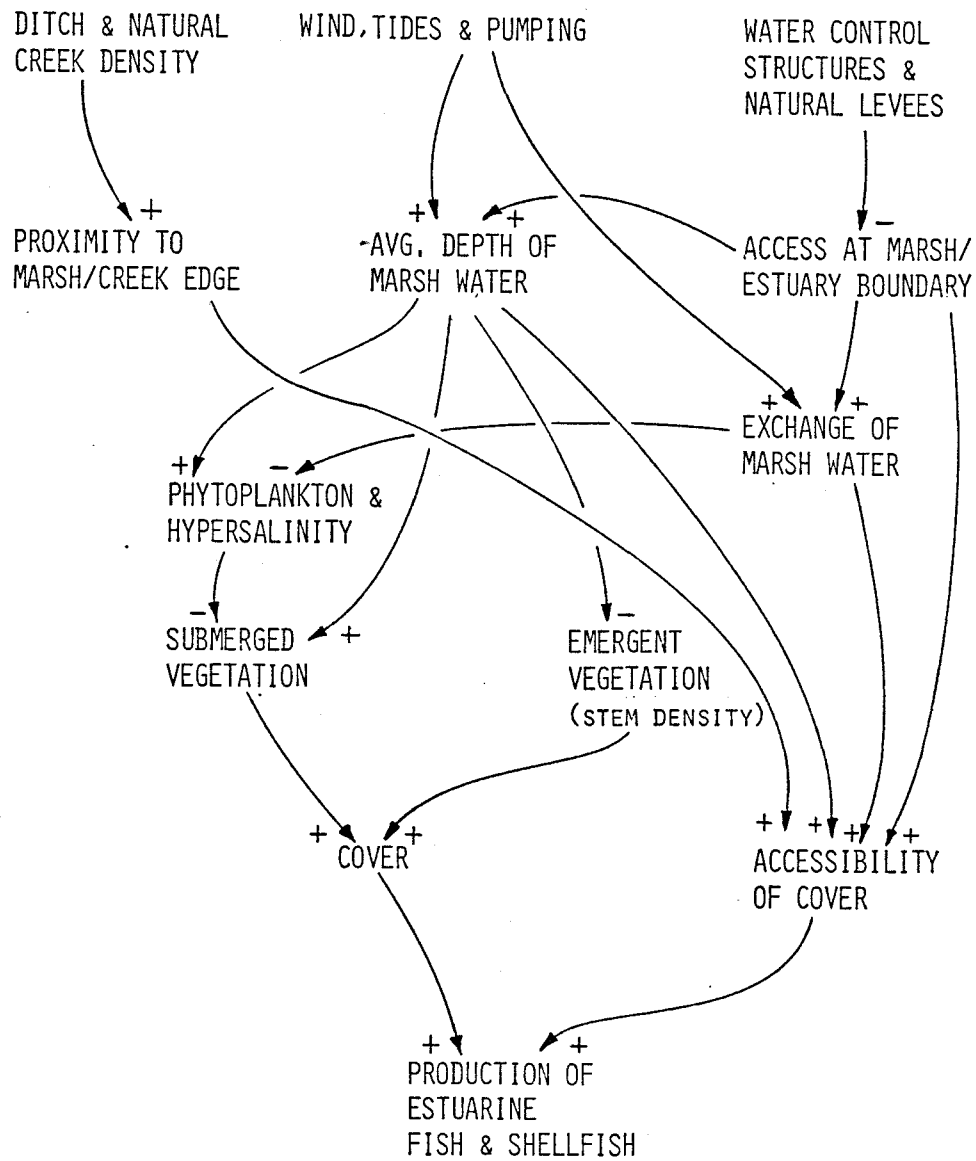


Figure 11. Conceptual Model of Major Influences on Cover for Estuarine Fish and Shellfish. Note the importance of accessibility of cover.

when too low, submerged vegetation is eliminated, and when too high, emergent vegetation is eliminated. Submerged vegetation may also be reduced by dense phytoplankton, which reduce light penetration to the seagrasses. If either phytoplankton or its nutrients are greater in marsh water than in estuarine water, exchange of marsh water with the estuary will reduce phytoplankton growth.

Resident marsh organisms account for considerable decomposition of detritus within the marsh itself, leaving perhaps a small fraction available for export. Exported detritus will be greater when more has accumulated on the marsh, and when exchange of marsh water is greater. Export will also be greater from marsh area closer to the edges of tidal creeks.

Accessibility of foods by estuarine fish and shellfish is enhanced by: 1) increased water depth; 2) proximity to the edge of a marsh creek; 3) exchange of marsh water with the estuary; and 4) increased access at the marsh-estuary boundary. The average depth of inundation of the marsh can be higher with greater tides, wind, or pumping, or if water outlets at the marsh-estuary boundary are sufficiently restrictive. Proximity to an edge of a marsh creek is greater where densities of creeks or man-made ditches are greater. Note in both Figures 10 and 11 the number of different aspects of estuarine fish production that are enhanced by proximity to edges of marsh creeks. Exchange of marsh water also influences several components in the diagrams. Exchange is enhanced by tides, wind, and pumping, and by increased access at the marsh-estuary boundary. Access is restricted by the size of creek mouths, the size of water control structures (trunks and culverts) and the time they are open, and the extent of natural levees and man-made dikes.

Cover

In Figure 11, production of estuarine fish and shellfish is shown as a function of cover and accessibility of cover. Cover is dependent on the quantity of submerged and emergent vegetation. Again, hypersalinity and phytoplankton can reduce growth of submerged vegetation, but these effects are reduced with greater exchange of marsh water with the estuary. Accessibility of cover is enhanced by exactly the same things that enhance accessibility to food and control of these is the same as in Figure 10.

Ideas for Impoundment Management to Enhance Estuarine Fish

Production of estuarine fish and shellfish should be enhanced by allowing greater ingress and egress. The enhanced access to food and cover within vegetated impoundments caused by perimeter ditches and flooding should be beneficial to estuarine fish if ingress and egress are enhanced.

Possible ways to enhance food, cover, and ingress and egress to marshes and impoundments include: 1) more submerged cross-sectional area of open access and more time open during times of high water; 2) keeping culverts open during the seasonal fall of water in January and letting the marsh drain completely in as many impoundments as possible (i.e. where mosquito control is needed, but waterfowl management is not); 3) breaching

dikes, or removing water control structures wherever possible (i.e. where neither mosquito control nor waterfowl management is essential or where rotary ditching provides adequate mosquito control and potholes provide adequate waterfowl habitat); 4) adding more ditches; and 5) leaving culverts at least partially open, with continuous pumping with a small pump or occasional pumping with a large pump. Culverts can be left "partially open" to allow egress and ingress using Neely's (1960) "leaky trunk" technique whereby a lower riser board is replaced with chock blocks.

Analysis of Commercial Landings for the Inshore Fisheries of Brevard and Volusia Counties, 1951-1982

Impoundment of Merritt Island marshes has been conjectured to be detrimental to the fisheries of the Indian River lagoonal system. To evaluate this possibility, we analyzed commercial landings statistics (recorded by the National Marine Fisheries Service) for the five fisheries considered by Anderson and Gehringer (1965) to be dominant in the "inside" (i.e. lagoonal) catch of the Merritt Island area. These are spotted seatrout (Cynoscion nebulosus), blue crab (Callinectes sapidus), spot (Leiostomus xanthurus), mullet (Mugil curema and M. cephalus, combined for this analysis), and Florida pompano (Trachinotus carolinus). These species continued to be dominant components of the fishery in the 1970's (Snelson 1980).

Impoundment of Merritt Island marshes occurred primarily between 1959 and 1966 (Leenhouts 1983). Because the species considered here are relatively short-lived and enter the commercial fishery at an early age, impacts on recruitment (by alteration or removal of nursery habitat or by trophic degradation of the estuary) should be evident in landings soon thereafter. We examined landings of the five dominant fisheries in Brevard and Volusia counties for sustained declines greater than normal variation during the period following impoundment.

Landings data are easily confounded especially in the absence of information on fishing effort expended to accrue the catches. Adequate effort data on these fisheries do not exist. However, an indication of trends in effort can be inferred from trends in numbers of commercial vessels registered (Ricker 1975). Available information on numbers of vessels registered for commercial use in Brevard and Volusia counties (courtesy of Florida Department of Natural Resources) are shown in Figure 12. From 1963 to 1978, the number of commercial vessels registered in Brevard county remained stable overall (with annual fluctuations), but declined steadily in Volusia County. We readily acknowledge that the usefulness of these data for estimating fishing effort are equivocal for a number of reasons; e.g., varying proportions of vessels may operate off-shore, shifts in species-specific effort are not apparent, and changes in gear efficiency may occur. Nevertheless, their consideration is probably more useful than their omission.

Spotted Seatrout

Juvenile spotted seatrout do not inhabit marshes and are therefore not considered dependent on marshes for cover. However, spotted seatrout prey on a variety of forage organisms (Moody 1950; Tabb 1966; Lorio and Perret

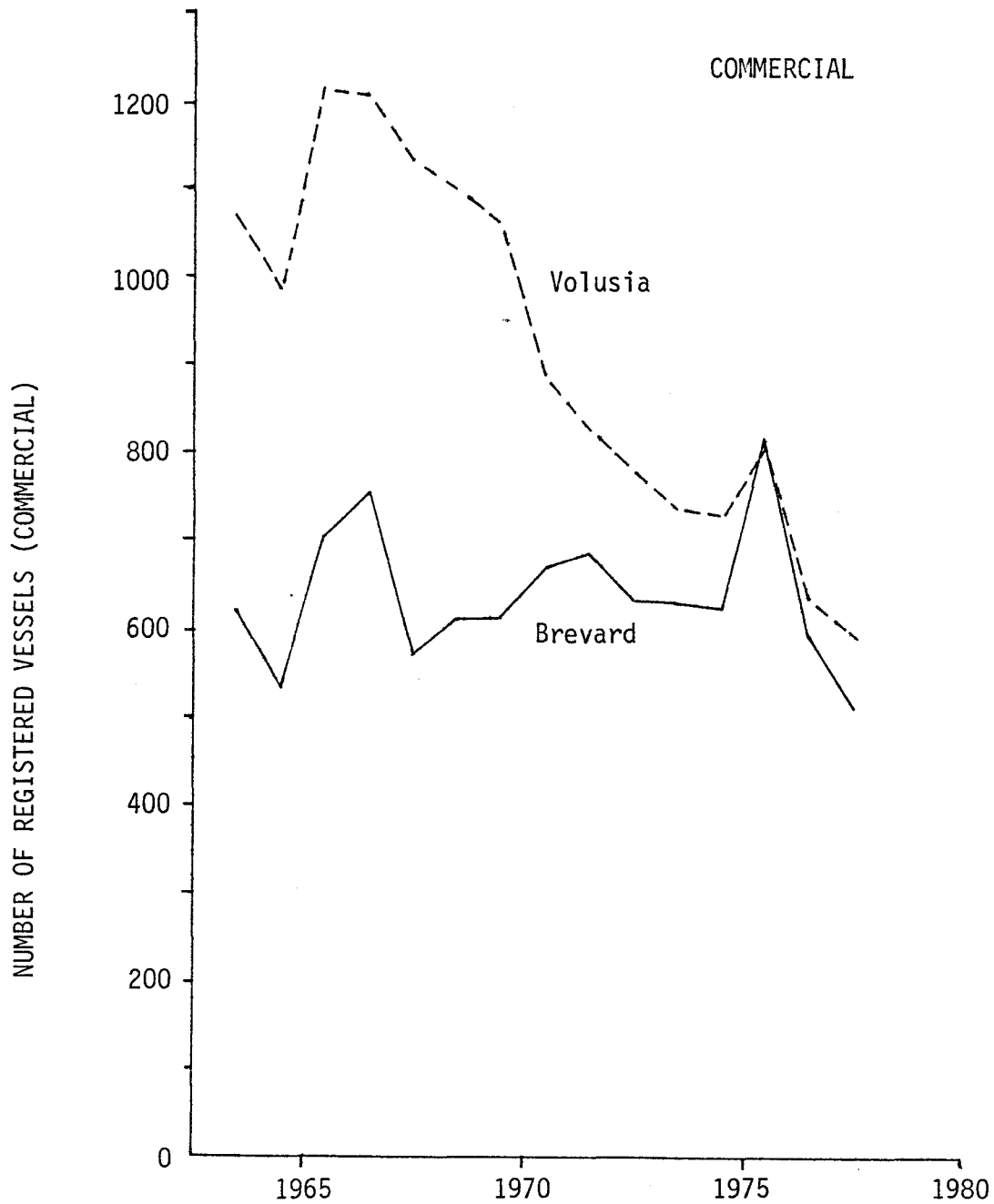


Figure 12. Numbers of vessels registered for commercial use in Brevard and Volusia counties, 1963 to 1978. Data courtesy of Florida Department of Natural Resources.

1980), many of which may spend part of their life cycle in marshes. Therefore, if impoundment has any effect on their forage, this species may be expected to decline following impoundment construction.

For both counties combined, landings of spotted seatrout declined in the 1950's prior to impoundment but have remained stable since (Fig. 13). However, catches increased in Volusia County whereas a gradual decline was evident in Brevard County since the period of impoundment. As commercial "effort" in Brevard County was stable, the declining landings suggest that impoundment may have negatively impacted this fishery. However, Anderson and Gehringer (1965) estimated that during the early 1960's, the recreational catch of spotted seatrout in the Merritt Island area was about twice that of the commercial catch. As the number of pleasure boats (and therefore anglers) in Brevard County quadrupled from 1963 to 1983 (Fig. 14), and the spotted seatrout is avidly sought by anglers, it is likely that the proportion of the total spotted seatrout catch taken by anglers increased. Therefore, the decline in commercial landings may have resulted from increasing sportfishing pressure and harvest. That the decline was gradual (as was the increase in sportfishing pressure) and not abrupt (as was impoundment of the marshes) lends further credence to the hypothesis that the decline was caused by increased sportfishing and not by impoundment. Increased commercial landings of spotted seatrout in Volusia County, concurrent with declining commercial "effort" and probable increased angling pressure, offer no evidence that impoundment has affected this fishery in Volusia County. Therefore, no clear evidence (from landings and boat registration data) exists suggesting that impoundment of Merritt Island marshes caused a deterioration of the spotted seatrout fishery.

Blue Crab

Blue crabs reside in or near salt marshes throughout much of their life cycle (Weinstein 1979; Van Den Avyle and Fowler 1984) and could be expected to be deleteriously affected by loss or degradation of marsh habitats. Landings analysis for this species was hindered by the lack of differentiation between landings in the two counties between 1958 and 1962 (Fig. 15).

The blue crab fishery in Volusia County has apparently never been very large compared to that in Brevard County (Fig. 15), or crabs taken there are brought to fish houses elsewhere. Crab landings in Volusia County during the 1970's and 1980's appear to be somewhat lower than landings reported in the 1950's.

Beginning in the mid-1960's, blue crab landings in Brevard County oscillated regularly (perhaps as a density-dependent response) but were considerably greater than during the 1950's and early 1960's. The increased landings perhaps resulted from a shift in local effort to this fishery, or perhaps impoundment enhanced this fishery by unknown means. Because landings improved so markedly during the 1960's, following the period of impoundment, it is unlikely that impoundment of Merritt Island marshes negatively impacted this fishery. Increased landings could be due to increased demand or increased production. Demand could be greater because of increased development concurrent with impoundment of the marshes.

LANDINGS (LBS), BREVARD (B) AND VOLUSIA (V) COUNTIES, 1951-1982
 T = TOTAL OF BOTH COUNTIES COMBINED
 SPOTTED SEATROUT

PLOT OF TROUT*YEAR SYMBOL IS VALUE OF COUNTY

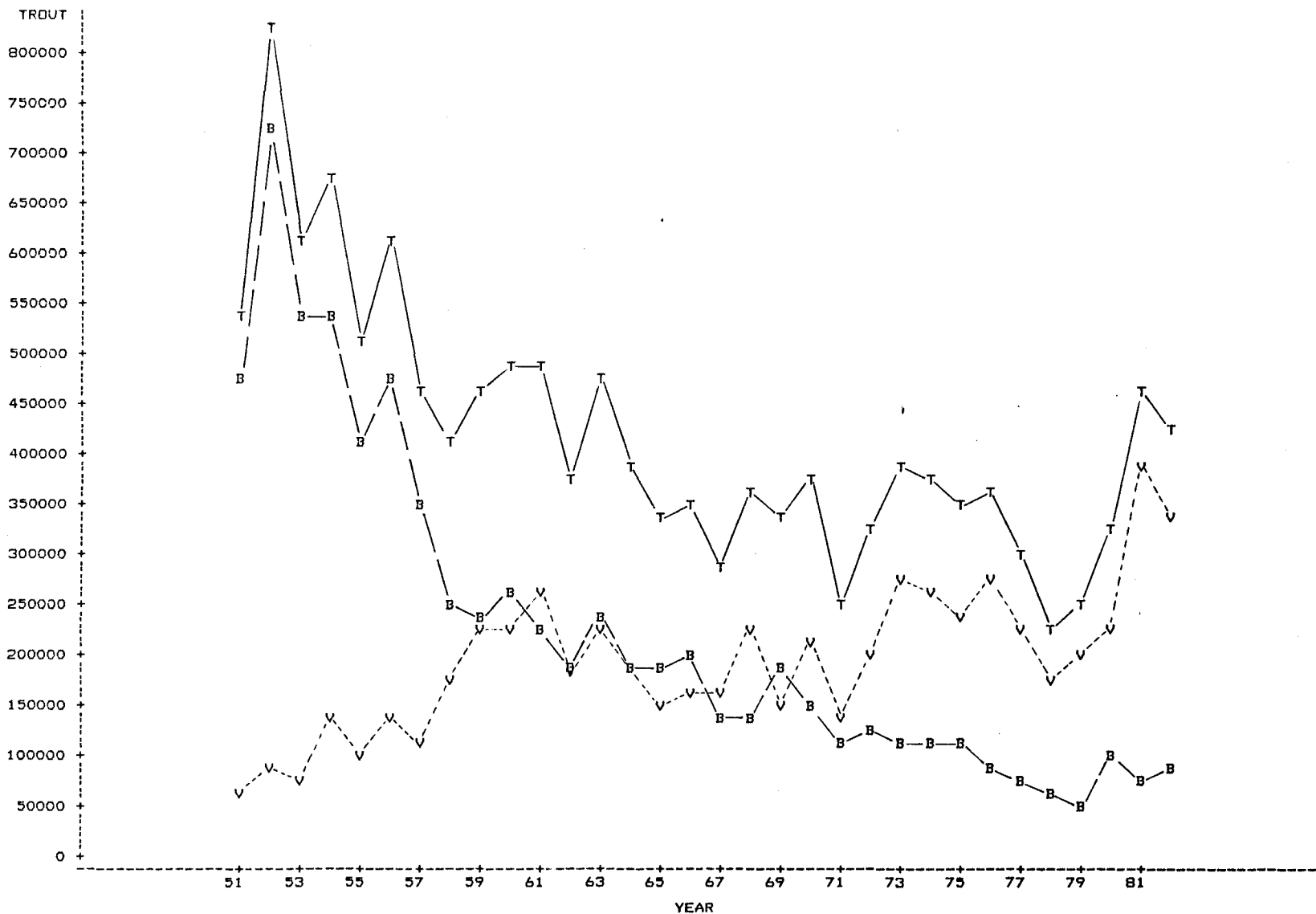


Figure 13. Commercial landings (pounds) of spotted seatrout in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982.

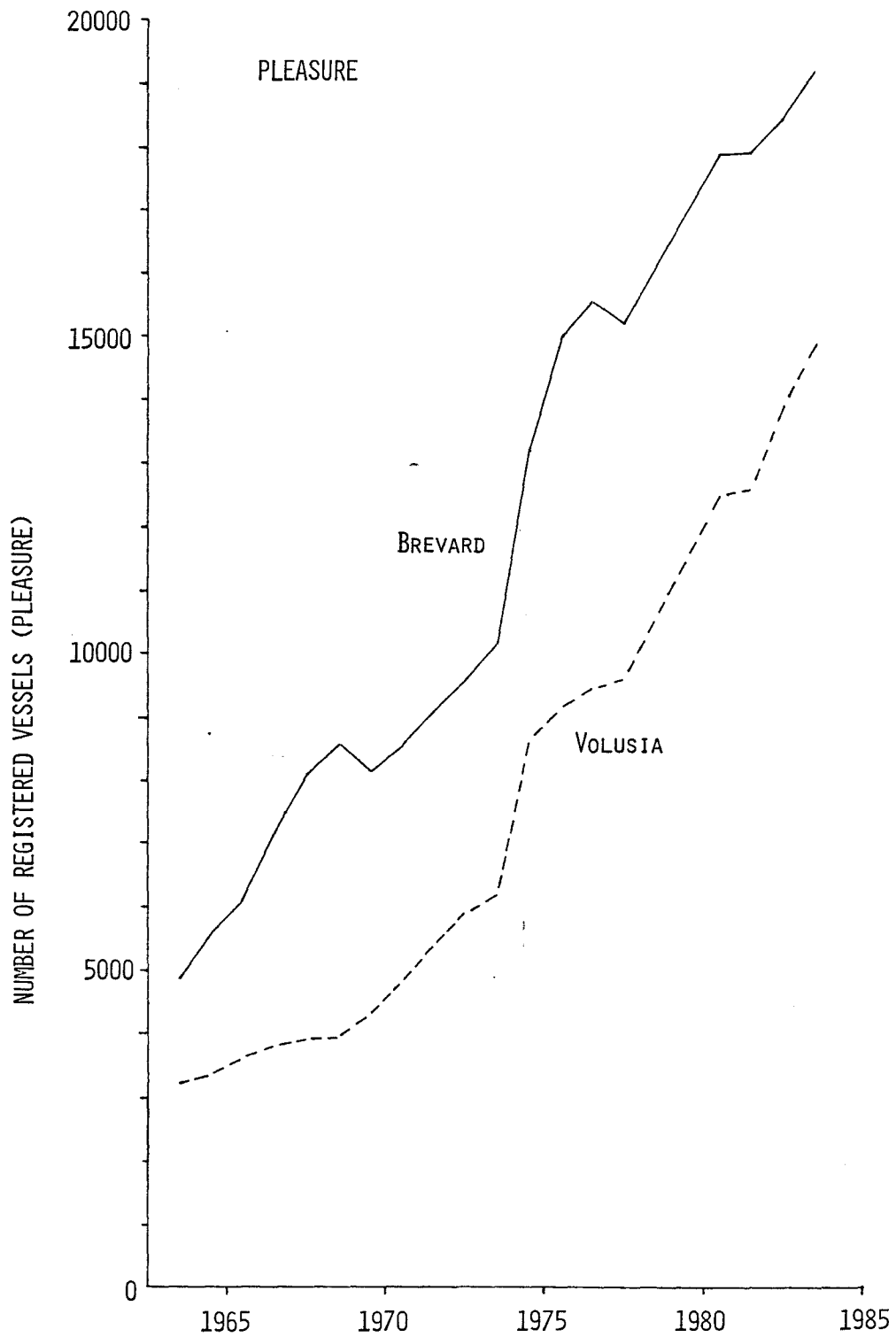


Figure 14. Numbers of vessels registered for recreational use in Brevard and Volusia counties, 1963 to 1983. Data courtesy of Florida Department of Natural Resources.

LANDINGS (LBS), BREVARD (B) AND VOLUSIA (V) COUNTIES, 1951-1982
 T = TOTAL OF BOTH COUNTIES COMBINED
 BLUE CRABS (HARD)

PLOT OF CRABS*YEAR SYMBOL IS VALUE OF COUNTY

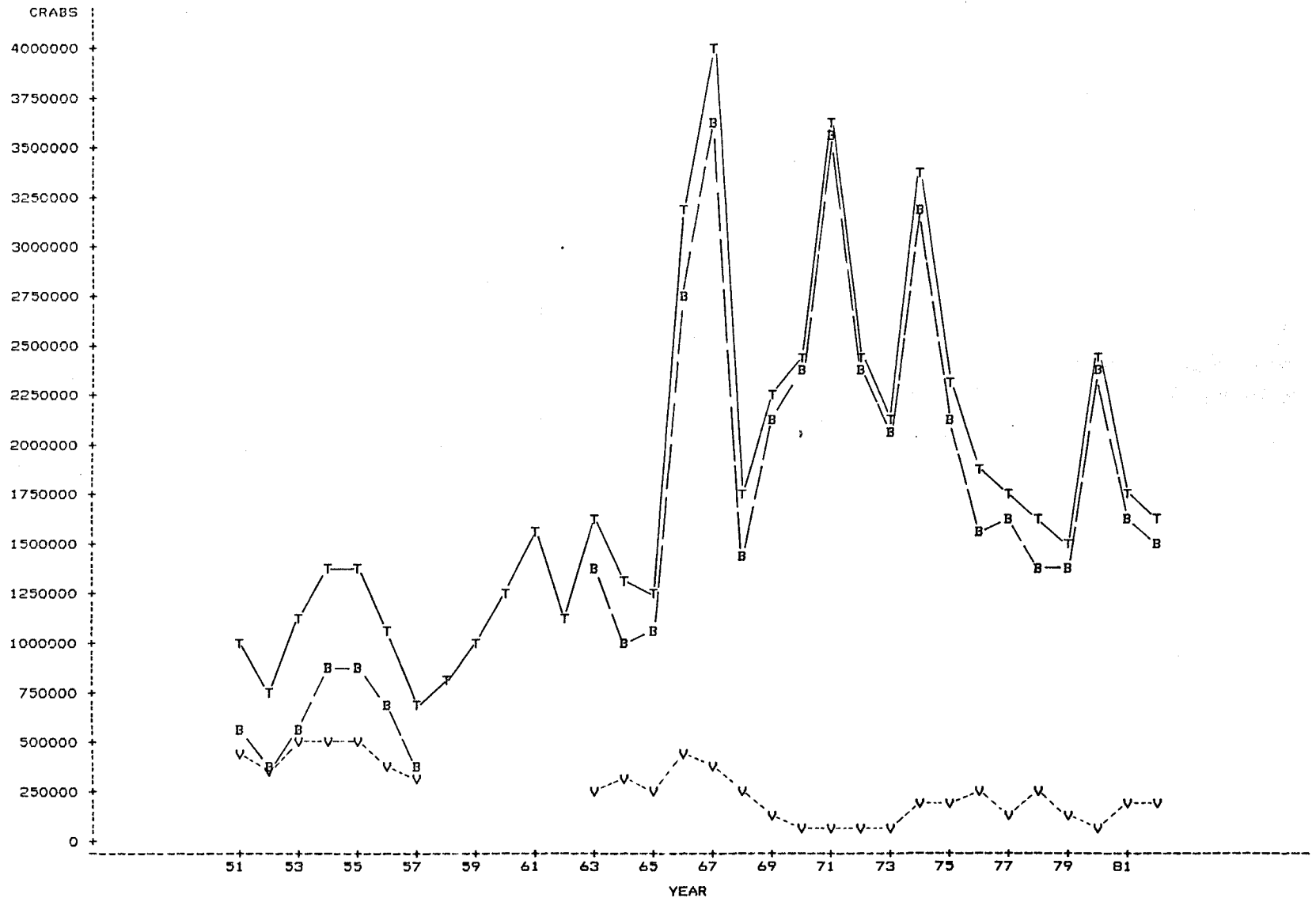


Figure 15. Commercial landings (pounds) of blue crabs (hard) in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982. From 1958 to 1962, landings data for the two counties were not reported separately.

Spot

Along the Atlantic coast north of Florida and the Gulf coast of northern Florida, juvenile spot are one of the most common components of salt marsh tidal creek fish assemblages (Subrahmanyam and Drake 1975; Weinstein 1979; Weinstein et al. 1980). However, they are notably absent from marshes in the southern part of the Indian River system (Harrington and Harrington 1961; Gilmore 1983). Consequently, the degree of their dependence on marshes in the vicinity of Merritt Island (or perhaps anywhere) is unclear. Stickney and Cuenco (1982) suggest that juvenile spot are "adapted to, and live in virtually all portions of estuaries", with habitat suitability decreasing with increasing depth.

The spot fishery in Volusia County remained small and stable from the 1950's to the 1980's (Fig. 16). Landings in Brevard County generally increased through the 1960's and declined in the 1970's but skyrocketed dramatically in the early 1980's (Fig. 16). The astronomical landings reported in 1982 were checked and confirmed by Ernie Snell of the National Marine Fisheries Service. Apparently, this species was underfished historically in the Merritt Island area and recently became more marketable. No evidence exists in these data to suggest that this fishery has been negatively impacted by impoundment of Merritt Island marshes.

Mullet

Juvenile mullet commonly inhabit salt marsh creeks and were selected as the indicator species for the transient fish guild in the WELUT AEA Workshop (Hamilton et al. 1985). Gilmore (1983) considered the striped mullet, Mugil cephalus (landings of which greatly exceeded those of white mullet, Mugil curema) a marsh dependent species.

Since the late 1950's, mullet landings in both counties were equivalent and constant (Fig. 17). Supply exceeds demand in this fishery (Cato et al. 1976) and fish house operators limit landings by assigning fishermen quotas (Anderson and Gehringer 1965; Snelson 1980). Therefore, the landings data do not reflect abundances of mullet in the Indian River system and offer no insight into the effects of impoundment on this fishery. However, it is apparent that current conditions in the system are adequate to maintain mullet stocks at levels resistant to overexploitation given current demand.

Florida pompano

Florida pompano do not regularly inhabit marshes, but do feed on organisms which commonly spend part of their life cycle in the marsh. Florida pompano command a high price (Anderson and Gehringer 1965) and are regularly sought by commercial fishermen. Because of this high demand, landings of Florida pompano (Fig. 18) probably reflect the relative abundances of this species in the Merritt Island area.

LANDINGS (LBS), BREVARD (B) AND VOLUSIA (V) COUNTIES, 1951-1982
 T = TOTAL OF BOTH COUNTIES COMBINED
 SPOT

PLOT OF SPOT*YEAR SYMBOL IS VALUE OF COUNTY

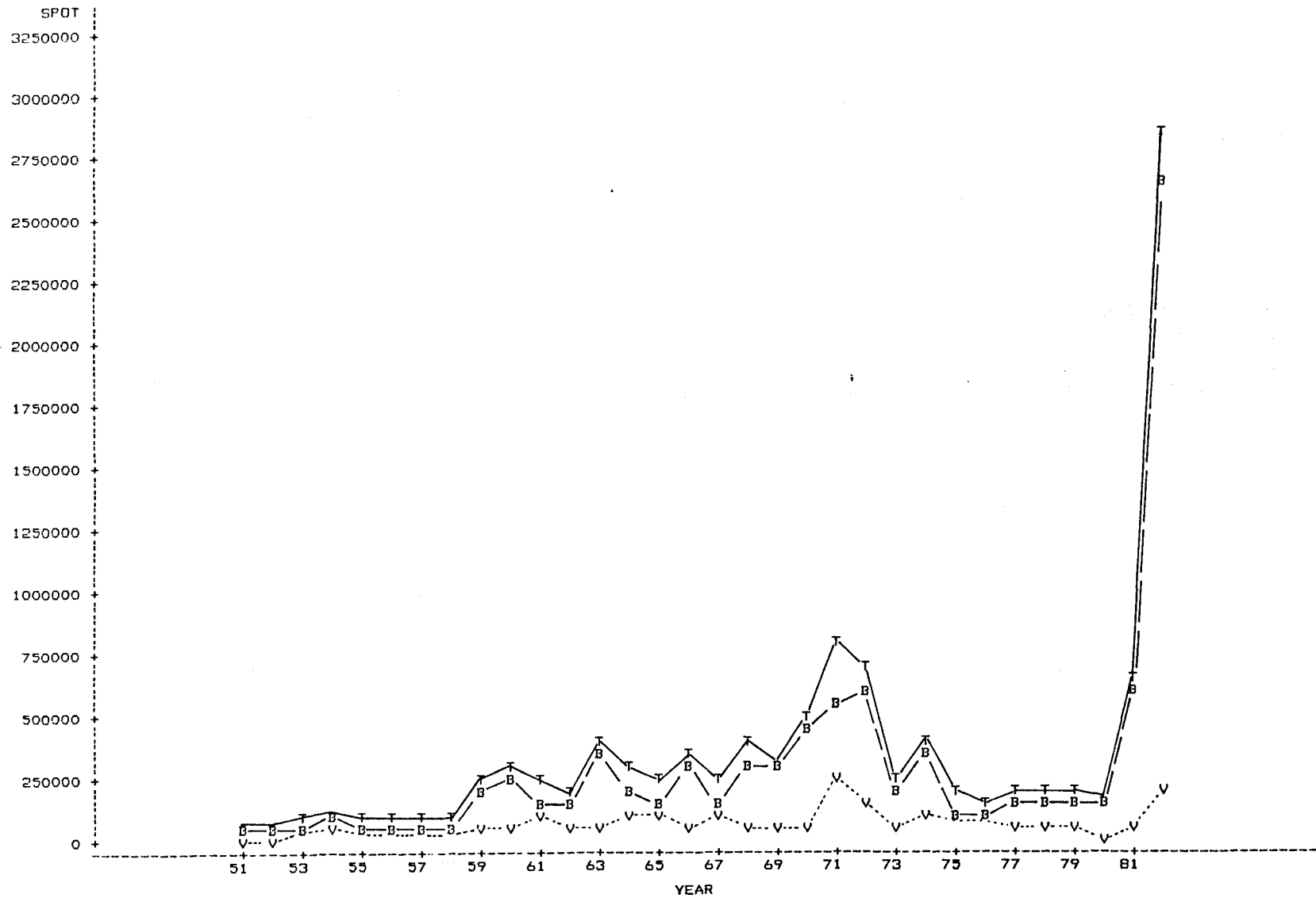


Figure 16. Commercial landings (pounds) of spot in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982. Note the substantial increase in landings in Brevard County in the 1980's.

LANDINGS (LBS), BREVARD (B) AND VOLUSIA (V) COUNTIES, 1951-1982
 T = TOTAL OF BOTH COUNTIES COMBINED
 MULLET: M. CUREMA AND M. CEPHALUS COMBINED
 PLOT OF MULLET*YEAR SYMBOL IS VALUE OF COUNTY

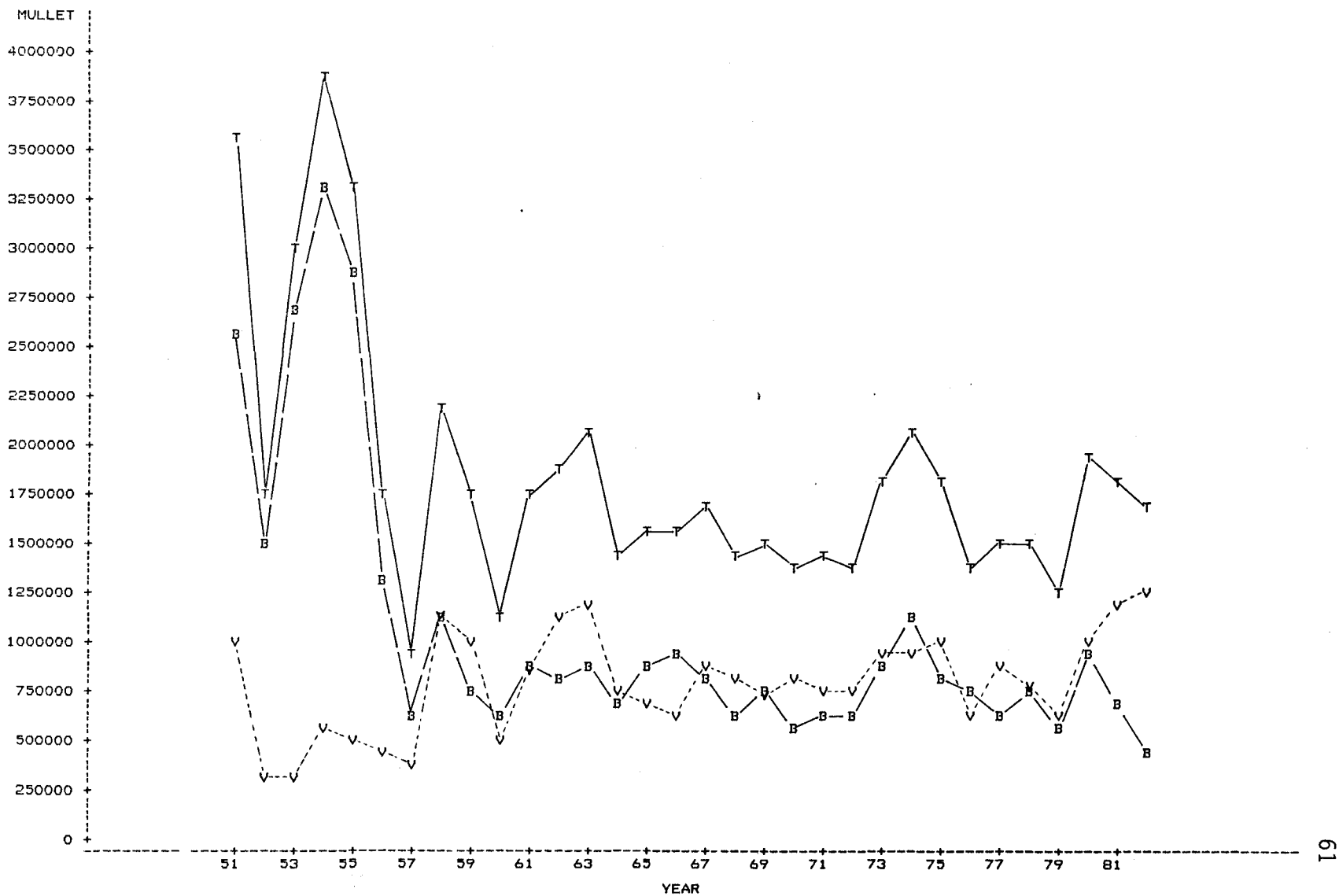


Figure 17. Commercial landings (pounds) of mullet (both white and striped combined) in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982.

LANDINGS (LBS), BREVARD (B) AND VOLUSIA (V) COUNTIES, 1951-1982
 T = TOTAL OF BOTH COUNTIES COMBINED
 POMPANO

PLOT OF POMPANO*YEAR SYMBOL IS VALUE OF COUNTY

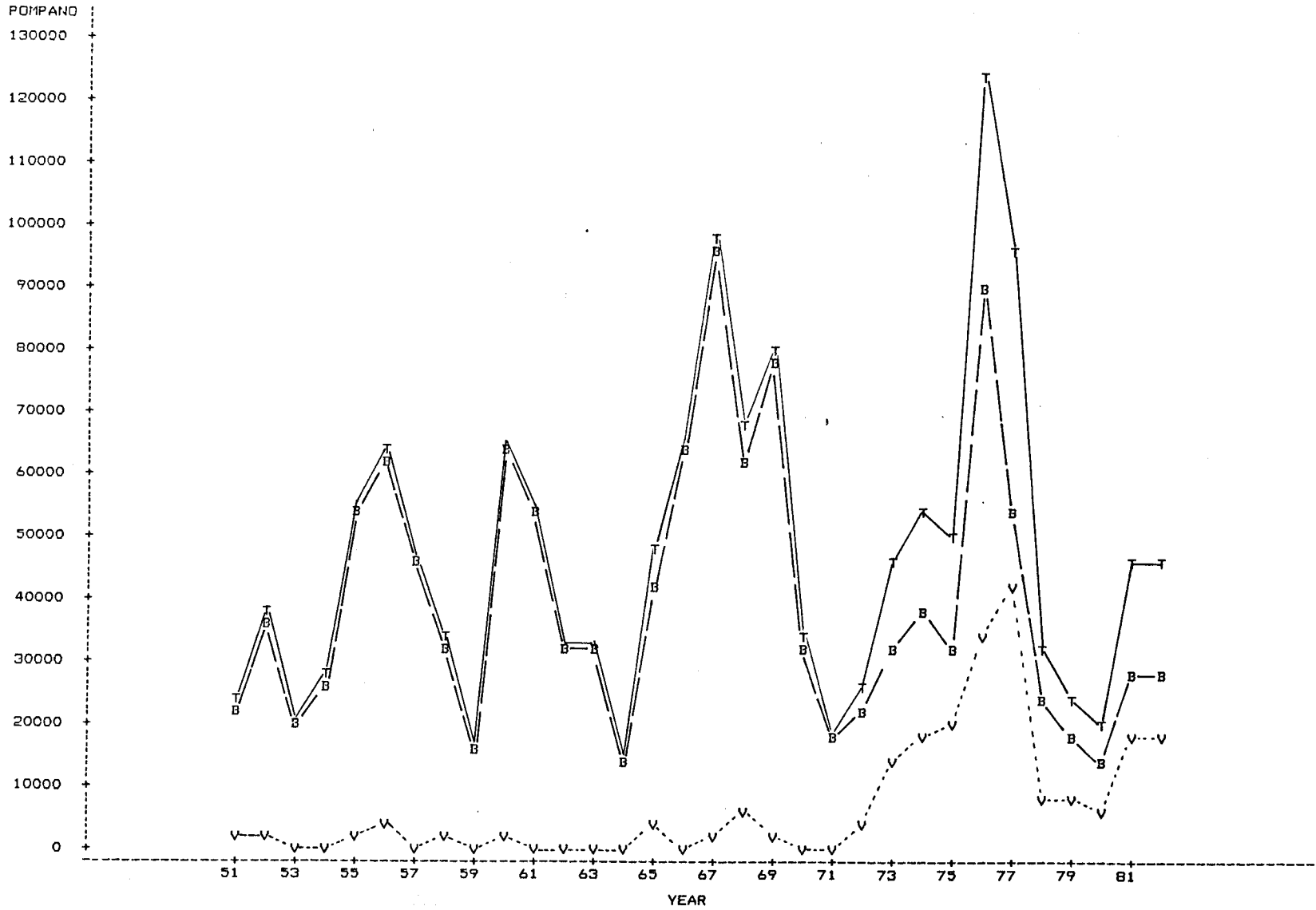


Figure 18. Commercial landings (pounds) of Florida pompano in Brevard (B), Volusia (V), and both counties combined (T), 1951 to 1982.

Until the mid-1970's, very few Florida pompano were landed in Volusia County, the bulk of landings in this area taking place in Brevard County. Since the 1950's, landings of Florida pompano oscillated regularly every few years, probably in response to density-dependent factors. No decline in the fishery following the 1959-1966 impoundment period is apparent. In fact, the fishery appears to have improved since this period.

Summary

With the exception of spotted seatrout in Brevard County, commercial landings data for the five dominant inshore fisheries of the Merritt Island area show no evidence of significant declines in these fisheries despite the impoundment of virtually all marshes in the area between 1959 and 1966. The spotted seatrout commercial landings may have declined because of increased recreational catch as suggested by the four-fold increase in registered pleasure boats between 1963 and 1984.

These findings are perhaps as much a reflection of the confounding of these data as they are an indication of the lack of effect of impoundments, but in any case the concern over fishery effects is not apparent in the actual commercial landings records. Confounding arises from concomitant changes in development, sportfishing pressure, climatic abnormalities, gear efficiency, market value, and regulations. However, the absence of dramatic declines and the presence of increases in some of these fisheries suggest that any effects of impoundment may be much more subtle or even different from the declines speculated.

Effects of Impoundments on Waterfowl

Demographically, two major factors - births and deaths - control population growth. In waterfowl management, the historical approach has been to provide and protect suitable breeding habitat, protect key wintering habitat, and regulate harvest. Increasing pressures on both breeding and wintering habitats, maintenance of hunter demand, and the realities of involvement with at least three nations and numerous state and provincial governments complicate continental management of waterfowl. Until Anderson and Burnham's (1976) classic publication on the subject, harvest of waterfowl was managed largely on the assumption that hunting mortality was additive to natural mortality and thus was negatively correlated with survival. The notion that hunting mortality of mallards is compensatory but may exceed some threshold and actually become additive to total annual mortality (Anderson and Burnham 1976) revolutionized waterfowl management. That notion was important in prompting increased attention to wintering waterfowl ecology and management and habitat preservation both in breeding and wintering habitats. The debate has now shifted (e.g. Nichols, et al. 1984) to examination of the reliability of the current evidence of compensatory mortality and its applicability to species other than the mallard.

Management to enhance waterfowl food plants has been described most extensively for such areas as Louisiana (e.g., Chabreck 1960; Yancey 1964; Joanen and Glasgow 1965; Baldwin 1967; Wicker et al. 1983) and the Carolinas (e.g., Neely 1960, 1968; Yancey 1964; Morgan 1974; Morgan et al. 1975; Heitzman 1978; Prevost et al. 1979; Miglarese and Sandifer 1982;

Swiderek et al. 1985). Techniques described as "moist soil management" are similar to the management of freshwater coastal impoundments and are currently being employed in inland impoundments (Green et al. 1964; Fredrickson et al. 1984; Fredrickson, pers. comm.). Managed impoundments provide food, cover, and security for waterfowl and are definitely attractive to them. Impoundment management is being used as a tool on refuges, wildlife management areas, and private hunting areas. In many cases we know the foods being used by waterfowl and they are generally the plants targeted for management. Fredrickson et al. (1984) calculated nutritional values of many of the native food plants encouraged by moist soil management and concluded (Fredrickson, pers. comm.) that such impoundments may provide more beneficial nutrition than grain crops which heretofore had been recommended for such situations. In addition, these natural foods can be produced in adequate supply much less expensively than by flooding grain crops. The water management techniques being employed for moist soil management are not unlike those long in use along the south Atlantic Seaboard in coastal impoundments. Fredrickson is providing a link between waterfowl management and waterfowl ecology.

Attractiveness of impoundments to waterfowl has beneficial aspects such as public viewing, control of hunting opportunity (and perhaps harvest), and possible energetic/nutritional benefits. Negative aspects include possible increases in harvest, increases in exposure to spent lead shot (Shillinger and Cottam 1937; Bellrose 1975; Baker and Thompson 1975; Feierabend 1983), and increased probability of disease. We know that waterfowl are attracted to Merritt Island National Wildlife Refuge. We do not have strong data to demonstrate a net gain of current populations over past populations, though Chamberlain (1960) and local authorities (e.g., J. Salmela, pers. comm.) suggest a positive response. Likewise, we do not know if the attractiveness of MINWR is actually competitive with other wetlands in the surrounding region nor, especially, whether we have actually enhanced continental populations.

For an individual area one may be able to demonstrate positive population responses. However, for the immediate regional population or the continental population we do not have the ability to determine impact. For the numbers attracted to a specific location there are areas from which an equal number were subtracted. Only when winter survival is enhanced has population growth been positively affected. Evidence exists for increasing populations of some Canada geese and snow geese populations which were attracted to more northern wintering habitats because of easy access to high energy foods and security of refuges. Obviously, those migrational shifts, referred to by some as "short-stopping", were advantageous to survival in these populations (see e.g., Crider 1967; Hankla and Rudolph 1967; Reeves et al. 1968). Geese are large, gregarious, visible, and limited in distribution; these factors allow ease of monitoring by aerial counts. Characteristics of most ducks are considerably different, and changes in population sizes or demography are much more difficult to detect.

Aspects surrounding effects on regional or continental populations are extremely elusive but nevertheless an important future research objective. For example, much effort has been expended on the question of compensatory mortality in waterfowl populations. This work has been done principally

using some of the largest and best banding and recovery data sets available for continental populations of waterfowl, yet even the foremost researchers in this area (Nichols et al. 1984) exercise caution in interpreting the results.

In the case of a private waterfowl hunting area, the latter concerns may not be, nor must they be, an issue to the owner and manager. For public areas, impacts on populations should be considered. At this point such consideration would be speculative but management decisions must often be made on speculation hopefully well spiced with intuition and logic.

Most waterfowl management of impoundments has been directed at wintering waterfowl. Limited opportunities exist for management of locally breeding species, notably the wood duck and mottled duck. In the case of Merritt Island, those opportunities are probably limited to the mottled duck. Montalbano (pers. comm.) suggests that nesting densities for this species is low throughout its range and suspects above range-wide average nesting densities on MINWR. Potential exists for successful management of breeding habitat for mottled ducks on MINWR (Johnson, pers. comm.) and efforts to enhance breeding success should be encouraged. More information is needed on breeding habitat requirements, brood ecology, and survival of locally produced birds to recommend breeding habitat management procedures.

Earlier studies of mottled ducks on MINWR indicated rather high nesting densities on spoil islands in the Indian River. Management of the islands to enhance mottled duck production was recommended (Stieglitz and Wilson 1968). Estimates of nesting densities for Merritt Island itself are not available, but most assuredly are low compared to the islands (W. Leenhouts, pers. comm.). Even in the case of known nesting on the spoil islands, estimates of recruitment are unavailable and are suspected to be low (F. Montalbano, pers. comm.). Any efforts to enhance breeding habitats for mottled ducks should be directed toward more freshwater areas until more information is available on brood survival in more saline habitats. Swanson et al. (1984) found that young ducklings could not survive at conductivities above 20 mmhos/cm in prairie lakes without access to fresh water. The lack of survival of ducklings produced on the islands could be due to salinity as well as a number of other factors - all of which should be investigated further before committing to their intensive management for mottled duck production.

Thomas (1982) suggests that wintering mottled ducks use different habitat types than do other waterfowl. Though these observations were inconclusive, the hypothesis that mottled ducks have special wintering habitat requirements is certainly worth investigation if this species became the subject of intensive management on Merritt Island.

Research information on wintering waterfowl and other migratory birds is seriously lacking. Anderson (1976) and Fretwell (1972) both indicated the need for such data and Rogers (1979) emphasized the importance of an understanding of total annual mortality. The reasons for this void of knowledge are attributable to the past philosophy of migratory bird management which was centered on the reproductive cycle (Pospahala et al. 1974). That focus probably was engendered because of serious, rapid, and conspicuous alteration of surrounding habitat that was occurring in the 1930's - 50's, particularly within the prairie pothole regions of the mid-western

U.S. and south-central Canada. Any changes within the wintering range at that time were small in scale, isolated, and resultingly inconspicuous. However, in the late '60's and '70's, technology allowed significant and large scale alteration of wintering range habitats such as coastal ecosystems (Tiner 1984) and bottomland hardwoods (Harris et al. 1984).

These changes precipitated accelerated research beginning circa 1975. Only 8 percent of over 2500 titles of publications on waterfowl and wetlands reviewed by Reinecke (1981) involved study within the wintering range of waterfowl. Our own experience with that small volume of literature indicates that the majority relate to habitat management techniques to attract wintering waterfowl. Those studies which concerned waterfowl biology were generally on wood ducks and mottled ducks and these principally involved the reproductive cycle as well. In the recent symposium, Waterfowl in Winter, held in January 1985, in Galveston, TX, a wealth of papers were presented. In a 10 year span, considerable progress has been made toward filling the void, though not sufficiently to elucidate many of the arguments surrounding coastal impoundments.

This surging interest in avian wintering ecology indicates that birds have special requirements in wintering habitats as well as those that have been identified for the breeding season. Jeske and Percival (1985) suggest that waterfowl have evolved "wintering strategies" that are expressed in a complex combination of characteristics such as anatomy, migration distance, and survival rates. White and James (1978) and Thomas (1982) have shown that waterfowl species are spatially distributed within specific wintering habitats and probably have varying habitat requirements. Alexander and Hair (1979) and Alexander (1983) have shown that even sexes of the same species may vary in geographical distribution and habitat use. More recent evidence for niche separation among species and between sexes have been based on morphometric variation (Livezey and Humphrey 1984; Nudds and Bowlby 1984; Nudds and Kaminsky 1984).

Three geographic areas and impoundments specific to these areas can be defined: the coastal deltaic marshes of Louisiana; coastal marshes and abandoned rice fields of Georgia and the Carolinas; and impounded high marsh and mangrove of eastern Florida. Whereas impoundments of the former two areas have been managed specifically for wildlife - namely waterfowl, furbearers, and crayfish - the latter were designed to control nuisance salt marsh mosquitos. In these situations, attractiveness to wildlife has been a serendipity to mosquito control objectives and impoundment management has been opportunistic around the schedule designed for effective mosquito control rather than specifically managed for waterfowl.

Effective management of wetlands depends on control of salinity and water levels. In the absence of control over salinity, water level management is essential for intensive management of desired waterfowl food plants. In the case of MINWR, most of the impoundments were previously "grassy" marshes which are high elevation, infrequently flooded wetlands. In this area, "lunar tidal action is negligible" (Stieglitz and

Wilson 1968) and these marshes are usually flooded only on storm tides and in the fall when water levels are normally higher. As such, water control is expensive to attain (compared to many of the coastal impoundments in Georgia, Louisiana, and the Carolinas, for example) since pumping or distribution of stored rain water are required for flooding. In addition, many of the impoundments are extremely large which complicates the ability to manage water for most effective plant management. Nevertheless, MINWR impoundments have provided an immense amount of waterfowl habitat when, in other areas of the State, some waterfowl habitat has been degraded.

The ecological value of impoundments is currently being debated. Obviously, for any management action, one is faced with acceptance of the consequences as well as the rewards for those actions. In many cases consequences may be mitigated to some degree but never fully mitigated at least not until they are identified. We can identify some of these trade-offs, but in most cases we cannot determine the magnitude. Based on the options available a number of consequences and alternatives are possible. Management alternatives which provide positive benefits for mosquito control, wildlife, and fisheries are possible but will require innovation and commitment.

MANAGEMENT OPTIONS FOR MARSHES ON MERRITT ISLAND NATIONAL WILDLIFE REFUGE

The current objectives of marsh management on MINWR are to preserve, maintain, enhance, and restore marsh and aquatic wildlife habitat and populations and to provide opportunity for wildlife-oriented recreation while maintaining established mosquito-control health and safety standards (Leenhouts 1983).

Specific objectives listed by Leenhouts (1983) are: 1) to maintain saltmarsh mosquito populations at levels which do not pose health or safety dangers to populated areas of Brevard and Volusia counties or to work areas of the Kennedy Space Center; 2) to maintain wildlife productivity and diversity within marine communities at 1980 levels; 3) to provide habitat for endangered and threatened species of plants and animals and migratory and resident wildlife according to established USFWS policy; 4) to optimize wildlife and wildlife habitat productivity and diversity within the mosquito control impoundments; and 5) to provide opportunities for wildlife oriented recreation and interpretation in marsh and aquatic habitats open to public access.

To date, the primary objective of marsh management on MINWR has been mosquito control. Its successful achievement by impoundment of marshlands has eliminated the use of insecticides (only mosquito-specific hormonal larvicides are used currently). Impoundment has been considered the best mosquito-control strategy to date (Brevard Mosquito Control District 1951; Florida Anti-mosquito Association 1970; correspondence from J. Salmela to D. Carlson, 23 July 1984). In addition, the impoundments provide habitat for a variety of fish and wildlife and provide distinct areas of marsh that may be used for other purposes (e.g., wastewater treatment, controlled access and observation points for hunters, anglers, and wildlife observers).

With a wide range of management objectives in mind, the following management alternatives are identified and discussed. The first four alternatives are currently practiced on some of more than 20,000 acres of MINWR marshes. The remainder are suggested in addition to these. These alternatives should promote discussion resulting in research and management trials leading to satisfactory multiple-objective management of marshes on MINWR.

Options

Permanent Flooding

This option entails closure of water-control structures throughout the year, except when water levels in the estuary exceed those in the impoundment. Flooding of the marsh is maintained at all times (via rainfall-capture, pumping, and passive estuarine inflow) to control saltmarsh mosquitos and provide habitat and foods (especially *Chara*) for wintering waterfowl. *Chara* grows best with constant inundation (Leenhouts pers. comm.). This option corresponds to that exercised on most MINWR marshes in the past. Currently, over 16,000 acres of MINWR improvements are scheduled for this type of management (MINWR Annual Water Management Program 1985).

There include several very large impoundments (T-16, 17, 18, and T-24-D). Although effective for mosquito control, waterfowl attraction, and freshwater fish management (in low salinity impoundments), it severely limits the accessibility of the marshes to estuarine fish and shellfish and inhibits or precludes growth of natural saltmarsh vegetation.

Impoundment Elimination

Removal of all dikes as was done in T-10-K would come closest to restoring MINWR marshes to a natural state, allowing growth of natural saltmarsh vegetation and access by estuarine fish and shellfish. However, it would also restore natural abundances of saltmarsh mosquitos and decrease habitat for wintering waterfowl and freshwater sportfish. Open marsh water management techniques could be instituted to negate the resultant mosquito problem, but perhaps not nearly as effectively as did impoundment (letter from J. Salmela to D. Carlson, 23 July 1984).

Vestigial Impoundments

By removing portions of dikes, or leaving all water-control structures open at all times, an effect similar to that brought about by impoundment elimination could be produced, but perimeter ditches would remain intact. These would serve as additional habitat for estuarine fish and shellfish and also would provide some protected, albeit minimal, aquatic habitat for wintering waterfowl. This option would also facilitate restoration of water control in the future if desired. The beach impoundments T-38, T-39, T-39-South and the "salt cell" (T-10-H) are currently of this type on Merritt Island.

Seasonal Flooding

In this option (proposed by Clements and Rogers 1964; Provost 1973b, and Lewis et al. in press), water-control structures are kept closed during the mosquito breeding season (about May to October) whenever estuarine water levels are below those in impoundments to ensure adequate mosquito control by keeping the marshes flooded. Estuarine inflows, pumping, and rainwater capture are used to maintain impoundment water levels. At the end of the mosquito breeding season (October), water-control structures are opened and remain so until the following May (or later if adequate pumping is available so that water does not have to be stockpiled in anticipation of later needs; J. Salmela, pers. comm.) thereby allowing water levels to fluctuate naturally. During this period, estuarine organisms can enter the marshes with the fall rise in water levels and use the cover and food found therein (though the marsh will generally be dry). Egress is possible when water levels decline or during cold weather. This option provides adequate mosquito control, restores the nursery value of the marsh, and allows perpetuation of natural saltmarsh vegetation. However, it results in less flooded area for both fish and wintering waterfowl, precludes development of *Chara*, and, by increasing salinity, renders the habitat unsuitable for freshwater sportfish.

Seasonal Flooding With Added Potholes

This option modifies the seasonal flooding strategy via the addition of man-made potholes (e.g., by blasting; Provost 1948). It offers the same

advantages of seasonal flooding but mitigates the deleterious effect on wintering waterfowl by producing more potential waterfowl habitat and Chara-producing areas. None of the MINWR marshes are currently managed in this way.

Leaky Impoundments

In this option, water-control structures are modified to allow constant, but limited, water exchange with the estuary by replacement of a lower riser board with chock blocks. A prescribed water level in the impoundment is maintained by constant pumping with a small pump, or the level is allowed to fluctuate between limits by intermittent pumping with a large pump. All riser boards can be removed during the peak of the fall inundation. This option provides mosquito control, acceptable habitat for wintering waterfowl and Chara production, and at least some opportunity for ingress and egress by estuarine fish and shellfish. However, it would result in the removal of habitat for freshwater sportfish and would most likely impair production of natural saltmarsh vegetation. This management strategy would be expensive and time-consuming, but would satisfy, at least in part, demand for the three major uses of MINWR marsh areas impacted by impoundments: mosquito control, wintering waterfowl attraction, and estuarine fish and shellfish nursery habitat. Although continuous free access by estuarine fish and shellfish would perhaps be at most times less than in a natural marsh, the availability of aquatic habitat in the marsh throughout the year might mitigate this difference.

Intensive Management For Waterfowl Foods

In this option, small impoundments, or diked-off sections of large impoundments (subimpoundments), would be intensively managed for preferred duck foods such as Ruppia, Chara, Sesuvium, or Scirpus robustus. Currently, waterfowl food management in MINWR marshes is largely a serendipity of mosquito control, and is relatively ineffective compared to impoundments elsewhere managed specifically for waterfowl foods. Intensive management of small areas may provide amounts of duck food comparable to those currently produced throughout the refuge. Concentration of waterfowl in such areas might also enhance recreational opportunities. Because only a small acreage of marsh would be managed in this fashion, deleterious impacts on other uses would be negligible. This option is particularly attractive if modifications in the management of other impoundments results in decreased waterfowl food production there.

Integrated Marsh Management

This option requires: 1) determination of the desired uses of marshes on MINWR (e.g., mosquito control, attraction of wintering waterfowl, nursery areas for estuarine fish and shellfish, maintenance of depleted or scarce habitat wildlife observation, sportfishing, endangered and threatened species management, wastewater treatment); 2) determination of the relative importance of each of these uses; 3) allocation of areas of marsh to each of these uses by their perceived importance; and 4) appropriate management of these areas, possibly by the options listed above. For example, areas within 4 miles of human activity centers could be managed primarily for mosquito control, areas frequented by refuge

visitors could be managed for waterfowl or other wildlife, etc. Management of each impoundment, or formerly impounded area, would be tailored to the specific use or combination of uses dictated for that area. Determination of the best areas for some uses (e.g., best nursery areas for estuarine fish and shellfish) would be difficult to predict a priori and would require monitoring and comparisons. Integrated marsh management would result in multiple-objective management of MINWR marshes for all uses deemed desirable or necessary. Both simultaneous multiple-objective management within marshes and multiple objective management among marshes for specialized purposes are possible.

RESEARCH AND DATA NEEDS

The paucity of scientifically collected data on impoundments and natural marshes in the Merritt Island area, together with the singularities of Merritt Island marshes (regime of inundation, sediments, climate, vegetation, lack of water movement) necessitate original data collection and analysis before any speculations and deductions (including those presented in this report) can be reliably applied. Below is a brief list of experiments and correlation analyses that if performed would considerably enhance understanding of the energetics, biogeochemistry, fish and wildlife use, and effects of various perturbations and management schemes in Merritt Island marshes (natural and impounded), and the relationship of these marshes to adjacent estuarine water.

1. Understand impounded salt marsh under different management regimes:
 - a) fish and wildlife use, including estuarine fish and shellfish
 - b) overall primary production
 - c) macrophyte diversity
 - d) relationship to estuary (import/export of biota, chemical constituents, detritus).
2. Comparison of impounded and unimpounded marsh with respect to above.
3. Quantitative determination of limiting nutrients and assessment of potential energy subsidies (wind, water movement) and stresses (salinity) on overall primary production.
4. Assessment of the influences of degree of temporal and spatial variability in water level and salinity on diversity of macrophytes.
5. Determine pump-passage mortality of estuarine biota.
6. Determine the optimal ditch density or edge per unit area of marsh.
7. Assess the use of man-made (blasted) potholes in natural marsh as a water and marsh bird management technique.
8. Track crude vegetative changes with an annual fly-over and correlate changes to management and environment. The level of detail included in such fly-overs must be chosen by considering the need for a time frame that can allow efficient adjustments in management. Detailed mapping of vegetation, while useful, is not essential for this purpose; rapid promulgation of results is.
9. Management trials should be accompanied by record keeping of what was done. Minimize confounding so that the effects of particular techniques can be evaluated. Response variables ideally should include:
 - a) water level
 - b) salinity
 - c) diurnal dissolved oxygen (or possibly dusk-dawn)
 - d) fish and wildlife use including estuarine biota
 - e) macrophyte diversity (number of species, % cover of each)
 - f) flux of chemical constituents and detritus to and from estuary.

LITERATURE CITED

- Alexander, W.C. 1983. Differential sex distributions of wintering diving ducks (Aythyini) in North America. *American Birds* 37:26-29.
- Alexander, W.C., and J.D. Hair. 1979. Winter foraging behavior and aggression of diving ducks in South Carolina. *Proc. Annu. Conf. S.E. Assoc. Fish and Wildl. Agencies* 31:226-232.
- Anderson, D.R., and K.P. Burnham. 1976. Population ecology of the mallard. VI. The effect of exploitation on survival. U.S. Fish and Wildlife Service Resource Publ. 128. Washington, D.C. 66 pp.
- Anderson, W.W., and J.W. Gehringer. 1965. Biological-statistical census of the species entering fisheries in the Cape Canaveral area. U.S. Fish and Wildlife Service Special Scientific Report - Fisheries No. 514. 79 pp.
- Aston, S.R. 1980. Nutrients, dissolved gases, and general biogeochemistry in estuaries. Pages 233-262 in E. Olausson and I. Cato (eds.). *Chemistry and Biogeochemistry of Estuaries*. John Wiley and Sons, New York, NY.
- Bahr, L.M. 1976. Energetic aspects of the intertidal oyster reef community at Sapelo Island, Georgia. *Ecology* 57:121-131.
- Bahr, L.M., and W.P. Lanier. 1981. The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-81/15. 105 pp.
- Baldwin, W.P. 1967. Impoundments for waterfowl on south Atlantic and Gulf coastal marshes. Pages 127-133 in J.D. Newsom, ed., *Proceedings of the marsh and estuary management symposium*. Louisiana State Univ., Baton Rouge.
- Ballard, R.W. 1977. Notes on a major oceanographic find. *Oceanus* 20:35-44.
- Beckman, D.W., and J.M. Dean. 1984. The age and growth of young-of-the-year spot, Leiostomus xanthurus Lacepede, in South Carolina. *Estuaries* 7:487-496.
- Bellrose, F. 1975. Impact of ingested lead pellets on waterfowl. Pages 163-167 in *Proc. 1st Int. Waterfowl Symp., Ducks Unlimited*, St. Louis, MO.
- Bidlingmayer, W.L. 1982. Surveying salt marsh mosquito control impoundments in central Florida. *J. Florida Anti-mosquito Assoc.* 53(1):4-7.

- Blum, J.L. 1969. Nutrient changes in water flooding the high salt marsh. *Hydrobiologia* 34: 95-99.
- Boesch, D.F., and R.E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7:460-468.
- Borey, R.B., P.A. Harcombe, and F.M. Fisher. 1983. Water and organic carbon fluxes from an irregularly flooded brackish marsh on the upper Texas coast, U.S.A. *Estuarine, Coastal and Shelf Science* 16:379-402.
- Bozeman, E.L., Jr., and J.M. Dean. 1980. The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek. *Estuaries* 3:89-97.
- Brevard Mosquito Control District. 1951. Policy of the Florida State Board of Health pertaining to present mosquito control practices and recommendations for a long-range plan to bring about more effective control in the state. Adopted by Florida State Board of Health 18 November 1951. 12 pp.
- Britton, R.H., and M.E. Moser. 1982. Size specific predation by herons and its effect on the sex-ratio of natural populations of the mosquito fish Gambusia affinis Baird and Girard. *Oecologia* 53: 146-151.
- Brock, T.D. 1979. *Biology of microorganisms*. Prentice-Hall, Inc. Englewood Cliffs, NJ.
- Browder, J.A., H.A. Bartley, and K.S. Davis. Unpublished manuscript. A probabilistic model of the relationship between marshland-water interface and marsh disintegration. 18 pp.
- Buresh, R.J., R.D. DeLaune, and W.H. Patrick, Jr. 1980. Nitrogen and phosphorus distribution and utilization by Spartina alterniflora in a Louisiana Gulf coast marsh. *Estuaries* 3:111-121.
- Burkholder, P.R., and G.H. Bornside. 1957. Decomposition of marsh grass by aerobic marine bacteria. *Bull. Torrey. Bot. Club* 84: 366-383.
- Burns, R.W. 1974. Species abundance and diversity of larval fishes in a high-marsh tidal creek. MS Thesis, Univ. of South Carolina, Columbia, SC.
- Byron, M.M. 1968. Net nutrient exchange between high marsh areas and an estuary. M.S. Thesis, North Carolina State University, Raleigh, North Carolina. 22 p.
- Cadle, R.D., and E.R. Allen. 1970. Atmospheric photochemistry. *Science* 167:243-249.

- Cain, R.L., and J.M. Dean. 1976. Annual occurrence, abundance, and diversity of fish in a South Carolina tidal creek. *Mar. Biol.* 36:369-379.
- Carlson, D.B. 1983. The use of salt-marsh mosquito control impoundments as wastewater retention areas. *Mosquito News* 43:1-6.
- Cato, J.C., P.B. Youngberg, and R. Raulerson. 1976. Production, prices, and marketing: an economic analysis of the Florida mullet fishery. Pages 15-62 in J.C. Cato and W.E. McCullough (eds.). *Economics, biology, and food technology of mullet*. Florida Sea Grant Progress Report No. 15.
- Chabreck, R.H. 1960. Coastal marsh impoundments for ducks in Louisiana. *Proc. Ann. Conf. S.E. Assoc. Game Fish Comm.* 14:24-29.
- Chamberlain, E.B., Jr. 1960. Florida waterfowl populations, habitats, and management. *Fla. Game and Fresh Water Fish Comm. Tech. Bull.* No. 7, 62 p.
- Chynoweth, L.A. 1975. Net primary production of *Spartina* and species diversity of associated macroinvertebrates of a semi-impounded salt marsh. Tech. Rep. No. 1, Grant No. NGR 10-019-009. National Aeronautics and Space Administration, Kennedy Space Center, Florida. 147 pp.
- Clements, B.W., Jr., and A.J. Rogers. 1964. Studies of impounding for the control of salt marsh mosquitos in Florida, 1958-1963. *Mosquito News* 24:265-276.
- Costanza, R., C. Neill, S.G. Leibowitz, J.R. Fruci, L.M. Bahr, Jr., and J.W. Day, Jr. 1983. Ecological models of the Mississippi Deltaic Plain Region: data collection and presentation. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, DC FWS/OBS-82/68. 342 pp.
- Crabtree, R.E., and J.M. Dean. 1982. The structure of two South Carolina estuarine tidal pool fish assemblages. *Estuaries* 5:2-9.
- Currin, B.M., J.P. Reed, and J.M. Miller. 1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: a comparison of tidal and nontidal nursery areas. *Estuaries* 7:451-459.
- Dahlberg, M.D. 1972. An ecological study of Georgia coastal fishes. *Fish. Bull.* 70:323-353.
- Daiber, F.C. 1974. Salt marsh plants and future coastal salt marshes in relation to animals. Pages 475-508 in R.J. Reimold and W.H. Queen (eds.). *Ecology of halophytes*. Academic Press, Inc., New York, NY.
- Dame, R.F. 1976. Energy flow in an intertidal oyster population. *Estuarine and Coastal Marine Science*. 4:243-283.

- Dame, R.F. 1979. The abundance, diversity and biomass of macrobenthos on tidal oyster reefs. *Proc. Natl. Shellfish. Assoc.* 69:6-10.
- Dame, R.F., and D. Stilwell. 1984. Environmental factors influencing macrodetritus flux in North Inlet Estuary. *Estuarine, Coastal and Shelf Science* 18:721-726.
- Dankers, N., M. Binsbergen, K. Zegers, R. Laane, and M.R. van der Loeff. 1984. Transportation of water, particulate and dissolved organic and inorganic matter between a salt marsh and the Ems-Dollard Estuary, the Netherlands. *Estuarine and Coastal Shelf Science* 19:143-165.
- Darley, W.M., C.L. Montague, F.G. Plumley, W.W. Sage, and A.T. Psalidas. 1981. Factors limiting edaphic algal biomass and productivity in a Georgia salt marsh. *J. Phycol.* 17:122-128.
- Darnell, R. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. *Publ. Inst. Mar. Sci. Univ. Tex.* 5:353-416.
- Darnell, R. 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology* 42:553-568.
- DeLaune, R.D., and W.H. Patrick, Jr. 1980. Rate of sedimentation and its role in nutrient cycling in a Louisiana salt marsh. Pages 401-412 in P. Hamilton and K.B. MacDonald (eds.). *Estuarine and wetland processes with emphasis on modeling.* Marine science series, Vol. 11. Plenum Press, New York, NY.
- Delwiche, C.C. 1970. The nitrogen cycle. Pages 71-80 in *The biosphere, a collection of reprints from Scientific American.* W.H. Freeman, San Francisco.
- Dransfield, P. 1968. *Engineering systems and automatic control.* Prentice-Hall, Inc. Englewood Cliffs, NJ. 429 pp.
- Dubbelday, P.S. 1975. Lagoonal circulation. Ch. 3 in *An ecological study of the lagoons surrounding the John F. Kennedy Space Center Brevard County, Florida, April 1972 to September 1975.* Volume I. Experimental results and conclusions. December 31, 1975. Final report to NASA from Florida Institute of Technology, Project #NGR 10-015-008.
- East Central Florida Regional Planning Council. 1975a. *Florida Regional Coastal Zone Management Atlas, Region 6, East Central Florida.* Bureau of Coastal Zone Planning, Division of Resource Management, Florida Department of Natural Resources.
- East Central Florida Regional Planning Council. 1975b. *Florida Regional Coastal Zone Environmental Quality Assessment. Region 6, East Central Florida.* Bureau of Coastal Zone Planning, Division of Resource Management, Florida Department of Natural Resources.

- Emlen, J.M. 1973. Ecology: an evolutionary approach. Addison-Wesley, Reading, Mass. 493 pp.
- Feierabend, J.S. 1983. Steel shot and lead poisoning in waterfowl. National Wildlife Federation Scientific and Technical Services No. 8. 62 pp.
- Ferrigno, F. 1970. Preliminary effects of open marsh water management on the vegetation and organisms of the salt marsh. Proc. Ann. Mtg. N.J. Mosq. Exterm. Assoc. 57:79-94
- Ferrigno, F., and D.M. Jobbins. 1968. Open marsh water management. Proc. Ann. Mtg. N.J. Mosq. Exterm. Assoc. 55:104-115.
- Ferrigno, F., L.G. MacNamara, and D.M. Jobbins. 1969. Ecological approach for improved management of coastal meadowlands. Proc. Ann. Mtg. N.J. Mosq. Exterm. Assoc. 56:188-202.
- Fisher, R.A., A.S. Corbet, and C.B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 12:42-58.
- Florida Anti-mosquito Association. 1970. Statement of policy on mosquito control in Florida. Concurred in by the Bureau of Entomology, Division of Health, Department of Health and Rehabilitative Services. 3 pp.
- Fredrickson, L., M. Heitmeyer, and F. Reid. 1984. Applications of moist-soil management techniques for waterfowl management. Information Transfer Update, Office of Information Transfer, U.S. Fish and Wild. Serv., Ft. Collins, CO. 79 pp.
- Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton Univ. Press. Princeton, NJ. 217 pp.
- Fritz, E.S., W.H. Meredith, and V.A. Lotrich. 1975. Fall and winter movements and activity level of the mummichog, Fundulus heteroclitus, in a tidal creek. Chesapeake Science 16:211-214.
- Fry, B. 1981. Natural stable carbon isotope tag traces Texas shrimp migrations. Fish. Bull. 79:337-345.
- Gallagher, J.L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of Spartina alterniflora and Juncus roemerianus. Amer. J. Bot. 62:644-648.
- Gallagher, J.L., R.J. Reimold, R.A. Linthurst, and W.J. Pfeiffer. 1980. Aerial production, mortality, and mineral accumulation-export dynamics in Spartina alterniflora and Juncus roemerianus plant stands. Ecology 61:303-312.
- Gardner, L.R. 1975. Runoff from an intertidal marsh during tidal exposure: regression curves and chemical characteristics. Limnol. Oceanogr. 20:81-89.

- Gilmore, R.G. 1983. Fishes and macrocrustacean population dynamics in a tidally influenced impounded sub-tropical marsh. in D.B. Carlson, R.G. Gilmore, and J. Rey. Impoundment management. Final Report: CM-47 and CM-73. unpublished report to Florida Department of Environmental Regulation, Coastal Zone Management Department.
- Gilmore, R.G., D.W. Cooke, and C.J. Donohoe. 1982. A comparison of the fish populations and habitat in open and closed salt marsh impoundments in east-central Florida. *Northeast Gulf Science* 5:25-37.
- Gilmore, R.G., C.J. Donohoe, and D.W. Cooke. 1983. Observations on the distribution and biology of east-central Florida populations of the common snook, Centropomus undecimalis (Bloch). *Fla. Sci.* 46: 313-336.
- Gosselink, J.G. and C.J. Kirby. 1974. Decomposition of salt marsh grass Spartina alterniflora Loisel. *Limnol. Oceanogr.* 19:825-832.
- Gosselink, J.G., E.P. Odum, and R.M. Pope. 1973. The value of the tidal marsh. Center for Wetland Resources, Louisiana State University, Baton Rouge, LA. 30 pp.
- Green, W.E., L.G. MacNamara, and F.M. Uhler. 1964. Water off and on. Pages 557-568 in J.P. Linduska (ed.). *Waterfowl tomorrow*. U.S. Dept. of Interior, Washington, D.C. 770 pp.
- Haines, B.L., and E.L. Dunn. 1976. Growth and resource allocation responses of Spartina alterniflora Loisel to three levels of $\text{NH}_4\text{-N}$, Fe, and NaCl in solution culture. *Bot. Gaz.* 137:224-230.
- Haines, E.B. 1977. The origins of detritus in Georgia salt marsh estuaries. *Oikos* 29:254-260.
- Haines, E.B. 1979a. Growth dynamics of cordgrass, Spartina alterniflora Loisel., on control and sewage sludge fertilized plots in a Georgia salt marsh. *Estuaries* 2:50-53.
- Haines, E.B. 1979b. Interactions between Georgia salt marshes and coastal waters: a changing paradigm. Pages 35-46 in R.J. Livingston (ed.). *Ecological processes in coastal and marine systems*, Plenum, New York, NY.
- Haines, E.B., A. Chalmers, R. Hanson, and B. Sherr. 1977. Nitrogen pools and fluxes in a Georgia salt marsh. Pages 241-254 in M. Wiley (ed.). *Estuarine processes*, Vol. II, Academic Press, New York, NY.
- Haines, E.B., and R.B. Hanson. 1979. Experimental degradation of detritus made from the salt marsh plants Spartina alterniflora Loisel, Salicornia virginica L. and Juncus roemerianus Scheele. *J. Exp. Mar. Biol. Ecol.* 40:27-40.

- Haines, E.B., and C.L. Montague. 1979. Food sources of estuarine invertebrates analyzed using $^{13}\text{C}/^{12}\text{C}$ ratios. *Ecology* 60: 48-56.
- Hamilton, D.B., A.K. Andrews, G.T. Auble, R.A. Ellison, A.H. Farmer, and J.E. Roelle. 1985. Environmental systems and management activities on the Kennedy space Center, Merritt Island, Florida: results of a modeling workshop. USFWS, Western Energy and Land Use Team, WELUT-85/W05, 130 pp.
- Hanson, R.B. 1977a. Comparison of nitrogen fixation activity in tall and short *Spartina alterniflora* salt marsh soils. *Appl. Environ. Microbiol.* 33:596-602.
- Hanson, R.B. 1977b. Nitrogen fixation (acetylene reduction) in a salt marsh amended with sewage sludge and organic carbon and nitrogen compounds. *Appl. Environ. Microbiol.* 33:846-852.
- Hanson, R.B. 1982. Organic nitrogen and caloric content of detritus II. Microbial biomass and activity. *Est. Coast. Shelf Sci.* 14: 325-336.
- Hardisky, M.A., R.M. Smart, and V. Klemas. 1983. Growth response and special characteristics of a short *Spartina alterniflora* salt marsh irrigated with freshwater and sewage effluent. *Remote sensing of Environment* 13:57-67.
- Harrington, R.W., Jr., and E.S. Harrington. 1961. Food selection among fishes invading a high subtropical salt marsh: from onset of flooding through progress of a mosquito brood. *Ecology* 42:646-666.
- Harrington, R.W., Jr., and E.S. Harrington. 1982. Effects on fishes and their forage organisms of impounding a Florida salt marsh to prevent breeding by salt marsh mosquitos. *Bull. Mar. Sci.* 32:523-531.
- Harris, L.D., R. Sullivan, and L. Badger. 1984. Bottomland hardwoods: valuable, vanishing, vulnerable. Florida Cooperative Extension Service, Gainesville, FL 18 pp.
- Hatton, R.S., W.H. Patrick, and R.D. DeLaune. 1982. Sedimentation, nutrient accumulation, and early diagenesis in Louisiana Barataria basin coastal marshes. Pages 255-267 in V.S. Kennedy (ed.). *Estuarine Comparisons*. Academic Press, New York, NY.
- Heitzman, B. 1978. Management of salt marsh impoundments for waterfowl in North Carolina. North Carolina Wildlife Resources Commission. 35 pp.
- Heald, E.J. 1970. The Everglades estuary: an example of seriously reduced inflow of freshwater. *Trans. Am. Fish. Soc.* 99:847-848.
- Heinselman, M.L. 1971. The natural role of fire in conifer forests. Pages 61-72 in C.W. Slaughter, R.J. Barney, and G.M. Hansen (eds.). *Fire in the northern environment*. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

- Herke, W.H. and B.D. Rogers. 1984. Comprehensive estuarine nursery study completed. *Fisheries* (Bethesda) 9(6):12-16.
- Hill, J., IV, and S.L. Durham. 1978. Input, signals and control in ecosystems. Pages 1-6 in Proc. 1978 IEEE Intl. Conf. on Acoustics, Speech, and Signal Processing. April 1978. Tulsa, OK.
- Hoffmeister, J.E. 1974. Land from the sea: the geologic story of south Florida. University of Miami Press, Coral Gables, Florida. 143 pp.
- Howarth, R.W. 1979. Pyrite: its rapid formation in a salt marsh and its importance to ecosystem metabolism. *Science* 203:49-51.
- Howarth, R.W. 1984. The ecological significance of sulfur in the energy dynamics of salt marsh and coastal marine sediments. *Biogeochemistry* 1:5-27.
- Howarth, R.W., and J.E. Hobbie. 1982. The regulation of decomposition and heterotrophic microbial activity in salt marsh soils: a review. Pages 183-207 in V.S. Kennedy (ed.). *Estuarine comparisons*. Academic Press, New York, NY.
- Howarth, R.W., and J.M. Teal. 1979. Sulfate reduction in a New England salt marsh. *Limnol. Oceanogr.* 24:999-1013.
- Howarth, R.W., and J.M. Teal. 1980. Energy flow in a salt marsh ecosystem: the role of reduced inorganic sulfur compounds. *Am. Nat.* 116:862-872.
- Imberger, J., T. Berman, R.R. Christian, E.B. Sherr, D.C. Whitney, L.R. Pomeroy, R.G., Wiegert, and W.J. Wiebe. 1983. The influence of water motion on the distribution and transport of materials in a salt marsh estuary. *Limnol. Oceanogr.* 28: 201-214.
- Jeske, C.W., and H.F. Percival. 1985. Wintering strategies of Anatinae. Presented at the Waterfowl in Winter symposium, 7-10 January 1985, Galveston, TX.
- Joanen, T., and L.L. Glasgow. 1965. Factors influencing the establishment of widgeongrass stands in Louisiana. *Proc. Ann. Conf. S.E. Assoc. Game Fish Comm.* 19:78-92.
- Johannes, R.E. 1964. Phosphorus excretion and body size in marine animals: microzooplankton and nutrient regeneration. *Science* 146: 923-924.
- Johannes, R.E. 1968. Nutrient regeneration in lakes and oceans. Pages 203-213 in M.R. Droop and E.J.F. Wood (eds.). *Advances in microbiology of the sea*. Academic Press, New York, NY.
- Kalber, F.A., Jr. 1959. A hypothesis of the role of tide-marshes in estuarine productivity. *Estuarine Bulletin* 4(1):3.

- Lasater, J.A. 1975. Water chemistry studies of the Indian River Lagoons. Chapter 6 in An ecological study of the lagoons surrounding the John F. Kennedy Space Center, Brevard County, Florida, April 1972 to September 1975. Volume I. Experimental results and conclusions. December 31, 1975. Final report to NASA from Florida Institute of Technology, Project #NGR 10-015-008.
- Leenhouts, W.P. 1983. Marsh and water management plan, Merritt Island National Wildlife Refuge. Titusville, FL.
- Leenhouts, W.P., and J.L. Baker. 1982. Vegetation dynamics in dusky seaside sparrow habitat on Merritt Island National Wildlife Refuge. *Wildl. Soc. Bull.* 10:127-132.
- Levinton, J.S. 1982. Marine ecology. Prentice-Hall, Inc., Englewood Cliffs, NJ. 526 pp.
- Lewis III, R.R., R.G. Gilmore, Jr., D.W. Crewz, and W.E. Odum. In press. Mangrove habitat and fishery resources of Florida. in Proceedings of the Florida Fishery Habitat Symposium. Florida Chapter American Fisheries Society, Gainesville, FL.
- Lewis, V.P., and D.S. Peters. 1984. Menhaden - a single step from vascular plant to fishery harvest. *J. Exp. Mar. Biol. Ecol.* 84:95-100.
- Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399-418.
- Livezey, B.C., and P.S. Humphrey. 1984. Sexual dimorphism in continental steamer-ducks. *Condor* 86:368-377.
- Livingston, R.J. 1984. Trophic response of fishes to habitat variability in coastal seagrass systems. *Ecology* 75:1258-1275.
- Lorio, W.J., and W.S. Perret. 1980. Biology and ecology of the spotted seatrout (*Cynoscion nebulosus* Cuvier). Pages 7-13 in R.O. Williams, J.E. Weaver, and F.A. Kalber (eds.). Proceedings: a colloquium on the biology and management of the red drum and seatrout. Gulf States Mar. Fish. Comm. No. 5.
- Lotka, A.J. 1922a. Contribution to the energetics of evolution. *Proc. Nat. Acad. Sci.* 8:147-151.
- Lotka, A.J. 1922b. Natural selection as a physical principle. *Proc. Nat. Acad. Sci.* 8:151-154.
- Lovelock, J.E. 1979. Gaia: a new look at life on earth. Oxford University Press, New York, NY. 157pp.
- MacIntyre, F. 1970. Why the sea is salt. Pages 104-115 in Ocean science: readings from Scientific American. W.H. Freedman and Co., San Francisco, CA.

- Marinucci, A.C. 1982. Trophic importance of Spartina alterniflora production and decomposition to the marsh-estuarine ecosystem. *Biol. Conserv.* 22:35-58.
- Meade, R.H., P.L. Sachs, T.T. Manheim, J.C. Hathaway, and D.W. Spencer. 1975. Sources of suspended matter in water of the middle Atlantic Bight. *J. Sed. Petrol.* 45:171-188.
- Migliarese, J.V., and P.A. Sandifer (eds.). 1982. An ecological characterization of South Carolina wetland impoundments. South Carolina Marine Resources Center Tech. Rep. No. 51. 132 pp.
- Mion, P., G.R. Best, and C.R. Hinkle. 1985. Low-energy wastewater recycling through wetland ecosystems: experimental use of a marsh ecosystem at Kennedy Space Center. Abstract in *Ecol. Bull.* 66(2):233.
- Montague, C.L. 1980. The net influence of the mud fiddler crab, Uca pugnax, on carbon flow through a Georgia salt marsh: the importance of work by macroorganisms to the metabolism of ecosystems. Ph.D. Diss., Univ. of Georgia, Athens, GA. 157 pp.
- Montague, C.L., S.M. Bunker, E.B. Haines, M.L. Pace, and R.L. Wetzel. 1981. Aquatic macroconsumers. Pages 69-85 in L.R. Pomeroy and R.G. Wiegert (eds.). *The ecology of a salt marsh*. Springer-Verlag, New York, NY.
- Montague, C.L., A.V. Zale, H.F. Percival, and T. Hingtgen. 1984a. A categorized bibliography for a conceptual model of salt marsh management on Merritt Island, Florida. Florida Cooperative Fish and Wildlife Research Unit Technical Report No. 9. 98 pp.
- Montague, C.L., A.V. Zale, and H.F. Percival. 1984b. Photographic analysis of natural and impounded salt marsh in the vicinity of Merritt Island, Florida. Florida Cooperative Fish and Wildlife Research Unit Technical Report No. 11. 23 pp.
- Moody, W.D. 1950. A study of the natural history of the spotted seatrout, Cynoscion nebulosus, in the Cedar Key, Florida area. *Q. J. Fla. Acad. Sci.* 12:147-171.
- Morgan, P.H. 1974. A study of tidelands and impoundments within a three-river delta system - the South Edisto, Ashepoo and Combahee rivers of South Carolina. MS Thesis, Univ. of Georgia, Athens, GA. 92 pp.
- Morgan, P.H., A.S. Johnson, W.P. Baldwin, and J.L. Landers. 1975. Characteristics and management of tidal impoundments for wildlife in a South Carolina estuary. *Proc. Ann. Conf. S.E. Assoc. Game Fish Comm.* 29:526-539.
- Mulholland, R. 1984. Habitat suitability index models: hard clam. U.S. Fish Wildl. Serv. FWS/OBS-82/10.77. 21 pp.

- Neely, W.W. 1960. Managing Scirpus robustus for ducks. Proc. S.E. Assoc. Game Fish Comm. 14:30-34.
- Neely, W.W. 1968. Planting, disking, mowing, and grazing. Pages 212-221 in J.D. Newsom (ed.). Proc. LSU Marsh and Estuary Management Symposium, Louisiana State University Division of Continuing Education, Baton Rouge, LA.
- Nichols, J.D., M.J. Conroy, D.R. Anderson, and K.P. Burnham. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Trans. N. Amer. Wildl. Nat. Res. Conf. 49:535-554.
- Nielsen, E.T., and A.T. Nielsen. 1953. Field observations on the habits of Aedes taeniorhynchus. Ecology 34:141-156.
- Nixon, S.W. 1980. Between coastal marshes and coastal waters - a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. Pages 437-525 in P. Hamilton and K.B. MacDonald (eds.). Estuarine and wetland processes, Plenum, New York, NY.
- Nixon, S.W. 1982. The ecology of New England high salt marshes: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-81/55. 70 pp.
- Nudds, T.D., and J.N. Bowlby. 1984. Predator-prey size relationships in North American dabbling ducks. Can. J. Zool. 62:2002-2008.
- Nudds, T.D., and R.M. Kaminski. 1984. Sexual size dimorphism in relation to resource partitioning in North American dabbling ducks. Can. J. Zool. 62:2009-2012.
- Odum, E.P. 1971. Fundamentals of ecology. W.B. Saunders, New York, NY.
- Odum, E.P. 1974. Halophytes, energetics and ecosystems. Pages 599-602 in R.J. Reimold and W.H. Queen (eds.). Ecology of halophytes. Academic Press, Inc., New York, NY.
- Odum, E.P., J.B. Birch, and J.L. Cooley. 1983. Comparison of giant cutgrass productivity in tidal and impounded marshes with special reference to tidal subsidy and waste assimilation. Estuaries 6: 88-94.
- Odum, E.P., and A.A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh - estuarine ecosystem. Pages 383-388 in G.H. Lauff (ed.). Estuaries. AAAS Publ. No. 83.
- Odum, E.P., and M.E. Fanning. 1973. Comparison of the productivity of Spartina alterniflora and Spartina cynosuroides in Georgia coastal marshes. Bull. Georgia Acad. Sci. 31:1-12.

- Odum, E.P., J.T. Finn, and E.H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. *BioScience* 29:349-352.
- Odum, E.P., and A.E. Smalley. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. *Proc. Nat. Acad. Sci.* 45:617-622.
- Odum, H.T. 1967. Biological circuits and the marine systems of Texas. Pages 99-157 in Burgess and Olson (eds.). *Pollution and marine ecology*. John Wiley and Sons, New York, NY.
- Odum, H.T. 1984. *Systems ecology*. John Wiley and Sons, New York, NY. 744 pp.
- Odum, H.T. In press. Self organization of estuarine ecosystems in marine ponds receiving treated sewage. North Carolina Sea Grant No. GH103, Project UNC-10. Data from experimental pond studies at Morehead City, NC, 1968-72.
- Odum, W.E. 1966. The food and feeding of the striped mullet, Mugil cephalus, in relation to the environment. MS Thesis, Univ. of Miami, Miami, FL. 118 pp.
- Odum, W.E. 1968. The ecological significance of fine particle selection by the striped mullet, Mugil cephalus. *Limnol. Oceanogr.* 13:92-98.
- Odum, W.E. 1969. The structure of detritus based food chains in a south Florida mangrove system. Ph.D. Diss., Univ. of Miami, Miami, FL.
- Odum, W.E. 1970a. Insidious alteration of the estuarine environment. *Trans. Am. Fish. Soc.* 99:836-847.
- Odum, W.E. 1970b. Utilization of the direct grazing and plant detritus food chain by the striped mullet Mugil cephalus. Pages 222-240 in J.H. Steele (ed.). *Marine food chains, a symposium*. Oliver and Boyd, Edinburgh.
- Odum, W.E., J.S. Fisher, and J.C. Pickral. 1979. Factors controlling the flux of particulate organic carbon from estuarine wetlands. Pages 69-80 in R.J. Livingston (ed.). *Ecological processes in coastal and marine systems*. Plenum, New York, NY.
- Odum, W.E., and E.J. Heald. 1972. Trophic analyses of an estuarine mangrove community. *Bull. Mar. Sci.* 22:671-738.
- Odum, W.E., and E.J. Heald. 1975. The detritus based food web of an estuarine mangrove community. Pages 265-286 in *Estuarine research*. Academic Press, New York, NY.
- Odum, W.E., and M.A. Heywood. 1978. Decomposition of intertidal freshwater marsh plants. Pages 89-97 in R.E. Good, D.F. Whigham and R.L. Simpson (eds.). *Freshwater wetlands: ecological processes and management potential*. Academic Press, Inc., New York, NY.

- OTA (Office of Technology Assessment) 1984. Wetlands: their use and regulations. U.S. Congress OTA-0-206. 208 pp.
- Onuf, C.P., M.L. Quammen, G.P. Shaffer, C.H. Peterson, J.W. Chapman, J. Cermak, and R.W. Holmes. 1979. An analysis of the values of central and southern California coastal wetlands. Pages 186-199 in P.E. Greeson, J.R. Clark, and J.E. Clark (eds.). Wetland functions and values: the state of our understanding. Proceedings of the National Symposium on Wetlands, 7-10 November 1978, Lake Buena Vista, FL.
- Orth, R.J., K.L. Heck, Jr., and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator - prey relationships. *Estuaries* 7:339-350.
- Parker, R.R., J. Sibert, and T.J. Brown. 1975. Inhibition of primary productivity through heterotrophic competition for nitrate in a stratified estuary. *J. Fish Res. Board Can.* 32:72-77.
- Patrick, W.H., Jr., and R.D. DeLaune. 1976. Nitrogen and phosphorus utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Est. Coast. Mar. Sci.* 4:59-64.
- Patrick, W.H., Jr., and R.A. Khalid. 1974. Phosphate release and absorption by soils and sediments: effect of aerobic and anaerobic conditions. *Science* 186:53-55.
- Peterson, B.J., R.W. Howarth, and R.H. Garritt. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* 227:1361-1363.
- Pomeroy, L.R. 1970. The strategy of mineral cycling. *Ann. Rev. Ecol. Syst.* 1:171-190.
- Pomeroy, L.R. 1980. Detritus and its role as a food source. Pages 84-102 in R.K. Barnes and K.H. Mann (eds.). *Fundamentals of aquatic ecosystems*. Blackwell Scientific Publications, Oxford.
- Pomeroy, L.R. and R.G. Wiegert (eds.). 1981. *The Ecology of a Salt Marsh*. Ecological Studies 38, Springer-Verlag, New York 271 pp.
- Pomeroy, L.R., E.E. Smith, and C.M. Grant. 1965. The exchange of phosphate between estuarine water and sediments. *Limnol. Oceanogr.* 10:167-172.
- Pomeroy, L.R., R.E. Johannes, E.P. Odum, and B. Roffman. 1969. The phosphorus and zinc cycles and productivity of a salt marsh. Pages 412-419 in D.J. Nelson and F.C. Evans (eds.). *Symposium on radioecology*. U.S. Atomic Energy Comm., Washington, DC.
- Pomeroy, L.R., L.R. Shenton, R.D. Jones, and R.J. Reimold. 1972. Nutrient flux in estuaries. *Amer. Soc. Limnol. Oceanogr. Spec. Symp.* 1:274-291.

- Pomeroy, L.R., K. Bancroft, J. Breed, R.R. Christian, D. Frankenberg, J.R. Hall, L.G. Maurer, W.J. Wiebe, R.G. Wiegert, and R.L. Wetzel. 1977. Flux of organic matter through a salt marsh. Pages 270-279 in M. Wiley (ed.). Estuarine processes, Vol. II. Academic Press, New York, NY.
- Pospahala, R.S., D.R. Anderson, and C.J. Henry. 1974. Population ecology of the mallard. II. Breeding habitat conditions, size of the breeding populations and population indices. U.S. Fish & Wildl. Serv. Res. Publ. 115. Washington, DC. 73 pp.
- Postma, H. 1980. Sediment transport and sedimentation. Pages 153-186 in E. Olausson and I. Cato (eds). Chemistry and biogeochemistry of estuaries. John Wiley and Sons, New York, NY.
- Presley, B.J., and J.H. Trefry. 1980. Sediment-water interactions and the geochemistry of interstitial waters. Pages 187-232 in E. Olausson and I. Cato (eds). Chemistry and biogeochemistry of estuaries. John Wiley and Sons, New York, NY.
- Prevost, M.B., A.S. Johnson, and J.L. Landers. 1978. Production and utilization of waterfowl foods in brackish impoundments in South Carolina. Proc. Ann. Conf. S.E. Assoc. Fish Wildl. Agencies 32:60-70.
- Provost, M.W. Undated. Charles H. Trost's study of wildlife usage of salt marsh on the east coast of Florida before and after impoundment for mosquito and sandfly control. Appendix: analysis by marsh and by species. Bureau of Sport Fisheries and Wildlife, Contract No. 14-16-0008-623. 26 pp.
- Provost, M.W. 1948. Marsh-blasting as a wildlife management technique. J. Wildl. Manage. 12:350-387.
- Provost, M.W. 1959. Impounding salt marshes for mosquito control - and its effects on bird life. Fla. Nat. 32:163-169.
- Provost, M.W. 1968. Managing impounded salt marsh for mosquito control and estuarine resource conservation. Pages 163-171 in J.D. Newsom (ed.). Proc. L.S.U. Marsh and Estuary Management Symposium, Louisiana State University Division of Continuing Education, Baton Rouge, LA.
- Provost, M.W. 1969a. Ecological control of salt marsh mosquitoes with side benefits to birds. Proc. Tall Timbers Conf. on Ecological Animal Control by Habitat Management 1:193-206.
- Provost, M.W. 1969b. Man mosquitos and birds. Fla. Nat. April 1969: 63-67.
- Provost, M.W. 1973a. Mean high water mark and use of tidelands in Florida. Fla. Sci. 36:50-66.

- Provost, M.W. 1973b. Salt marsh management in Florida. Proc. Tall Timbers Conf. on Ecological Animal Control by Habitat Management 5:5-17.
- Provost, M.W. 1977. Source reduction in salt-marsh mosquito control: past and future. Mosquito News 37:689-698.
- Rae, K.M., and R.G. Bader. 1960. Clay-mineral sediments as a reservoir for radioactive materials in the sea. Proc. Gulf Carib. Fish. Inst. 12:55-61.
- Rapport, D.J., H.A. Regier, and T.C. Hutchinson. 1985. Ecosystem behavior under stress. Am. Nat. 125:617-640.
- Reeves, H.M., H.D. Dill, and A.S. Hawkins. 1968. A case study in Canada goose management: the Mississippi valley population. Pages 701-722 in R. L. Hine and C. Schoenfeld (eds). Dembar Educational Research Services, Madison, WI.
- Reimold, R.J. 1972. The movement of phosphorus through the salt marsh cord grass, Spartina alterniflora Loisel. Limnol. Oceanogr. 17: 606-611.
- Reimold, R.J., and F.C. Daiber. 1970. Dissolved phosphorus concentrations in a natural salt-marsh of Delaware. Hydrobiologia 36: 361-371.
- Reinecke, K.J. 1981. Winter waterfowl research needs and efforts in the Mississippi Delta. Pages 231-235 in Fourth international waterfowl symposium, 30 January - 1 February 1981, New Orleans, LA. Ducks Unlimited.
- Reis, R.R. 1977. Temporal variation in utilization of a high marsh intertidal creek by larval and juvenile fish. MS Thesis, Univ. of South Carolina, Columbia, SC. 68 pp.
- Reis, R.R., and J.M. Dean. 1981. Temporal variation in the utilization of an intertidal creek by the bay anchovy (Anchoa mitchilli). Estuaries 4:16-23.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191. 382 pp.
- Rogers, J.P. 1979. Symposium summary and comments on the future of waterfowl and wetlands. Pages 143-147 in T.A. Bookhout (ed.). Waterfowl and wetlands: an integrated review. Proc. 1977 Symp., Madison, WI. N. Cent. Sect., The Wildlife Society.
- Rozas, L.P., and C.T. Hackney. 1984. Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. Estuaries 7:213-224.

- Ryther, J.H. 1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. *Biol. Bull.* 106:198-209.
- Ryther, J.H. 1956. Photosynthesis in the ocean as a function of light intensity. *Limnol. Oceanogr.* 1:61-70.
- Ryther, J.H., and W.M. Dunstan. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science* 171: 1008-1013.
- Sanders, H.L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102:243-282.
- Shenker, J., and J.M. Dean. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variations. *Estuaries* 2:154-163.
- Shillinger, J.E., and C.S. Cottam. 1937. The importance of lead poisoning in waterfowl. *Trans. N. Am. Wildl. Conf.* 2:398-403.
- Sikora, W.B., and J.P. Sikora. 1982. Ecological implications of the vertical distribution of meiofauna in salt marsh sediments. Pages 269-282 in V.S. Kennedy (ed.). *Estuarine comparisons*. Academic Press, New York, NY.
- Smalley, A.E. 1959. The growth cycle of *Spartina* and its relation to the insect population in the marsh. Pages 96-100 in *Proc. Salt Marsh Conf., Marine Inst., University of Georgia, Athens, GA.*
- Snelson, F.F., Jr. 1980. Volume III of IV: Part I - Ichthyological studies; ichthyological survey of lagoonal waters. A continuation of base-line studies for environmentally monitoring space transportation systems (STS) at John F. Kennedy Space Center. 119 pp.
- Snelson, F.F., Jr. 1983. Ichthyofauna of the northern part of the Indian River lagoon system, Florida. *Fla. Sci.* 46:187-206.
- Stickney, R.R., and M.L. Cuenco. 1982. Habitat suitability index models: juvenile spot. U.S. Dept. Int. Fish Wildl. Serv. FWS/OBS-82/10.20. 12 p.
- Stieglitz, W.O., and C.T. Wilson. 1968. Breeding biology of the Florida duck. *J. Wildl. Manage.* 32:921-934.
- Strong, D.R., Jr., D. Simberloff, L.G. Abele, and A.B. Thistle. 1984. *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Press, Princeton, NJ. 614 pp.
- Subrahmanyam, C.B., and S.H. Drake. 1975. Studies on the animal communities in two north Florida salt marshes. *Bull. Mar. Sci.* 25: 445-465.

- Sweet, H.C. 1976. Botanical studies of Merritt Island. Final report NGR10.019 004 to NASA from Florida Technological University, Orlando, Florida. 258 p.
- Swiderek, P.K., A.S. Johnson, P.E. Hale, and R.L. Joyner. 1985. Sea purslane, gulf coast muskgrass, and widgeongrass in brackish impoundments. draft manuscript presented at Waterfowl in Winter symposium and workshop, 7-10 January 1985, Galveston, TX.
- Tabb, D.C. 1966. The estuary as a habitat for spotted seatrout (Cynoscion nebulosus). Pages 59-67 in R.S. Smith (chairman). A symposium on estuarine fishes. Am. Fish. Soc. Spec. Publ. No. 3.
- Talbot, C.W., and K.W. Able. 1984. Composition and distribution of larval fishes in New Jersey high marshes. *Estuaries* 7:434-443.
- Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614-624.
- Teal, J.M. 1980. Primary production of benthic and fringing plant communities. Pages 67-83 in R.K. Barnes and K.H. Mann (eds.). *Fundamentals of aquatic ecosystems*. Blackwell Scientific Publications, Oxford.
- Tenore, K.R., L. Cammen, S.E.G. Findlay, and N. Phillips. 1982. Perspectives of research on detritus: do factors controlling the availability of detritus to macroconsumers depend on its source? *J. Mar. Res.* 40:473-490.
- Thayer, G.W. 1974. Identity and regulation of nutrients limiting phytoplankton production in the shallow estuaries near Beaufort, N.C. *Oecologia* 14:75-92.
- Thayer, G.W., W.J. Kenworthy, and M.S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic coast: a community profile. U.S. Fish Wildl. Serv. FWS/OBS-84/02. 147 pp.
- Thayer, G.W., P.L. Parker, M.W. LaCroix, and B. Fry. 1978. Stable carbon isotope ratio of some components of an eelgrass, Zostera marina, bed. *Oecologia* 35:1-12.
- Thomas, C. 1982. Winter ecology of dabbling ducks in central Florida. MS Thesis, Univ. of Missouri, Columbia, MO. 60 pp.
- Tiner, R.W., Jr. 1984. Wetlands of the United States: current status and recent trends. U.S. Fish and Wildlife Service, National Wetlands Inventory. 59 pp.
- Trost, C.H. Undated. Study of wildlife usage of salt marsh on the east coast of Florida before and after impoundment for mosquito and sandfly control. Final report. Bureau of Sport Fisheries and Wildlife, Contract No. 14-16-0008-623. 30 pp.
- Turner, R.E. 1976. Geographic variation in salt marsh macrophyte production: a review. *Contrib. Mar. Sci.* 20:47-68.

- Valentine, J.W. 1973. Evolutionary ecology of the marine biosphere. Prentice-Hall, Inc. Englewood Cliffs, N.J. 511 pp.
- Valiela, I. 1984. Marine ecological processes. Springer-Verlag, New York, NY.
- Valiela, I., J.M. Teal, and N.Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: belowground biomass. *Limnol. Oceanogr.* 21:245-252.
- Valiela, I., and J.M. Teal. 1979a. Inputs, outputs and interconversions of nitrogen in a salt marsh ecosystem. Pages 399-414 in R.L. Jefferies and A.J. Davy (eds.). *Ecological processes in coastal environments*. Blackwell, London.
- Valiela, I., J.M. Teal, S. Volkmann, D. Shafer, and E.J. Carpenter. 1978. Nutrient and particulate fluxes in a salt marsh ecosystem: Tidal exchanges and inputs by precipitation and groundwater. *Limnol. Oceanogr.* 23: 798-812.
- Valiela, I., and J.M. Teal. 1979b. The nitrogen budget of a salt marsh ecosystem. *Nature* 280:652-656.
- Valiela, I., S. Vince, and J.M. Teal. 1976b. Assimilation of sewage by wetlands. Pages 234-253 in M. Wiley (ed.). *Estuarine processes*.
- Van Den Avyle, M.J., and D.L. Fowler. 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) -- blue crab. U.S. Fish Wildl. Serv. FWS/OBS-82/11.19. U.S. Army Corps of Engineers TR EL-82-4. 16 pp.
- Vince, S., I. Valiela, N. Backus, and J.M. Teal. 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. *J. Exp. Mar. Biol. Ecol.* 23:255-266.
- Voigts, D.K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. *Am. Midl. Nat.* 95:313-322.
- Vogal, R.J. 1980. The ecological factors that produce perturbation-dependent ecosystems. Pages 63-94 in J. Cairns, Jr. (ed.). *The recovery process in damaged ecosystems*. Ann Arbor Science, Ann Arbor, MI.
- Walker, R.L. and K.R. Tenore. 1984. The distribution and production of the hard clam, *Mercenaria mercenaria*, in Wassaw Sound, Georgia. *Estuaries* 7:19-27.
- Weinstein, M.P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *U.S. Fish. Bull.* 77:339-357.

- Weinstein, M.P., L.S. Scott, S.P. O'Neil, R.C. Siegfried II, and S.T. Szedlmayer. 1984. Population dynamics of the spot, Leiostomus xanthurus, in polyhaline tidal creeks of the York River Estuary, Virginia. Estuaries 7:444-450.
- Weinstein, M.P., and M.P. Walters. 1981. Growth, survival and production in young-of-year populations of Leiostomus xanthurus Lacpede residing in tidal creeks. Estuaries 4:185-197.
- Weinstein, M.P., S.L. Weiss, and M.F. Walters. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River Estuary, North Carolina, USA. Mar. Biol. 58:227-243.
- Welsh, B. 1975. The role of grass shrimp, Palaemonetes pugio, in a tidal marsh ecosystem. Ecology 56:513-530.
- Wetzel, R.G. 1975. Limnology. W.B. Saunders, Co., Philadelphia, PA. 743 pp.
- Wetzel, R.L. 1975. An experimental study of detrital carbon utilization in a Georgia salt marsh. Ph.D. Diss., Univ. of Georgia, Athens, GA.
- Wetzel, R.L. 1977. Carbon resources of a benthic salt marsh invertebrate, Nassarius obsoletus Say (Mollusca: Nassaridae). Estuarine processes. Vol. 2:293-308. Academic Press, New York, NY.
- White, D.H., and D. James. 1978. Differential use of freshwater environments by wintering waterfowl of coastal Texas. Wilson Bull. 90:99-111.
- Whitman, W.R. 1976. Impoundments for waterfowl. Occas. Pap. No. 22, Canadian Wildl. Serv. 22 pp.
- Whitney, D.E., A.G. Chalmers, E.B. Haines, R.B. Hanson, L.R. Pomeroy, and B. Sherr. 1981. The cycles of nitrogen and phosphorus. Pages 163-182 in L.R. Pomeroy and R.G. Wiegert (eds.). The ecology of a salt marsh. Ecological Studies 38, Springer-Verlag, New York, NY.
- Wicker, K.M., D. Davis, and D. Roberts. 1983. Rockefeller State Wildlife Refuge and Game Preserve: evaluation of wetland management techniques. Louisiana Dept. Nat. Res., Baton Rouge, LA.
- Wiegert, R.G. 1979. Ecological processes characteristic of coastal Spartina marshes of the south-eastern U.S.A. Pages 467-490 in R.L. Jefferies and A.J. Davy (eds.). Ecological processes in coastal environments. Blackwell, London.
- Wiegert, R.G., A.G. Chalmers, and P.F. Randerson. 1983. Productivity gradients in salt marshes: the response of Spartina alterniflora to experimentally manipulated soil water movement. Oikos 41:1-6.

- Wilkinson, P.M. 1983. Nesting ecology of the American alligator in coastal South Carolina. Study completion report, August 1978 - September 1983. South Carolina Wildlife and Marine Resources Department. 113 pp.
- Wilson, J.A. 1972. Principles of animal physiology. MacMillan Publishing Co., New York, NY. 842 pp.
- Yancey, R.K. 1964. Matches and marshes. Pages 619-626 in J.P. Linduska (ed.). Waterfowl tomorrow. U.S. Dept. Int. Washington, DC. 770 pp.
- Zieman, J.C. 1982. The ecology of the seagrasses of south Florida: a community profile. U.S. Fish and Wildlife Services, Office of Biological Services, Washington, D.C. FWS/OBS-82/85. 158 pp.
- Zilberberg, M.H. 1966. Seasonal occurrence of fishes in a coastal marsh of northwest Florida. Contrib. Mar. Sci. 11:126-134.