

AN OVERVIEW OF MAJOR WETLAND FUNCTIONS AND VALUES

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CONTENTS

	Page
INTRODUCTION.....	1
References.....	2
HYDROLOGY.....	3
General.....	3
Flood Control.....	3
Ground Water Recharge and Discharge.....	6
Shoreline Anchoring and Dissipation of Erosive Forces.....	6
References.....	8
WATER QUALITY.....	11
General.....	11
Wastewater Treatment.....	11
Toxic Substances.....	13
Nutrients.....	14
References.....	16
FOOD CHAIN SUPPORT/NUTRIENT CYCLING.....	21
General.....	21
Primary Production.....	21
Decomposition.....	24
Nutrient Export.....	25
Nutrient Utilization.....	27
References.....	28
HABITAT.....	40
General.....	40
Invertebrates and Poikilothermal Vertebrates.....	43
Fisheries.....	44
Mammals.....	45
Nongame Birds.....	47
Game Birds.....	47
References.....	48
SOCIO-ECONOMIC.....	58
General.....	58
Nonconsumptive Use Value.....	58
Consumptive Use Value.....	61
References.....	62

TABLES

<u>Number</u>		<u>Page</u>
1	Summary of current status of knowledge of selected wetland functions - hydrology.	4
2	Summary of current status of knowledge of selected wetland functions - water quality.	12
3	Summary of current status of knowledge of selected wetland functions - food chain support/nutrient cycling.	22
4	Summary of current status of knowledge of selected wetland functions - habitat.	42
5	Summary of current status of knowledge of selected wetland functions - socio-economic.	59

INTRODUCTION

This report was prepared to provide background information for participants at the National Wetland Values Assessment Workshop held at Alexandria, Virginia in May 1983 (Sather and Stuber 1984). The Wetlands Values Bibliographic Database (created by U.S. Fish and Wildlife Service National Wetland Inventory) proved to be of inestimable value in the initial stages of the literature search. Annotations of each referenced document can be found in the Database.

In this report we have viewed wetlands as being those habitats that fall within the Cowardin et al. (1979) definition of wetlands. That definition is as follows:

Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is covered by shallow water. For purposes of this classification wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soil; and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year.

A number of recent papers have addressed a broad range of wetland functions. Several of these papers have included extensive literature reviews (Reppert et al. 1979; Larson 1981, 1982; Linder and Hubbard 1982; National Wildlife Federation 1982; Zinn and Copeland 1982; Adamus 1983). When these comprehensive reviews are combined with reviews that are specific to one or two functions, the result is an up-to-date and reasonably complete picture of what is currently known about wetland functions. This report is an attempt to briefly summarize the information available in these literature reviews.

This review is divided into the following major headings: hydrology; water quality; food chain; habitat; and socio-economic. We are aware of the fact that there is a considerable amount of overlap among some of these broad categories; however, this type of arrangement was deemed most appropriate to assist participants in their preparation for deliberations at the Wetland Values Assessment Workshop.

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HYDROLOGY

GENERAL

It is generally accepted that natural wetland functions are closely linked to hydrology. Wetland primary productivity; nutrient cycling; wildlife habitat; harvest of fiber, fin, and fur; and aesthetics are unquestionably tied to the presence, movement, quality, and quantity of water in the wetland (Clark and Clark 1979). It is also generally agreed that wetlands are among the most difficult hydrologic environments to assess (Remson and Stonestrom 1978) and that the difficulty in assessment largely accounts for the fact that the hydraulic and hydrologic characteristics of wetlands are not well understood. Methodologies developed for the study of the hydrologic properties of rivers, lakes, and mineral soils are not satisfactory for studying wetlands and organic soils. Despite the fact that the importance of prairie potholes and lakes to waterfowl has been recognized for a long time, very little is known about the hydrologic functions of those wetlands (Winter 1981).

In the following discussion, we have chosen to review the hydrologic literature as it pertains to the following major wetland functions: ground water recharge and discharge; flood storage and desynchronization; and shoreline anchoring and dissipation of erosive forces. This is consistent with the manner in which the hydrology review is handled in the Adamus (1983) report. We have also attempted to summarize the current status of knowledge regarding these functions in Table 1. The status of knowledge is broken into three categories to which studies are assigned based upon interpretation of the authors' statements in the paper. A listing of some assessment systems that address these functions is also included in Table 1.

FLOOD CONTROL

Any depression in the landscape has the potential to store water and, thereby, plays a role in flood control. Many depressions contain wetlands, and any basins that are not already filled to capacity will perform a flood control function. There is general agreement that wetlands associated with streams provide flood storage, slow flood waters, reduce flood peaks, and increase the duration of the flow (Carter et al. 1978; Verry and Boelter 1978; Clark and Clark 1979; Larson 1981, 1982; Zinn and Copeland 1982).

Table 1. Summary of current status of knowledge of selected wetland functions - hydrology.

Function	Well authenticated	Fairly well authenticated	Poorly authenticated	Existing assessment methods	Remarks
1. Ground water recharge and discharge		Linder and Hubbard 1982	Carter et al. 1978 Reppert et al. 1979 Larson 1981 Adamus 1983	U.S. Army Engineer Div., N.E. 1972 Dee et al. 1973 Larson 1976 Solomon 1977 Galloway 1978 Kibby 1978 US. Soil Conservation Service 1978 Reppert et al. 1979 Schuldiner et al. 1979 Winchester 1979 Adamus 1983	The ground water recharge function of wetlands is by no means clear, but there is good evidence that many wetlands serve as ground water discharge areas. Wetlands perform a flood control function, but techniques for assessing the effectiveness and exact nature of their role have not been developed. There is some disagreement as to the effectiveness of wetlands in stabilization of shorelines, but recent studies indicate that wetland vegetation plays a significant role in dissipating erosion forces.
2. Flood control		Carter et al. 1978 Reppert et al. 1979 Verry and Boelter 1978 Clark and Clark 1979 Larson 1981 Adamus 1983			
3. Shoreline anchoring and dissipation of erosive forces	Carter et al. 1978 Clark and Clark 1979 Reppert et al. 1979 Knutsen et al. in press	Adamus 1983	Tilton et al. 1978 Larson 1981		

Studies of the Charles and Neponset River watersheds in Massachusetts are frequently cited to document the influence of wetlands on peak flows (Anderson-Nichols and Co., Inc. 1971; U.S. Army Corps of Engineers 1972; Larson 1981; Zinn and Copeland 1982). In the Charles River study, the U.S. Army Corps of Engineers (1972) determined that a loss of 40% of the wetlands within the basin would increase flood damage by at least \$3,193,000 annually. Loss of the entire 8,422 acres of wetland within the basin would result in average annual flood damages of \$17,084,606. On the basis of this study, the Corps determined that the most economical way to control flood losses in the basin was to protect the wetlands. The Neponset River study also indicated that a significant increase in downstream flood stages would occur with the loss of wetlands. The basinwide flood stage increase for the 100-year flood was predicted to range from 0.15 m with a 10% loss of wetlands to 0.9 m with a 50% loss.

Characteristics of wetlands that are most often cited as having a role in controlling flood waters are: size (the larger the wetland, the more area provided for flood storage and velocity reduction); location within the drainage basin; texture of the substrate, and lifeform of the wetland vegetation (Carter et al. 1978; Novitzki 1978; Clark and Clark 1979; Reppert et al. 1979). A thorough review of how different characteristics affect the role of wetlands in flood control is included in Novitzki (1978). Novitzki classified wetlands into four "hydrologic wetland classes" and then showed how the different characteristics of each class determine how the wetlands modify flood and base flows.

Although it is possible for an isolated wetland to perform a significant flood control function, effective flood control is more often the result of the interrelationship of a series of wetlands within a particular watershed. In Wisconsin, flood peaks were reduced by 60 to 80% in watersheds with a 30% wetland or lake area, as compared to watersheds with no wetland or lake area (Verry and Boelter 1978). It has also been reported that peak flows will be 60 to 65% lower if a watershed has 15% of its area in wetlands or lakes than if no wetlands or lakes are present (Zinn and Copeland 1982).

Although it is accepted that wetlands perform a flood control function, it is by no means clear how effective different types of wetlands are (Reppert et al. 1979). Larson (1981 and 1982) expressed the view that techniques have not yet been developed that will accurately assess the effectiveness of wetlands in flood control. Adamus (1983) identified some of the major factors that affect this function; however, he also indicated that there are only a few quantitative and qualitative approaches that examine the contributions of wetlands to flood storage. It is also apparent that existing studies of the flood control function of wetlands do not cover all geographic areas. Larson (1981 and 1982) notes that studies up to now have been restricted primarily to glaciated areas.

In summary, it appears that there is a significant lack of the type of information that would enable the measurement of the flood control effectiveness of a particular wetland.

GROUND WATER RECHARGE AND DISCHARGE

The role that wetlands play in ground water recharge is not clear. Hydrologists seem to agree that, while some wetlands recharge the ground water system, most do not (Carter et al. 1978; Clark and Clark 1979; Reppert et al. 1979; Larson 1981). Contrary to previous assumptions, there is very little evidence in the literature that indicates that wetlands perform a significant recharge function (Carter et al. 1978). Wetlands probably contribute less to ground water supplies than do undeveloped upland areas because the wetland evapotranspiration rate may be greater and the soils less permeable than in many upland areas (Clark and Clark 1979; Larson 1981).

Hydrologic studies conducted in Massachusetts indicate that wetlands in that region serve as valuable potential sources of ground water (Motts and Heeley 1973). Temporary or seasonal wetlands seem to be more likely to perform a recharge function than wetlands that are permanent or semipermanent (Lissey 1968; Sloan 1972; Carter et al. 1978; Novitzki 1978; Verry and Boelter 1978; Clark and Clark 1979; Reppert et al. 1979; Linder and Hubbard 1982).

The following wetland features are frequently mentioned as being closely associated with the ground water recharge function: water permanence; nature of the substrate; nature of surface outlets; the amount of edge; and the type and amount of vegetation. Adamus (1983) states that the recharge function of wetlands has been studied less than any other function and, in some regions, has apparently been totally unmeasured in systematic water budget studies. He concluded that more wetlands function as important ground water discharge areas than ground water recharge areas. Novitzki (1978) and Larson (1981) supported this view by noting that most wetlands occur where water is discharging to the surface. In addition, Carter et al. (1978) cited a number of studies that support the contention that many wetlands perform a ground water discharge function and that such wetlands are, therefore, good indicators of potential water supplies for communities or municipalities. It is generally accepted that wetlands are likely to be sites of significant ground water discharge.

As with the flood control function, much more work is needed in order to understand the interactions that exist between wetlands and ground water; this is especially true in the unglaciated sections of the country (Carter et al. 1978; Larson 1981; Linder and Hubbard 1982).

SHORELINE ANCHORING AND DISSIPATION OF EROSION FORCES

The role that vegetation plays in controlling shoreline erosion and the forces leading to shoreline erosion are well documented (Scoffin 1970; Wayne 1975; Allen 1978; Carter et al. 1978; Dean 1978; Clark and Clark 1979; Reppert et al. 1979; Knutsen et al. 1982; Zinn and Copeland 1982). On the basis of their examination of the literature, Carter et al. (1978) concluded that wetland vegetation plays three major roles in erosion

control: (1) it binds and stabilizes substrates; (2) it dissipates wave and current energy; and (3) it traps sediments. These authors also cite several references that indicate that the role played by vegetation in erosion control is the same for coastal as it is for inland lakes and riverine habitats. On the other hand, Larson (1981) indicated that experimental evidence of the shoreline stabilization role of wetlands appears to be lacking and that it is a subject that requires further study. Larson's conclusion was apparently influenced by the work of Tilton et al. (1978), who concluded that, where physical processes combine to produce shore erosion, those energies involved prevent the establishment of wetland communities.

Clark and Clark (1979) pointed out that there is not much information available on the relative erosion control values of various types of wetland plant communities; most of the information comes from studies of individual plant species. These authors concluded that the effectiveness of shoreline vegetation in controlling erosion depends on the particular plant species involved (e.g., its flood tolerance and resistance to undermining), the width of the vegetated shoreline band, the efficiency of the vegetated band in trapping sediments (based on growth form and diversity), the soil composition of the bank or shore, the height and slope of the bank or shore, and the elevation of the toe of the bank with respect to mean storm high water.

Silberhorn et al. (1974) stated that any marsh two feet (0.61 m) or more in average width has significant value as an erosion deterrent. Garbisch (1977) concurred about the erosion control value of wetland vegetation; however, he specified 10 ft (3.05 m) as the minimum width required to reduce erosion. Reppert et al. (1979) stated that the wider the area of the wetland, the greater the degree of shoreline protection. And they stated that the greater the lateral extent of the wetland along the coastline, the greater the potential for reducing soil erosion and wave damage over the entire adjacent inland area. These authors also stated that wetlands fringing coastal areas with long fetches are more important in protecting shorelines from wave action than are areas characterized by relatively short fetches.

In summary, it appears that wetlands perform a significant role in shoreline anchoring and erosion control; however, experimental evidence as to the exact nature of that role is inadequate for most types of wetland. Knutsen et al. (in press) recently described a technique to evaluate the erosion control effectiveness of marsh vegetation in terms of wave dissipation potential. Their work, to date, has been focused on smooth cordgrass marshes and has led them to conclude that such marshes play a significant role in controlling shoreline erosion. Expansion of this type of research to include other wetland plant species and plant communities may result in a clearer understanding of the role that wetlands play in shoreline anchoring and dissipation of erosive forces.

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WATER QUALITY

GENERAL

Wetlands are believed important in maintaining water quality because they function as filters to remove pollutants and sediments from moving waters. Water changes as it passes through wetlands. These changes occur primarily as a result of: (1) a reduction in the velocity of flowing water as it enters and/or passes through a wetland; (2) the decomposition of organic substances by micro-organisms; (3) the metabolic activities of plants and animals; (4) photosynthesis; and (5) sediment binding of particles.

This section reviews the wastewater treatment functions of wetlands and, more specifically, the role wetlands play in the improvement of water quality through the removal of toxic substances, sediments, and certain nutrients. The section on Food Chain Support/Nutrient Cycling contains a more detailed discussion of the changes in wetland water chemistry that are associated with nutrients. We have attempted to summarize the current status of knowledge regarding this function in Table 2. A listing of some assessment systems that address this function is also included in Table 2.

WASTEWATER TREATMENT

During the past decade, there has been a great deal of interest with regard to the possibility of utilizing natural and/or manmade wetlands for the treatment of wastewater. Studies related to this function have covered a variety of wetland types (e.g., cypress domes, brackish marshes, freshwater tidal marshes, freshwater inland marshes, bogs), located in a broad geographic range (Grant and Patrick 1970; Banus et al. 1975; DeJong 1976; Ewel and Odum 1978; Fetter et al. 1978; Craig et al. 1980; Thibodeau and Ostro 1981). Several reviews of the current status of knowledge about wetlands as wastewater treatment systems have appeared in recent years (Tilton et al. 1976; Valiela et al. 1976; Kadlec 1978; Sloey et al. 1978; Kadlec 1981; Whigham 1982).

The role that wetlands play as wastewater treatment systems is believed primarily dependent on the following wetland attributes: (1) high rates of primary productivity (plants take up pollutants from the water and/or substrate); (2) high rates of sedimentation and accumulation of sediments

Table 2. Summary of current status of knowledge of selected wetland functions - water quality.

Function	Well authenticated	Fairly well authenticated	Poorly authenticated	Existing assessment methods	Remarks
1. Wastewater treatment	Grant and Patrick 1970 Ewel and Odum 1978 Valiela et al. 1976 Kadlec 1978 Kadlec 1981 Whigham 1982			Fritz 1978 Dee et al. 1973 Galloway 1978 Kibby 1978 Reppert et al. 1979 Schuldiner et al. 1979 U.S. Soil Conservation Service 1978 Solomon et al. 1977 U.S. Army Eng. Div., LMV. 1980 Adamus 1983	General agreement exists that wetlands change water quality through retention and/or modification of sediments, toxic substances, and nutrients. The exact nature of the processes involved is not well understood in all cases.
2. Toxic substances	Lee et al. 1976 Lee et al. 1978 Kadlec and Kadlec 1978 Tchobanoglous and Culp 1980 Snyder and Snyder 1982				
3. Nutrients	Snyder and Snyder 1982 Adamus 1983				

(pollutants are readily absorbed by mineral and organic sediments which then become buried in the substrate); (3) anaerobic conditions within the bottom sediments (permits the conversion of soluble forms of heavy metals to insoluble forms and the elimination of nitrogen through denitrification); and (4) high populations of decomposers (which convert pollutants to harmless forms) (Boto and Patrick 1978; Burton 1981; Snyder and Snyder 1982). There is also good evidence indicating that the increased diversity of wetland types may be one of the major factors determining their ability to retain large amounts of nutrients (Blumer 1978).

Snyder and Snyder (1982) concluded that aquatic plants and animals bring about little direct treatment of wastewater. These authors indicated that submerged and emergent vascular plants result in an improved wastewater treatment capability of a wetland primarily by: (1) supplying substrates for bacterial growth; (2) providing a media for physical filtration and absorption; and (3) restricting algal growth and wave action. In other words, the primary role of plants in the wastewater treatment process is through their influence on the physical characteristics of the environment, rather than by their metabolic activities.

Despite the many examples of successful wastewater treatment by wetlands, the exact nature of the processes that contribute to water quality improvement are not well understood. Of particular concern is the lack of knowledge about the impact on the biota from the introduction of waste materials into a wetland over an extended period of time (Guntenspergen and Stearns 1981; Whigham 1982).

TOXIC SUBSTANCES

Heavy metals and various kinds of pesticides are examples of toxic substances that are introduced into wetlands through natural or artificial means. Through chemical and/or biological processes of various kinds, many of these substances are changed to a harmless nontoxic state. However, other substances become temporarily immobile and innocuous because they are buried in sediments.

Snyder and Snyder (1982) stated that heavy metals are removed from wastewater by three mechanisms: (1) ion exchange and adsorption to sediment clays and organic compounds; (2) precipitation as oxides, hydroxides, carbonates, phosphates, and sulfides; and (3) plant uptake. Although plants accumulate certain metals in leaves, roots, and stems under certain conditions, removal of metals by plants is usually small compared to removal by ion exchange, adsorption, and precipitation (Lee et al. 1976; Kadlec and Kadlec 1978; Lee et al. 1978). Plant uptake of metals represents a potential hazard to organisms in food chains, but there is insufficient data to evaluate the magnitude of this hazard (Clark and Clark 1979; Snyder and Snyder 1982). Heavy metal removal efficiencies of wetlands vary from 20 to 100%, depending on the metals involved and the

physical and biological variations in wetland habitats (Tchobanoglous and Culp 1980).

The fate of pesticides and other toxic substances entering wetlands is essentially similar to that of heavy metals. Some of them are immobilized and semipermanently buried in sediments, others are changed by chemical and/or biological processes into harmless forms, and some may enter the food chain.

In summary, many investigations have been conducted that deal with the fate of toxic substances introduced into wetlands. These studies have revealed that most of these toxic substances are either partially or totally assimilated by wetlands. The processes are complex, and the variability in the physical and biological characteristics of wetlands adds to the complexity. The long range capabilities of wetlands to perform such functions, and their long term impact on the biota, are largely unknown.

NUTRIENTS

In water quality studies nitrogen and phosphorus are the substances most commonly identified as pollutants; they are also classified as nutrients. Excess quantities of these nutrients degrade water quality directly through their promotion of algal blooms and population explosions of other undesirable aquatic plants. Nitrogen and phosphorous indirectly degrade water quality through the effects of these increased aquatic plant populations on drinking water, recreational activities, and the dissolved oxygen content of the water. Agricultural and/or urban runoff wastewater are the primary sources of high concentrations of dissolved nitrogen and phosphorus entering wetlands (van der Valk et al. 1978). The levels of these nutrients within a wetland are modified by a variety of processes, including the form of the nutrient, the wetland type, and the season of the year.

Snyder and Snyder (1982:107-109) summarized some of the modification processes as follows:

Phosphorus is removed in freshwater wetlands by plant uptake during the growing season and by several chemical adsorption and precipitation reactions at the sediment/water column interface. Chemical adsorption by organic detritus and precipitation appears to be the most significant phosphorus removal mechanism.

Plant uptake of phosphorus during spring and early summer only amounts to about 20% of the total amount available (Sutherland and Bevis 1979). This storage, however, is compensated for by the release of phosphorus from plant tissue decay during the winter. The net removal is rarely greater than 5 to 10 percent of the annual total loading (King and Burton 1979). Harvesting of plant tissue is a

feasible but uneconomical removal technique because only an average of one gram of phosphorus per square meter of plant biomass is removed from the marsh (Spangler et al. 1976). Regular plant harvest would also reduce the waterfowl habitat value of the wetland.

Wetlands receiving phosphorus loaded wastewater usually demonstrate relatively high removal efficiencies of phosphorus at first because of direct adsorption by organic bottom sediments. However, the removal process is finite and declines with time. When first put into use, ponds will show excellent phosphorus removal, but once all available adsorption sites are filled, there is no compensating mechanism in the system that allows continued phosphorus removal at the initial high levels.

The settling of metal phosphate precipitates is a removal mechanism that occurs at a pH greater than 8.0. The major factors determining how much phosphorus will be stored as metal-phosphate precipitates in an aquatic system are pH, redox potential, and the concentration of iron, aluminum, calcium and clay minerals.

The primary mechanism for nitrogen removal from wastewater is bacterial metabolism through nitrification/denitrification processes. Wetlands with standing water areas are typically very effective at removing the various forms of nitrogen. Removal efficiencies vary from 40 to 97 percent and often exceed 90 percent. Nitrification and denitrification occur at the water/substrate interface where bacteria are attached. This includes bottom sediments and submerged plant parts.

Nitrifying bacteria occupy aerobic zones where the dissolved oxygen is above 0.6 to 1.0 ppm. In aquatic systems, the rate of nitrification can be extremely variable and depends primarily on water temperature and the amount of bacteria support structure (plant stems and leaves) available in the oxygenated zone. At water temperatures below approximately 50 F, the rate of nitrification is very slow.

Denitrification is caused by anaerobic bacteria found in anoxic bottom sediments and detrital layers of the proper pH. The denitrification rate varies according to the water temperature, pH, organic carbon availability, and available bottom surface area.

Nitrogen uptake and removal by vascular plants and algae is comparatively insignificant on an annual basis. Like phosphorus, nitrogen is seasonally removed during the spring and then released during the winter by organic decay and leaching processes. Net annual biomass storage is low and insignificant.

Adamus (1983) did a thorough job of reviewing the nutrient retention and removal attributes of wetlands. By nutrient retention, he is referring primarily to the storage of nutrients (nitrogen and phosphorus) within the substrate or vegetation. By nutrient removal, he is referring to the elimination of nitrogen nutrients by conversion to gas. As a result of his extensive review of the literature, he concluded that wetlands valuable for nutrient retention and removal usually have the following characteristics (Adamus 1983. Vol. I:23):

(1) The wetland's vegetation, on a net annual basis, assimilates and transfers to deep sediments (via the roots) more nutrients than are subsequently released via leaching and decay. The wetland's plants are efficient at nutrient storage during the season (typically the growing season) when downstream or offshore systems are most sensitive to nutrient enrichment. (2) The substrate accumulates organic matter on a net annual basis (rather than most organic matter being released into the water column with decomposition). (3) Sediments accumulate (accrete) faster than they are removed, and once accumulated, the nutrients contained in these sediments remain intact and are not brought to the surface in significant quantities by plants and animals. (4) The rate of denitrification consistently exceeds that of nitrogen fixation.

In summary, wetlands function in varying degrees as "nutrient traps." In other words, they are capable of improving water quality through the removal of nutrients from runoff waters. Wetland efficiency in this regard varies with many factors, including vegetative characteristics, geographic location (especially latitude), nature of the substrate, size, water chemistry, temperature, and pH. Considerably more study is necessary to clarify the exact nature of the role of wetlands in this regard and the long term effects of nutrient pollutants on the wetland ecosystem.

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FOOD CHAIN SUPPORT/NUTRIENT CYCLING

GENERAL

The food chain support function of wetlands refers to the direct or indirect use of nutrient sources derived from wetlands by heterotrophic organisms. These organisms may be located permanently or temporarily in the wetland proper or in associated, downcurrent wetland or aquatic areas. Of primary interest with respect to this function is the cycling of carbon, phosphorus, and nitrogen in their organic and inorganic forms.

Wetlands, as with all ecosystems, have an inherent functional value in terms of food chain support. The basis for this value is, of course, the primary production of wetland autotrophs. Autotrophs provide the link between heterotrophs and the energy and nutrient sources of the ecosystem by performing two essential functions. First, plants utilize solar energy in the process of photosynthesis to fix carbon and store chemical energy in their tissues. Secondly, autotrophs take up inorganic nutrients from their environment and incorporate them into organic forms. The energy and nutrients stored in wetland autotrophs, directly or indirectly, supply the needs of all heterotrophic organisms in wetland-related food chains.

The production of organic materials by wetland autotrophs does not guarantee that the material will be incorporated into heterotrophic food chains. Additional factors, such as decomposition, export, and actual utilization by consumers, ultimately determine the fate of wetland net primary productivity (NPP).

The current state of knowledge regarding this function is summarized in Table 3, along with a listing of some assessment systems that address this function.

PRIMARY PRODUCTION

The underlying factor influencing the functional role wetlands play in the support of food chains is the quantity of NPP produced within the wetland and potentially available for incorporation into food chains.

Table 3. Summary of current status of knowledge of selected wetland functions - food chain support/nutrient cycling.

Function	Well authenticated	Fairly well authenticated	Poorly authenticated	Existing assessment methods	Remarks
1. Primary production	Westlake 1963 Brinson et al. 1981 Richardson 1979 Good et al. 1978 Dykjova and Kvet 1976 Westlake 1975 Keefe 1972 Adamus 1983	Whittaker and Likens 1975		Virginia Inst. Marine Sci. (undated) Galloway 1978 Reppert et al. 1979 Schuldiner et al. 1979 Adamus 1983	It is well documented that wetlands, in general, have high rates of net primary productivity (NPP). The energetic and nutrient connection between wetland NPP and wetland/aquatic secondary production is widely accepted but is based on qualitative evidence and speculation to a large degree. The assumption that nutrients exported from wetlands are important in food chain support has the least amount of supportive evidence. Only a few assessment methods include the food chain support function in their procedure. The Adamus (1983) system has this type of rating and uses high-medium-low ratings, but is based on many more predictors than other methodologies.
2. Nutrient export		Odum and Heald 1975 Odum and de la Cruz 1967 de la Cruz 1979	Nixon 1980 Brinson et al. 1981 Correll 1978 Haines 1979		
3. Secondary production (utilization)	Crow and MacDonald 1979 Weller 1979 Clark 1979 Martin and Uhler 1939 Shanholzer 1974 Ohmart and Anderson 1979	Turner 1977 Tihansky and Meade 1977			

Wetlands, in general, support high levels of NPP compared to other types of ecosystems (Westlake 1963; Whittaker and Likens 1975). High levels of NPP presumably indicate a high potential for food chain support. A number of studies have estimated the primary production of various coastal and inland freshwater wetland types (e.g., saltmarshes and cypress swamps), photosynthetic components (e.g., macrophytes and phytoplankton), and species (e.g., *Typha* spp. and *Spartina* spp.). Publications that effectively summarized this literature include Spence et al. (1971), Keefe (1972), Westlake (1975), Dykyjova and Kvet (1976), Turner (1976), Bagur (1977), Reimold and Linthurst (1977), Good et al. (1978), Richardson (1979), Brinson et al. (1981), and Adamus (1983). It should be noted that information gaps exist even though the literature is fairly extensive and that the quantity and quality of available primary production estimates are not equivalent for all wetland types and photosynthetic components.

Estimates of NPP for specific wetland types and plant species often vary widely. Several factors are at least partially responsible. First, the lack of standardized methods for estimating NPP contributes significantly to this variation (Linthurst and Reimold 1978; de la Cruz 1979; Hardisky 1981; Shew et al. 1981; Brinson et al. 1981). Soil and water chemistry factors can influence primary production. Productivity declines where critical inorganic nutrients (phosphorus and nitrogen) are limited (Broom et al. 1975; Valiela et al. 1975; Patrick and Delaune 1976; Loucks and Watson 1978; Schindler 1978; Valiela et al. 1978; Farnsworth et al. 1979; Linthurst and Seneca 1980). Large deviations from a neutral pH decrease productivity (Heinselman 1970; Small 1972; Darnell et al. 1976; Richardson 1979). Moderately high levels of alkalinity enhance freshwater aquatic plant growth (Moyle 1945; Darnell et al. 1976). Adamus (1983. Vol. I:71) cited numerous studies that documented decreased production in wetlands with high salinity. Adamus (1983. Vol. I:94) also cited a number of studies where turbidity, through a reduction in light penetration, decreased productivity in submerged aquatics. Other factors that influence productivity are climatic in nature. Latitudinal variation in primary production has been shown in several studies, to be related to one or more climatic factors (Bernard 1973; Gorham 1974; Turner 1976; Reader 1978). Factors related to hydrologic regime, such as tidal amplitude, flow velocity, and hydroperiod have often been cited as influencing primary production. Steever et al. (1976), Gosselink and Turner (1978), Hern and Lambou (1978), Brinson et al. (1981), and Adamus (1983. Vol. I:75,79,80) reviewed and discussed studies dealing with this relationship. A complex of factors, including nutrient removal, oxygen levels, and other factors, presumably account for this relationship between hydrologic regime and primary production.

Despite the gaps in knowledge and the variation in NPP estimates, the information available on wetland NPP is believed, by at least some researchers, to be adequate to establish credible value ranges of NPP for different wetland types and plant species (Richardson 1979; Adamus 1983).

DECOMPOSITION

The net primary production is just one of a number of factors that ultimately determine the functional value of a wetland in the support of food chains. Plant tissues may need to be chemically and physically altered through decomposition prior to utilization by consumers. Decomposition begins with the leaching of soluble substances from the tissues, followed by a gradual mechanical breakdown and biological oxidation of the tissues to particles of decreasing size and chemical complexity. These particles provide a substrate for bacteria, fungi, and other microorganisms, which add to the nutritive value of the so-called detritus (Odum 1970; Fenchel 1972; Mann 1972; Fell and Master 1973; Darnell et al. 1976; Gallagher et al. 1976; Adamus 1983). Certain consumers are thought to strip the attached microorganisms from detritus as the detritus passes through their digestive tract. The resulting feces become available for recolonization and ingestion by other microorganisms (Adams and Angelovic 1970; Odum and Heald 1975). In some studies, a large number and variety of heterotrophic consumers were found to utilize the dissolved nutrients and detritus particles produced by the decomposition process (Odum and Heald 1975; Clark 1979). These consumers, in turn, supply the nutrient requirements of higher trophic level consumers.

The relationship between decomposition and food chain support is not clearly understood. Under conditions suitable for rapid decomposition, nutrients presumably become quickly available for use in detritus food chains or reuse by wetland autotrophs. Under conditions of slow decomposition, a greater potential exists for nutrients to accumulate in organic sediment sinks. Depending on the other factors that control nutrient availability, the latter situation could limit NPP and the ability of a wetland to support food chains.

The decomposition rate of wetland plant materials is influenced by a number of species-specific and environmental factors. Physical and chemical characteristics of plants, such as total fiber content (Godshalk and Wetzel 1978), surface to volume ratio (Seliskar et al. 1977; Chamie and Richardson 1978), and component proteins (Handley 1961) influence the rate of decomposition. Decomposition rates for a number of freshwater and saltwater plant species have been documented (Visser 1964; Boyd 1970; Odum et al. 1972; Mason and Bryant 1975; Chamie and Richardson 1978; Davis and van der Valk 1978a,b; Godshalk and Wetzel 1978; Odum and Heywood 1978; de la Cruz 1979). In general, decomposition rates are greatest in algae and decrease through submerged aquatics to emergent and woody macrophytes (Gallagher 1978; Tilton and Schwegler 1979).

Several authors have suggested that temperature is the most important environmental factor affecting decomposition rates (Godshalk and Wetzel 1978; Montagna and Ruber 1980; Brinson et al. 1981). Decomposition rates of cellulose were shown to correlate with maximum and minimum water temperatures in at least one study (Brinson 1977). Moisture and oxygen levels also influence decomposition rates. The hydrologic regime of a wetland has a large measure of control over both these factors. Wetlands may contain a wide range of conditions from stagnant, oxygen-depleted

sediments and water column to fluctuating water levels with alternating anaerobic and aerobic conditions to exposed sediments with continually aerobic conditions. Adamus (1983) cited numerous studies that documented high decomposition rates under the aerobic conditions, often associated with temporary flooding, moving water, and exposed sediments. Periodic wet/dry cycles also enhance decomposition (Stevenson 1956; Birch 1958; Van Schreven 1967; Sorenson 1974). Decomposition is likely to be greatest under aerobic conditions, coupled with some optimal wet/dry cycle (Brinson et al. 1981). Factors that decrease decomposition rates include salinity (Odum and Heywood 1978; Odum et al. 1979) and acidity (Heinselman 1970; Chamie and Richardson 1978).

There is strong evidence that the process of decomposition is an important factor in determining the functional value of wetlands in the support of food chains. However, although the literature identifies the factors controlling the decomposition process, few attempts have been made to directly link decomposition to the food chain support function of wetlands.

NUTRIENT EXPORT

The export capability of a wetland is an important factor that needs to be included when considering the food chain support function of wetlands. Presumably, nutrient export increases the food chain support function by allowing a greater number and variety of heterotrophic organisms to make use of wetland-derived nutrients (de la Cruz 1979). Nixon (1980) indicated that, while the range of primary production in wetlands varies by a factor of approximately 10, the range of flushing capacity is much greater. Thus, in terms of food chain support, the capability of a wetland to export nutrients is potentially of greater importance than the level of NPP.

Nutrient export from wetlands has been studied most extensively in the Atlantic and Gulf coastal wetlands. Early studies of particulate organic carbon export in the salt marshes of Georgia provided a basis for the hypothesis that detritus from coastal marshes was important in the maintenance of secondary productivity in adjacent estuaries and coastal waters. Studies also have been conducted on nutrient export in Florida mangrove swamps (Heald 1969; Odum 1971; Odum and Heald 1975) and salt marshes in Louisiana (Day et al. 1973), Georgia (Reimold et al. 1975), and New England (Nixon and Oviatt 1973; Valiela et al. 1978). However, there is also documentation in the literature of coastal wetlands where no net export and, in some cases, a net import of nutrients occurred (Nadeau 1972; Heinle and Flemer 1976; Hackney 1977; Woodwell and Whitney 1977; Woodwell et al. 1977).

Nixon (1980) reviewed the literature relating to this subject and concluded that, while the amount of export varies significantly, the majority of coastal marshes export dissolved and particulate organic nutrients to adjacent estuaries and coastal waters. However, the importance of this exported material in the support of food chains is not

totally clear. There is recent evidence suggesting that detritus, exported from coastal wetlands, might not be the most important source of nutrients for estuarine and coastal heterotrophs, as has often been assumed. Several authors (Correll 1978; Haines 1979; Haines and Montagna 1979) reported that, in estuaries at least, the most important sources of nutrients are phytoplankton, submerged vasculars, and benthic or epiphytic algae, rather than detritus exported from tidal marshes. Nixon (1980) concluded that, at least in the case of Atlantic coastal marshes, there is no convincing evidence as yet to support the belief that these marshes play a significant role in the support of estuarine secondary productivity through detritus export. On the basis of the limited data available, it appears that nutrient export in Pacific coastal marshes is not significant in the support of secondary productivity (Onuf et al. 1979).

The export of nutrients from inland freshwater wetlands has not received the extensive study given coastal wetlands and, consequently, the subject is poorly documented. Several authors have suggested that floodplains are important to the productivity of rivers and streams (Marlier 1973; Hynes 1975; Sioli 1975, cited in Merritt and Lawson 1979). Brinson et al. (1981) shed light on this subject in an indirect manner. In reviewing the literature, these authors found that rivers that drain watersheds with a significant wetland component have higher dissolved organic carbon (DOC) and total organic carbon (TOC) concentrations than do rivers that drain watersheds with negligible wetlands. Levels of particulate organic carbon (POC) were not reported and were presumed to show no consistent pattern.

The export of nutrients from a wetland is influenced by a number of factors. Of primary importance is the flow of water through the wetland. Wetlands with water flow in the form of tides (Mason and Bryant 1975; Odum and Heald 1975; Gosselink and Turner 1978) and seasonal floodwater (Darnell et al. 1976; Brown et al. 1979; Frederickson 1979) have increased levels of nutrient export. Adamus (1983) cited a number of studies where nutrient export increased with an increase in the velocity of waterflow. Factors that increase water circulation in a wetland help keep the amount of nutrients available for export high. These factors include vertical mixing (Gallagher 1978; Gosselink and Turner 1978; Peterson and Peterson 1979), sediment disturbance by scouring (Adamus 1983), and activities of invertebrates and waterfowl (Lynch et al. 1947). The form of the nutrients also helps determine their likelihood to be exported; materials that are dissolved or suspended are more easily moved by water than heavy, sinking materials (Zieman et al. 1979).

Several authors have suggested that the variability in nutrient export exhibited by coastal marshes is due to factors such as the geomorphology of the wetland basin, tidal amplitude, freshwater input, and possibly other biological and chemical factors (Correll 1978; Odum et al. 1979; Odum 1980). In addition, Odum et al. (1979) stated that, if the "pulsed nature of particulates" and all forms of particulate transport (floating, suspended, and bed) are taken into consideration, the prediction of nutrient flux should be possible based on geomorphological and hydrologic factors.

The longstanding consensus that wetlands (particularly tidal wetlands) support aquatic food chains through the export of nutrients is now being questioned. While it appears that many coastal wetlands export nutrients, it is not clear how significant the export is in terms of total energy and nutrient budgets. It appears that the question of food chain support through the export of nutrients must be answered on a site-specific basis for different wetland types in different geographic locations. Information concerning nutrient export in freshwater wetlands is scarce and deals mainly with wetlands associated with rivers. A considerable research effort, in a variety of wetland types, is necessary to evaluate the overall importance of wetland nutrient export to heterotrophic food chains.

NUTRIENT UTILIZATION

If the food chain support function is to be realized, wetland-derived nutrients must actually be consumed by heterotrophs in wetlands or associated aquatic areas. Nutrients are incorporated into these food chains via one of two pathways. In the first pathway, often called the grazing pathway, living plant materials are consumed directly by herbivores. The other alternative, often called the detritus pathway and presumed by many researchers to be quantitatively more important, involves the consumption of dead plant materials in various stages of decomposition by low trophic level heterotrophs. These low trophic level consumers, in turn, become an indirect source of wetland-derived nutrients to higher trophic level consumers. The greatest number of studies concerning the utilization of wetland-derived nutrients have been conducted on higher trophic level species with commercial and/or recreational importance. Very few trophic relationships of heterotrophs in the detritus pathway have been studied; consequently, their role in food chain support, while often believed to be great, is largely undocumented and hypothetical (Crow and MacDonald 1979; Tilton and Schwegler 1979; Saunders et al. 1980). Crow and MacDonald (1979) and Weller (1979) recently published overviews of the important role wetlands play in the support of grazing and detritus food chains.

The role wetlands play in supplying nutrient resources is best documented for the grazing food chain, and the most extensive body of literature deals with wildlife species directly important to man. This literature is too voluminous to be discussed in detail in this report. Waterfowl use wetland plant (seeds, foliage, roots, and tubers) and animal (macroinvertebrates and fish) food sources extensively (Martin and Uhler 1939; McAtee 1939; Bellrose 1941; Moyle and Hotchkiss 1945; Collias and Collias 1963; McRoy 1966). Furbearers, such as muskrat, nutria, beaver, and raccoon, depend on certain types of wetlands for a large portion of their food requirements (Bellrose and Brown 1941; Baumgartner 1942; Harris and Webert 1962; Errington 1963; Shanholzer 1974). Big game species, such as moose, caribou, and bear, graze on wetland vegetation (Peterson 1955; U.S. Army Corps of Engineers 1978, cited in Crow and MacDonald 1979; Aho and Jordon 1979). Wetlands are also a source of food for nongame birds (Kahl 1964; Wharton et al. 1977; Ohmart and Anderson

1979) and small mammals (Toll et al. 1960; Birkenholz 1963; Crow and MacDonald 1979).

A few studies have dealt with the use of wetland food resources by insects. Marsh grasshoppers and planthoppers graze directly on saltmarsh cordgrass, *Spartina alterniflora* (Odum and Smalley 1959; Smalley 1960; Davis and Gray 1966; Marples 1966). Foster and Treherne (1976) concluded that insects consume less than 5% of the annual saltmarsh cordgrass NPP. Brinson et al. (1981) cited several investigations where insects consumed significant amounts of wetland NPP under certain conditions, such as frost damage (Haslam 1970), logging disturbance (Conner and Day 1976), and nutrient enrichment (Onuf et al. 1977).

Because of the complexity of detritus food chains, it is difficult to link the wetland-derived nutrients that follow this pathway to their actual utilization at higher trophic levels. The literature on this topic is less extensive and convincing than the literature available for the grazing food chain. There is documentary evidence that supports the longstanding belief that detritus is an important element in the food chains of coastal and freshwater wetland and aquatic ecosystems (Odum 1970; Melchiorro-Santolini and Hopton 1972; Odum and Heald 1975; Thayer et al. 1975; Kirby-Smith 1976). A number of studies have shown that wetland-derived detritus and/or detritivores serve as a source of food for coastal and freshwater finfish (McHugh 1966; Odum 1970; Jefferies 1972; Wiley et al. 1973; St. Amant 1973; Adams 1976; Marzolf 1978; Peters and Schaffe 1981), shellfish, and crustaceans (Mock 1967; Welsh 1975; Turner 1977).

The functional value of wetlands in terms of food chain support is not well understood at this time. This is due, in part, to the large number of factors and processes (e.g., NPP, decomposition, export, and utilization) that influence this function and, in part, to the lack of good information as to how these factors and processes are related to the support of food chains (especially the detritus food chain). More information is needed concerning the breakdown and movement of energy and nutrients through wetland and aquatic food chains before this function of wetlands can be properly understood and evaluated.

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HABITAT

GENERAL

Wetlands provide habitat for a variety of plants and animals. Some animals are completely dependent on wetlands for food, protection from weather and/or predators, resting areas, reproductive materials or sites, molting grounds, and other life requisites. Other animal species use wetlands for only part of their life functions. Some species spend their entire life within a particular wetland; other species are resident only during a particular period in their life cycle or during the year or travel from wetland to wetland. Some animals use wetland habitat throughout their lives, but reside primarily in deepwater or upland habitats (Chabrek 1971; Shanholtzer 1974; Clark and Clark 1979; Weller 1981; Zinn and Copeland 1982). Wetlands also provide necessary habitat for many rare and endangered plant and animal species. More than half the areas identified as critical habitat under provisions of the Endangered Species Act involve wetland areas (Zinn and Copeland 1982).

Many factors are of importance in determining the value of wetlands as habitat for animals, including the structure and species diversity of the vegetation, surrounding land uses, spatial patterns within and between wetlands, vertical and horizontal zonation, size, and water chemistry (Golet 1973; Schitoskey and Linder 1978; Clark and Clark 1979; Zinn and Copeland 1982). Knowledge of habitat values for all forms of wildlife associated with southwestern wetlands is reported to be little beyond the general survey stage (Ohmart and Anderson 1978) and, with the notable exception of pheasants (Gates and Hale 1974; Sather-Blair and Linder 1980; Linder and Hubbard 1982) and white-tailed deer (Sparrowe 1966; Rongstad and Tester 1969), there has been surprisingly little documentation of the use of wetlands by upland game species.

We have attempted to summarize the current status of knowledge of this function in Table 4. A listing of some assessment systems that address this function is also included in Table 4.

Table 4. Summary of current status of knowledge of selected wetland functions - habitat.

Function	Well authenticated	Fairly well authenticated	Poorly authenticated	Existing assessment methods	Remarks
1. Invertebrates and cold blooded animals (other than fishes)			Clark 1978 Thayer et al. 1978 Tilton and Schweger 1978 Clark and Clark 1979 Weller 1978	U.S. Army Eng. Div. NE. 1972 Dee et al. 1973 Golet 1973 Brown et al. 1974 Fried 1974 Larson 1976 Solomon et al. 1977	With the exception of certain species of commercial importance (e.g., shrimp, oysters, and crayfish), knowledge of the wetland habitat requirements of invertebrates is sketchy.
2. Fisheries		Niering 1970 Onuf et al. 1978 Weller 1978 Thayer et al. 1978 Clark and Clark 1979 Larson 1981 Zinn and Copeland 1982 Adamus 1983 Clark 1978		Galloway 1978 U.S. Soil Conservation Serv. 1978 Reppert et al. 1979 Winchester and Harris 1979 U.S. Army Eng. Div.. LMV 1980 U.S. Fish and Wildlife Service 1980 Virginia Inst. Marine Science (undated) Maryland Dept. Nat. Resour. (undated) Adamus 1983	The habitat value of wetlands to commercial and salt water sport fishes and to fishes of the Great Lakes is fairly well documented; however, similar values for fishes of the Pacific Coast and inland freshwater wetlands are not well known.
3. Mammals		Wharton et al. 1981 Clark and Clark 1979 O'Neil 1949 Errington 1963 Palmisano 1972 Chabrek 1962 Hair et al. 1979			With the exception of muskrats, nutria, and beaver, the habitat requirements of mammals are not well known. Individuals and some populations of several species of small mammal spend their entire lives in wetlands; however, their specific requirements are not well known. Several species of large mammals periodically, usually seasonally, visit wetlands.

Table 4. Concluded.

4. Nongame birds	Gaines 1977 Flake and Vohs 1979 Rundle and Frederickson 1981 Sprunt 1968 Pitelka 1979 Oriens 1961 Weller and Spatcher 1965 Adams and Quay 1958	Adams 1983	Kroodsma 1978	The general wetland habitat requirements of a few species of nongame birds and several species of game birds are well known. In most cases, specific details are missing.
5. Game birds	Sather-Blair and Linder 1980 Linder and Hubbard 1982 Adams 1983			

INVERTEBRATES AND POIKILOTHERMAL VERTEBRATES

It is generally agreed that the study of wetlands as habitat for invertebrates (particularly those making up the microfauna) and poikilothermal vertebrates has been largely ignored (Thayer et al. 1978; Tilton and Schweger 1978; Clark and Clark 1979). A tremendous variety of these types of organisms occur in wetlands, and there is great variation in the kinds and numbers of invertebrates and poikilothermal vertebrates that different types of wetlands will support. Some of the southern wetlands closely associated with riverine habitats support a rich variety of these organisms; whereas, acid bog lakes in northern areas may have reduced species diversity and density of invertebrates and poikilothermal vertebrates (Clark 1978; Frederickson 1978; Wharton et al. 1981).

Weller (1978) indicated that most studies of invertebrates inhabiting wetlands have been taxonomic and descriptive in nature and that little is known about habitat selection, niche segregation, factors influencing taxonomic diversity, indicator species for habitat conditions, and community structure. Weller also stated that a considerable amount of work remains to be done on niche segregation in wetland amphibian populations and that invertebrates are very important in the food chain function because of their role in the conversion of plant energy into animal food chains.

Clark (1978) presented an excellent review of current knowledge about freshwater wetlands as habitat for aquatic invertebrates, fishes (especially forage species, but also game species), amphibians, and reptiles. She concluded that the number of taxonomic groups associated with freshwater wetlands is large and that there apparently is no typical wetlands fauna. She stated that, for most wetland types, there are insufficient data to allow generalizations about the richness or poverty of the entire invertebrate and cold blooded vertebrate fauna. For a comprehensive review of invertebrates and vertebrates associated with bottomland hardwood habitats, see Wharton et al. (1981).

Krull (1970) reviewed some of the literature on aquatic invertebrates and found that many investigators commented on the general relationship between the abundance of aquatic invertebrates and the presence of hydrophytes. However, few studies focused specifically on the quantitative aspects of plant invertebrate associations in aquatic environments. Krull also observed that there is practically no differentiation in the literature between bottom fauna abundance in plant-free areas and in areas exhibiting a growth of submerged hydrophytes. His own studies revealed: that each plant species generally has several kinds of animals associated with it throughout its entire life, that the abundance of these animals reaches a peak soon after the plant appears, that their weight and numbers tend to decline as the season progresses, and that the number of organisms increases with an increase in plant surface area. Tilton and Schweger (1978) pointed out that studies of Great Lakes wetland ecosystems indicated that vegetated areas generally have higher densities of invertebrates than nearshore areas without vegetation, and emergent areas generally have

higher densities of invertebrates than submerged or floating-leaved aquatic plant habitats.

Clark (1978) singled out the following factors as important wetland features that control the abundance and diversity of wetland invertebrates and poikilothermal vertebrates: wetland size and location relative to other wetlands; wetland setting (relationship of the wetland to other aquatic and terrestrial systems); substrate; vegetation structure; water regime; water quality; competition; and predation. She pointed out that these are the same factors mentioned as habitat requirements of wetland birds and mammals.

FISHERIES

The value of wetlands for fish is well established for Atlantic and Gulf coast wetlands. Estuarine salt marshes in the Northern Pacific coastal area are known to be very important to the production of many animal species. However, little is known about the importance of coastal wetlands in the southern portions of the Pacific coast (Niering 1970; Onuf et al. 1978; Thayer et al. 1978; Clark and Clark 1979; Larson 1981; Zinn and Copeland 1982).

The bulk of the United States commercial and saltwater sport fish catch is probably dependent on coastal estuaries and their wetlands for food sources, spawning grounds, and nurseries for young (McHugh 1976; Larson 1981). The U.S. Department of Commerce estimated that, on the Atlantic and Gulf coast, 66 to 90 percent of the commercially important fish and shellfish species depend on coastal marshes or estuaries for at least part of their life cycle.

Clark (1978) pointed out that fishes of freshwater wetlands are usually dominated by forage species, such as killifish, shiner, mosquito fish, pigmy sunfish, and other sunfish. Clark stated that most of the larger fishes are nonpermanent residents of freshwater wetlands, entering the wetlands only to feed and/or spawn at certain times of the day or seasons of the year. Several workers have reported that many game fishes (e.g., northern pike, walleye, yellow perch, green sunfish, and bluegills) are wetland-dependent spawners (Clark 1978; Weller 1978; Clark and Clark 1979; Larson 1981; Zinn and Copeland 1982; Adamus 1983). The nursery function of wetlands for these larger game fish is well documented for the Great Lakes, but not as well documented for other freshwater wetlands (Clark 1978).

On the basis of an extensive review of the literature, Adamus (1983) concluded that the major factors influencing a wetland's habitat value for fisheries are the: (1) water quality (physical and chemical); (2) water quantity (hydroperiod, flow, and depth); and (3) cover, substrate, and interspersation. The water quality factors of greatest importance to marine and estuarine fisheries are salinity and temperature, with dissolved oxygen and turbidity occasionally playing an important role. Freshwater fisheries

are primarily influenced by temperature and dissolved oxygen, with turbidity, alkalinity, and pH sometimes important. Water quantity factors of importance to fisheries include depth, volume, velocity, width, and hydroperiod. "Cover" refers to areas used by animal species for protection from predators and climatic conditions or as a substrate for feeding and reproduction. Substrate is self-explanatory; interspersions refers to the relationships between open water and vegetation, various types of vegetation, and various types of substrates.

MAMMALS

Relatively few species of mammals are truly wetland-dependent; however, a large number of mammalian species have individuals and/or populations that are wetland-dependent in some areas and/or at certain times of the year. Muskrats, nutria, beavers, marsh rice rats, and swamp rabbits are examples of totally wetland-dependent species; otter, mink, raccoon, meadow mice, moose, and white-tailed deer are examples of partially wetland-dependent species (Weller 1978).

The muskrat is widely distributed throughout North America and has been the subject of many intensive studies (Johnson 1925; Baumgartner 1942; Lay and O'Neil 1942; Dozier et al. 1948; Gashwiler 1948; O'Neil 1949; Harris 1952; Dozier 1953; Sather 1958; Errington 1963; Palmisano 1972; Proulx 1982). The habitat requirements of the muskrat in both coastal and inland wetlands are well documented. Three of the major factors affecting the habitat value of wetlands for muskrats are: (1) water depth; (2) water quality; and (3) emergent aquatic plants. Muskrats are widely distributed in North America and range from the subtropical rivers and brackish coastal marshes of the Southeast to the Arctic tundra. Throughout this broad range, muskrats adjust to a surprising variety of habitat conditions. In general, however, they require water that is deep enough to enable them to remain active under the ice in winter at the more northern latitudes and to support the growth of emergent plants for food and cover. Large fluctuations in water levels pose serious problems for muskrats. High water levels may result in the flooding of bank burrows and/or the destruction of muskrat houses; low water levels may increase the vulnerability of muskrats to predators. Muskrats occur in both fresh and brackish wetlands. However, modifications in water quality that result in the loss of emergent vegetation have an adverse impact on a muskrat population. Emergent vegetation consisting of species suitable as forage and for house construction (e.g., cattails and bullrushes) appears to be essential in terms of supporting healthy muskrat populations. The size of the wetland is not a factor; muskrats occur in wetlands varying in size from small roadside pools to marshes covering thousands of acres.

The habitat requirements of two other economically important wetland-dependent mammals, nutria and beaver, have been fairly well documented. In coastal marshes of the Southeast, the habitat requirements of nutria are similar to those of muskrats; however, nutria prefer fresh over brackish water (Chabreck 1962; Garner 1962; Harris and Webert 1962; Milne and

Quay 1966; Lowry 1974; Brown 1975; Clark and Clark 1979; Shirley 1979; Willner et al. 1979; Love 1981; Simpson 1981).

Like muskrats, beaver have a very broad geographic range. They occur in a large variety of aquatic situations, many of which they create. Although they sometimes use the same habitat as muskrats, beavers are more dependent on the presence of woody vegetation (Bradt 1947; Swank 1949; Grasse 1950; Denney 1952; Retzer et al. 1956; Parrish 1959; Henderson 1960; Wilkinson 1962; Longley and Moyle 1963; Arner 1964; Rutherford 1964; Henry 1967; Byford 1974; Hair et al. 1979; Willis 1978; Hodgdon and Larson 1980; Echternach 1981).

There is surprisingly little information available concerning the life history and ecology of mink and river otter, two economically important species that are closely associated with wetland habitat. The river otter has been the subject of some recent studies in this country (Field 1971; Tabor 1973; Grenfell 1974; Modafferi and Yokum 1980; Anderson and Scanlon 1981; Beckel 1982). However, relatively few field studies have been conducted on mink. Allen (1983) gives a good review of what is known about the habitat requirements of mink. The raccoon, another economically important mammal associated with wetlands, has been extensively studied (Caldwell 1963; Johnson 1970; Urban 1970; Cowan 1973; Sanderson and Nalbando 1973; Fleming 1975; Fleming et al. 1978; Bigler et al. 1981; Greenwood 1981).

Several species of small mammals (e.g., short-tailed shrew, white-footed mouse, meadow mouse, bog lemming, cotton mouse, wood rat, cotton rat, and swamp rabbit) live in wetlands. In most cases, populations of these species live in a wetland, as well as in adjoining upland habitats. Wharton et al. (1981) reviewed what is known about the habitat requirements of many of these species in the bottomland hardwood habitats of the Southeast.

In some localities, several larger mammalian species (e.g., opossum, fox, coyote, white-tailed deer, and moose) are dependent to some degree on wetlands. Seasonal use of wetlands by white-tailed deer, particularly in the northern part of their range, is well documented (Kellogg 1956; Sparrowe 1966; Rongstad and Tester 1969). Forested wetlands, dominated by conifers, typically serve as winter yarding areas for deer in the Northern States. Moose also exhibit a close seasonal association with wetlands.

In summary, there is a surprising lack of specific information pertaining to the wetland habitat requirements of mammalian species with the exception of muskrat and nutria, and possibly beaver. This is true even for economically important species, such as mink and raccoon, that are totally wetland-dependent in some parts of their range.

NONGAME BIRDS

The importance of wetland habitats for nongame birds has been documented for riparian habitats (Carothers and Sharber 1976; Gaines 1977; Johnson and Jones 1977; Hehnke and Stone 1979) and for saltmarsh and estuarine habitats (Sprunt 1968; Pitelka 1979). There are a few studies that deal specifically with inland freshwater wetlands as habitat for nongame birds (Evans and Krebs 1977; Peterson and Flake 1977; Flake and Vohs 1979; Rundle and Frederickson 1981). Hair et al. (1979) and Reese and Hair (1976), in their studies of beaver pond complexes, showed that riparian wetlands are important habitat for a wide variety of game and nongame species of birds.

Among the passerine birds associated with wetlands, blackbirds, particularly red-winged blackbirds, have been studied the most intensively (Orians 1961; Meanley 1962; Case and Hewitt 1963; Meanley and Webb 1963; Weller and Spatcher 1965; Meanley and Mitchell 1966; Willson 1966; Goddard 1967; Holcomb and Twiest 1968; Orians and Horn 1969; Keeler 1970; Jackson 1971; Cutright 1973a,b; Albers 1978; Lederer 1978; Johnson 1979).

Several studies have been conducted on the Atlantic and Gulf coasts that dealt with the food habits and habitat requirements of rails (Oney 1951; Adams and Quay 1958; Bateman 1965; Meanley 1965; Roth et al. 1973).

In general, little is known about the requirements of most species of nongame birds that inhabit inland freshwater wetlands. Kroodsmma (1978) stated that about a third of the North American bird species use wetlands and that three-fourths of these species are nongame birds whose ecological significance remains poorly understood.

GAME BIRDS

Adamus (1983) surveyed the literature pertaining to the habitat requirements of game birds associated with wetlands. His analysis focused primarily on waterfowl, but also considered some other harvested game and nongame birds. The major habitat factors identified in this analysis (availability of cover, freedom from disturbance, availability of food, availability of specialized habitat needs, and interspersation) apply to all species that require wetland habitats. In fact, these requirements have long been recognized as the basic habitat needs of all wildlife species.

In summary, specific wetland habitat requirements are best known for some of the species of economic importance, such as finfish and shellfish of commercial and/or sport fishing value, furbearers (particularly muskrat and nutria), and gamebirds (particularly waterfowl); relatively little is known about the specific wetland habitat requirements of micro- and macroinvertebrates, poikilothermal vertebrates, mammals, game birds, and nongame birds with varying degrees of dependency on wetland habitats.

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SOCIO-ECONOMIC

GENERAL

The socio-economic category involves wetland functions that, in many cases, are the most obvious functions or values because individuals or groups are more likely to derive socio-economic benefits directly. For example, canoeists paddling through a wetland are probably much more aware of its scenic functional value than of its water quality or habitat functional value. Socio-economic functions can usually be separated into one of two categories, consumptive and nonconsumptive. The consumptive category includes those products, usually food, fuel, or fiber, whose production is significantly dependent on wetlands and that are physically removed (harvested) for human utilization. The nonconsumptive category includes the scenic, recreational, educational, aesthetic, archeological, heritage, and historical values of wetlands, experienced directly or vicariously (through art and literature) by individuals, while preserving the essential attributes of the wetland.

We have attempted to summarize the current status of knowledge of this function in Table 5. A listing of some assessment systems that address this function is also included in Table 5.

NONCONSUMPTIVE USE VALUE

Reimold et al. (1980:80) described the essence of the nonconsumptive use category as follows:

Socio-cultural values, then, are generally removed from the economic plane and involve mankind's higher aspirations: philosophy, beauty, learning, spiritual and humanitarian concerns -- those elusive elements that make up the equally elusive thing known as 'quality of life'.

There is often a considerable amount of overlap and intertwining of these values, and consequently a precise definition of each value is not possible, if even desirable. For this reason these values are often described as a group.

Table 5. Summary of status of knowledge of selected wetland functions - socio-economic.

Function	Well authenticated	Fairly well authenticated	Poorly authenticated	Existing assessment methods	Remarks
Consumptive	Ireland 1976 Boyce and Cost 1974 Farnham 1979 Diderikson et al. 1979 Peters et al. 1979 Chabreck 1979 Johnson 1979 Diedrick 1981 Turner et al. 1981.	Motts and Healy 1973 Mundorf 1950 Baker 1960		Litton et al. 1972 Smardon 1972 U.S. Army Eng. Div., NE. 1972 Dee et al. 1973 Gupta and Foster 1976 Larson 1976 Smardon and Fabos 1976 Solomon 1977 Lee 1977 U.S. Soil Conservation Serv. 1978 Galloway 1978 Reppert et al. 1979 Adamus 1983	The consumptive use values of wetlands are well documented by monetary value of the products harvested. However, there is no clearly agreed on method for assessing the functional value of the wetland from which products are harvested. Nonconsumptive use values have been recognized, but little work has been done in terms of defining or quantifying them. Some assessment methodologies include them in their procedures, assessing them as a group.
Nonconsumptive			Litton et al. 1972 Lee 1977 Smardon 1972 Reimold et al. 1980 Hammit 1978 Niering 1979 Reimold and Hardisky 1979 Niering and Palmisano 1979		

Nonconsumptive use values have, up to this time, been relegated to a secondary status when compared to functions linked directly to ecological or physical services or economic products. For instance, habitat or flood control functions are normally considered of greater importance than aesthetic or recreational functions. Significant exceptions to this rule do exist, but they are isolated. There are at least two reasons for the secondary status of nonconsumptive uses. First, the importance given to an intangible nonconsumptive function is directly related to a personal or cultural interaction with the wetland (Niering and Palmisano 1979; Reimold and Hardisky 1979). Second, abilities and experience in assessing human perceptions that define nonconsumptive values are minimal (Niering and Palmisano 1979; Reimold et al. 1980). There is also a lack of a standard measure for intangible and tangible functions that would allow comparisons between the two (Reimold and Hardisky 1979).

The literature dealing with nonconsumptive uses is not extensive and often is not rigorously scientific. This literature often consists of the perceptions of an individual or group concerning an intangible value. Several general literature reviews have been published in recent years on this topic (Gosselink et al. 1974; Fritzell 1979; Niering 1979; Niering and Palmisano 1979; Reimold and Hardisky 1979; Smardon 1979; Reimold et al. 1980). Other articles have considered one or two of the many possible nonconsumptive values. The scenic value of wetlands was considered by Errington (1957), Niering (1967), Rodgers (1970), Litton et al. (1972), Haslam (1973), Rowntree (1976), Cherem and Traweek (1977), Lee (1977), Hammitt (1978), and Palmer (1978). Recreational values were considered by Larson and Foster (1955), Shaw and Fredine (1956), Errington (1957), Haslam (1973), and Cheek and Field (1977), while educational values were discussed by Niering (1967), Wharton (1970), Odum (1971), and Randall and Brainerd (undated).

The evaluation of nonconsumptive use values of wetlands has been limited. The primary effort appears to have been in the Northeast, where Rodgers (1970), Smardon (1972), Smardon and Fabos (1976), and Hammitt (1978) attempted to evaluate visual-cultural values of wetlands. Similar evaluations were done in the Far South (Lee 1977) and on the West coast (Litton et al. 1972; Rowntree 1976). These evaluations were limited both in geographical scope and the potential number of nonconsumptive values considered. The U.S. Soil Conservation Service (1978) used a simplified version of a visual-cultural evaluation in the Connecticut River Region, based on the models developed by Gupta and Foster (1976) and Smardon and Fabos (1976).

The Heritage Panel of the National Symposium on Wetlands (Niering and Palmisano 1979) recommended the development of a methodology for the evaluation of nonconsumptive use values of wetlands. This recommendation suggested utilizing professionals in each of the fields associated with nonconsumptive values in order to obtain information concerning the basic principles of psychology, aesthetics, history, anthropology, landscape architecture, recreation, and related fields. This information would increase understanding and the ability to evaluate human users' experiences

in wetlands to a similar level as that for habitat, primary productivity, and related wetlands functions. Once the needed information has been gathered for each of the pertinent disciplines, professionals in those fields will need to integrate and correlate their findings. Only after the data gathering and integration has occurred can methodologies and instruments for assessing, rating, or scaling nonconsumptive values of wetlands be developed.

CONSUMPTIVE USE VALUE

Consumptive use values include a variety of harvestable resources produced in association with wetlands. Unlike nonconsumptive use values, which are often difficult to define and evaluate, consumptive use values have a tangible economic basis tied to the use of the wetland product by humans. Another significant difference between consumptive and nonconsumptive use values is that while consumptive uses, in some cases, may alter the wetland, nonconsumptive uses do not. This fact was significantly illustrated by Diderikson et al. (1979:634) when they remarked that, in a recent soil conservation survey inventory of wetlands and wet soils, it was assumed that "...once soils have been adequately drained for growing most common cultivated crops, they no longer qualify as wetlands...". In other words, the essence of the wetland was gone, and recovery, if possible, would presumably require an extended, but unknown period of time.

The value of wetlands in terms of their ability to produce harvestable resources has been qualitatively documented for timber (Boyce and Cost 1974; Ireland 1976; Johnson 1979; Turner et al. 1981), agricultural crops (Diderikson 1979; Diedrick 1981), energy (Bjork and Graneli 1978; Farnham 1979; Ryther et al. 1979; Pratt and Andrews 1981), finfish and shellfish (Carley and Frisbie 1968a,b; Newsom 1968; Chabreck 1973; Leitch and Scott 1977; Tihansky and Meade 1977; Peters et al. 1979), wildlife (Newsom 1968; Chabreck 1973; Leitch and Scott 1977; Chabreck 1979), and water supply (Mundorf 1950; Baker 1960; Motts and Healey 1973). Several attempts have been made to quantitatively assess the consumptive use value of wetlands by assigning a monetary value to harvestable products. One approach has been to divide the market value of products by total wetland acreage, thereby establishing a dollar per acre value (Wass and Wright 1969; Gosselink et al. 1974; MacDonald et al. 1979). Odum (1978) criticized this method as being based on an artificial, market place value that does not represent the true value of the wetland in an ecological sense (i.e., all products and services derived from wetlands are not recognized by size).

Shabman and Batie (1980) suggested that two basic errors are inherent in the dollar per acre value method. First, the method assumes that a reduction in wetland acreage directly affects the amount of a product harvested, which is not necessarily the case when factors other than wetland size limit the harvest. Second, the cost of harvesting the product is ignored, or more accurately, added to the value assigned to the wetland when the total monetary value of the product is allocated to wetland value.

Another approach to quantitatively assess the consumptive use of wetlands assumes that the actual dollar value of harvestable products includes the increasing dollar value generated as the product is processed, wholesaled, and retailed (Gosselink et al. 1974; Langdon et al. 1981). Shabman and Batie (1977) and Foster (1979) have critiqued this method. Lugo and Brinson (1979) concluded that evaluation based on the dollar value of the resource being harvested does not meet the three essential requirements for any evaluation scheme: ecological soundness; objectivity; and completeness of analysis.

It is obvious that standard methods have not been established for estimating the economic value of harvestable wetland products. Estimates that have been reported to date are widely divergent in terms of dollar value and dependent on the perspective of the evaluator (Shabman and Batie 1977; Foster 1979). Foster (1979) pointed out that the methodology, assumptions, and resultant value must pass a test of reasonableness in order for the conclusions to have sufficient validity to be useful in the decisionmaking process. This rationale is not restricted to consumptive use and should apply to the evaluation of all functions. Finally, a wetland may produce not one but several harvestable products that should be evaluated simultaneously. No methodology currently exists with this capability.

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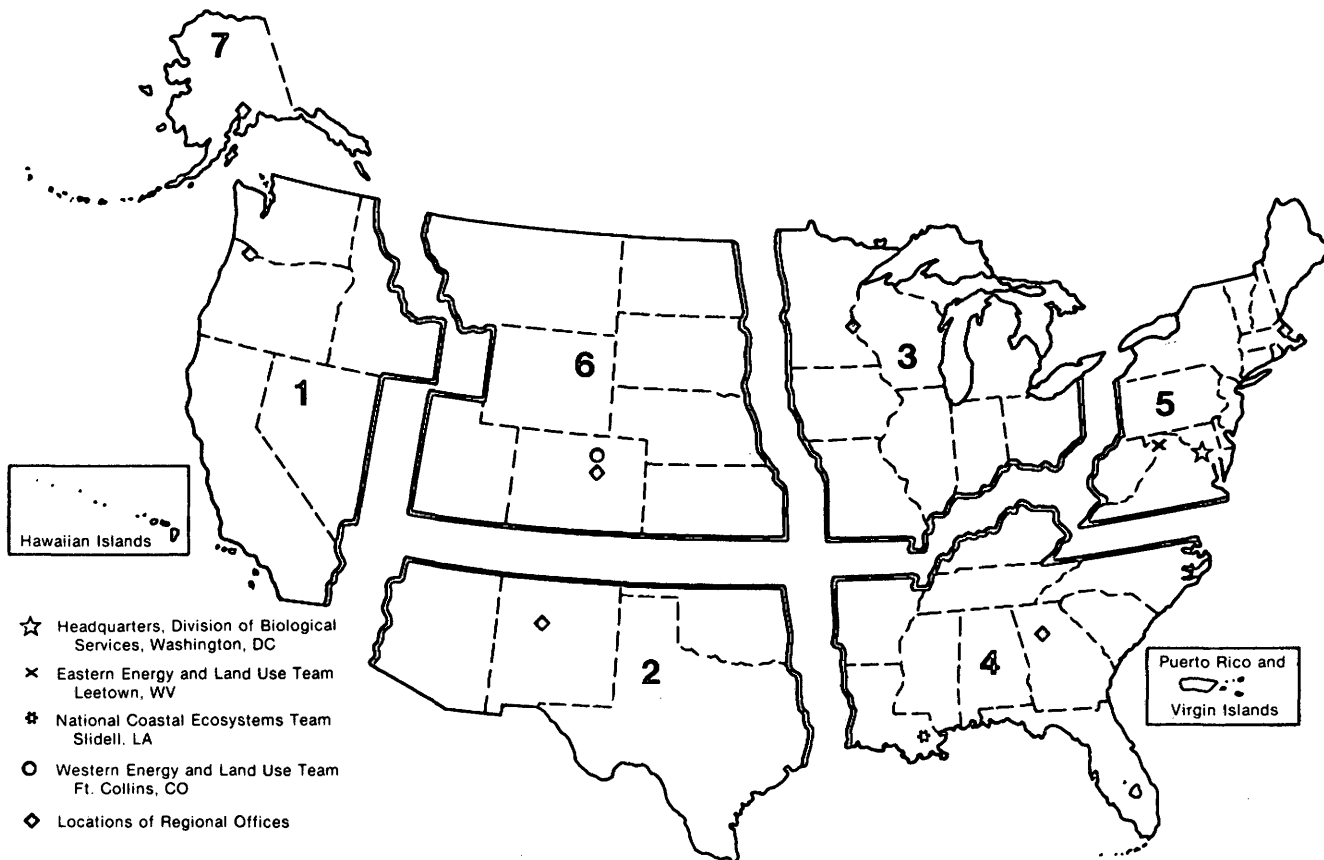
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