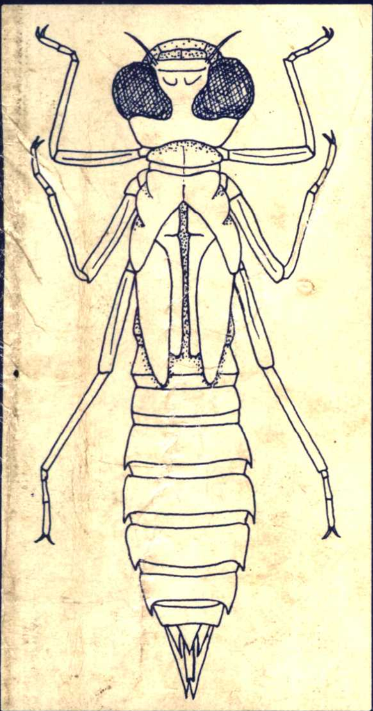
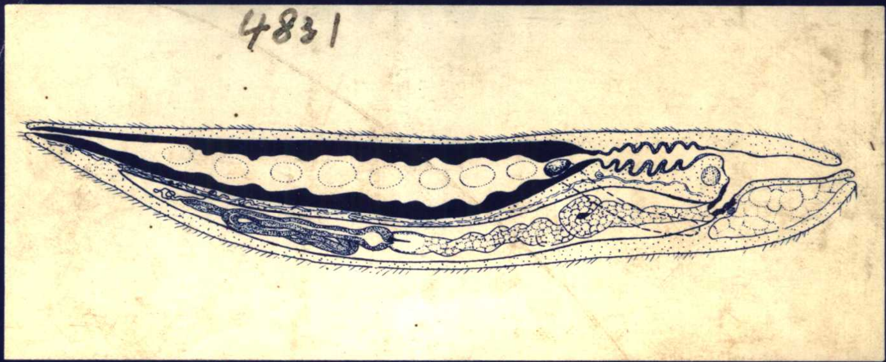
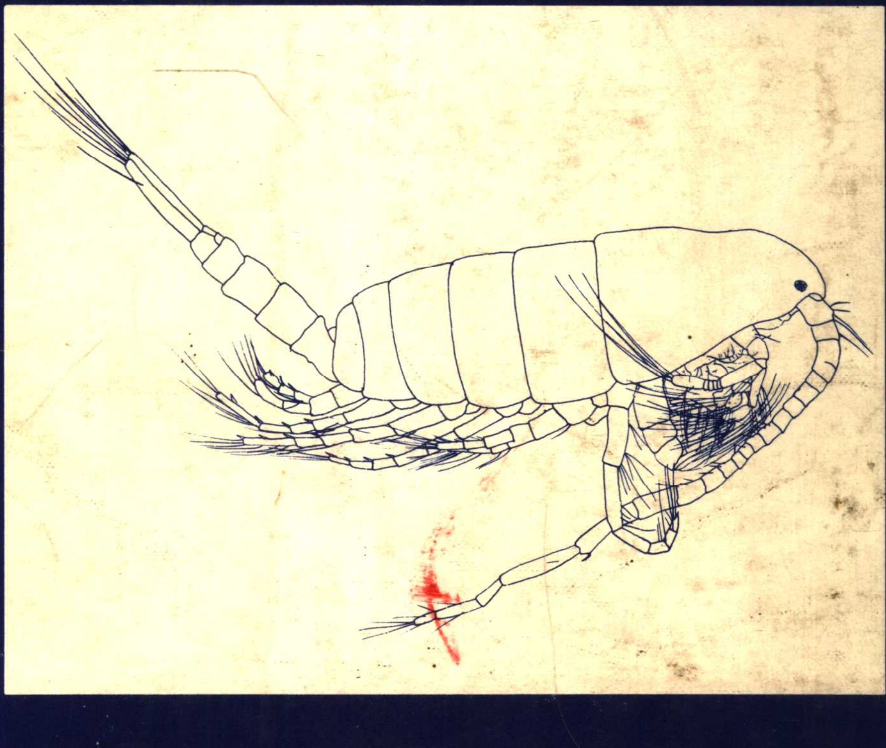
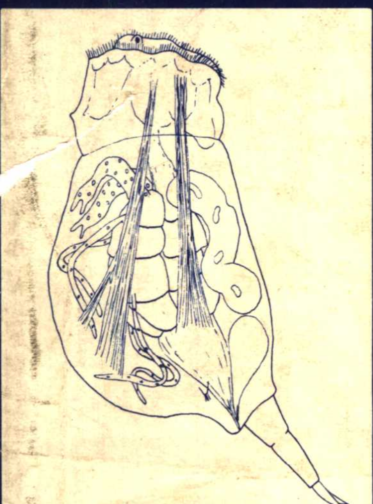
# FRESH-WATER INVERTEBRATES of the United States, 2nd Ed.











Robert W. Pennak

# FRESH-WATER INVERTEBRATES of the United States

SECOND EDITION

By

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A WILEY-INTERSCIENCE PUBLICATION
JOHN WILEY & SONS, New York • Chichester • Brisbane • Toronto

***Library of Congress Cataloging in Publication Data:***

Pennak, Robert William.
Fresh-water invertebrates of the United States.

"A Wiley-Interscience publication."
Includes bibliographies and index.
1. Freshwater invertebrates—United States.
I. Title.

QL141.P45 1978 592'.09'2973 78-8130
ISBN 0-471-04249-8

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

# FRESH-WATER INVERTEBRATES of the United States

To the memory of

C. JUDAY

"What's the use of their having names," the Gnat said, "if they won't answer to them?"

"No use to *them*," said Alice; "but it's useful to the people that name them, I suppose."

LEWIS CARROLL

"All cold-blooded animals . . . spend an unexpectedly large proportion of their time doing nothing at all, or at any rate, nothing in particular."

CHARLES ELTON

# PREFACE TO THE FIRST EDITION

No comprehensive work on American fresh-water invertebrates has appeared since 1918, and in the meantime much new information has steadily accumulated in a wide variety of biological periodicals. To me, therefore, the need for the present volume is obvious. I hope it will prove useful to biologists and zoologists generally, and to aquatic zoologists, limnologists, fish biologists, and entomologists particularly. It will also serve as a text and reference pitched toward the level of the college senior and beginning graduate student.

Original material resulting from my own field and laboratory research forms only a small fraction of this book. Rather, my role as an author has been one of arrangement, organization, and selection from a very large mass of published information. Indeed, my most perplexing problem has been how *much* material on each taxonomic group to include within the covers of a single volume. General policies, however, have been clear from the outset; I have emphasized natural history, ecology, and taxonomy; I have minimized details in the sections on anatomy and physiology; I have tried to be complete, accurate, concise, and consistent from one chapter to another. During the preparation of this volume all of the chapters have been continually revised and kept up to date in accordance with new material appearing in the literature.

For the most part, only free-living, fresh-water invertebrates that occur in the United States are included. Cestodes, trematodes, parasitic nematodes, etc. are all omitted; their inclusion would have necessitated a much more extensive work and additional years of preparation. Furthermore, most aquatic biologists seldom need to refer to parasitic groups as contrasted with free-living groups.

It will be noted that some chapters contain keys to species, while others contain keys only as far as genera. In general, the chapters in the former category deal with small or comparatively stable taxonomic groups that are fairly well known and in which few new species are being described from time to time in the United States. The chapters in the latter category, however, are all concerned with larger taxonomic groups, as well as those that are less well known in the United States and in which new forms are being described so abundantly that any key to species is quickly out of date. It is assumed that users of this manual are familiar with the fundamentals of taxonomy and the construction of keys. Incidentally, each half of a key couplet consists of but a single sentence; changes in subject within a sentence are indicated by semicolons.

The list of references at the end of each chapter consists only of especially significant and comprehensive works; these include older classical papers as well as recent contributions. Except where sections are especially valuable, I have not listed the larger standard reference works such as Hyman's *The Invertebrates,* Schulze's *Biologie der Tiere Deutschlands*, Bronn's *Tierreich*, Kükenthal and Krumbach's *Handbuch der Zoologie*, Dahl's *Die Tierwelt Deutschlands*, Grassé's *Traité de Zoologie*, and *Faune de France*.

Almost all of the chapters (with or without figures) were sent to at least one specialist for criticisms, corrections, and suggestions. I am deeply grateful to all these specialists, who were most encouraging, generous, and cooperative. Without their help and assurance I would have had much less confidence in my efforts. Following is a list of these specialists, with the sections examined by each.

John L. Brooks (Cladocera); Royal B. Brunson (Gastrotricha); C. F. Byers (Odonata); Fenner A. Chace, Jr. (Crustacea Introduction, Mysidacea); B. G. Chitwood (Nematoda); W. R. Coe (Nemertea); R. E. Coker (Copepoda); Ralph W. Dexter (Eubranchiopoda); W. T. Edmondson (Rotatoria); T. H. Frison [deceased] (Plecoptera); R. E. Gregg (Insecta Introduction); H. H. Hobbs, Jr. (Decapoda); C. C. Hoff (Ostracoda); Leslie Hubricht (Amphipoda, Isopoda); H. B. Hungerford (Hemiptera); Libbie H. Hyman (Coelenterata, Turbellaria); F. P. Ide (Ephemeroptera); O. A. Johannsen (Diptera); M. W. de Laubenfels (Porifera); H. B. Leech (Coleoptera); James E. Lynch (Eubranchiopoda); J. G. Mackin (Isopoda); Ruth Marshall (Hydracarina); H. B. Mills (Collembola); J. Percy Moore (Hirudinea); L. E. Noland (Protozoa); Mary D. Rogick (Bryozoa); H. H. Ross (Plecoptera, Trichoptera); Henry van der Schalie (Gastropoda, Pelecypoda); Waldo L. Schmitt (Crustacea Introduction, Mysidacea); L. H. Townsend (Megaloptera, Neuroptera); H. C. Yeatman (Copepoda).

The introductory chapter was criticized by A. S. Pearse and by several of my graduate students. Other people have helped me in one way or another. A group of eight protozoologists, for example, selected the 300 most appropriate and common genera of Protozoa to be included in the Protozoa key. These men are: William Balamuth, Gordon H. Ball, A. M. Elliot, Harold Kirby [deceased]; J. B. Lackey, L. E. Noland, K. L. Osterud, and D. H. Wenrich.

Obviously, a book of this sort is bound to have errors and ambiguities, and certainly such faults are clearly my own responsiblity. I hope readers will bring them to my attention.

In a sense, this book constitutes a plea and encouragement for more work on our rich but poorly known fresh-water invertebrate fauna. I hope these chapters will kindle sparks and raise questions in the minds of our students and beginning investigators in zoology, for it is among these young people that we shall find our authorities and specialists of tomorrow.

ROBERT W. PENNAK

Boulder, Colorado
1952

# PREFACE TO THE SECOND EDITION

About 25 years have elapsed since the publication of the first edition of this book. During this long interval I have done my best to gather the pertinent references and literature that would be necessary for the production of this second edition. This period has been characterized by a greatly increased interest in the biology of our fresh-water invertebrates. As a result, the germane literature since 1952 amounts to more than 5000 titles in technical journals. Colleagues and professional acquaintances everywhere have been generous in sending me reprints of their works, and I am greatly in their debt for such thoughtfulness. I am grateful to Dr. John Bushnell for his comments and patience in helping me with anatomical and nomenclatural problems in the Ectoprocta. Dr. Perry Holt generously supplied the key to the genera of Branchiobdellida.

Several of the shortest chapters have required only few changes, but most chapters have had a major overhaul. Nearly all keys have been rewritten and made longer in accordance with maturing systematics. A few of the old figures have been deleted, especially where I could find or make more suitable illustrations. Many new figures have been added, especially to clarify difficult key couplets. Lists of references at the end of each chapter have been revised and enlarged; about half of the citations are new.

When we refer to fresh-water invertebrates of the United States, we are including complete data only for the 48 contiguous states. In general, however, this volume covers essentially all the Alaskan fauna. The Hawaiian fresh-water fauna is impoverished and poorly known.

The Ronald Press Co. and I have been surprised and continuously gratified by the acceptance of the first edition by such a very broad spectrum of users. We hope this second edition will receive similar acceptance.

My greatest personal reward derived from producing the two editions of this book is the host of professional acquaintances I have made, not only in the United States but also in many foreign countries.

ROBERT W. PENNAK

Boulder, Colorado
March 1978

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# Chapter 1

# INTRODUCTION

EXCLUDING Protozoa and all parasitic classes but including aquatic insects, it is estimated that the fresh-water invertebrate fauna of the United States consists of about 10,000 described species. Twenty-five years ago the figure was 8,500 species. Probably no aquatic biologist is of the opinion that this fauna is well known; certainly the total is bound to increase markedly in coming years, especially when the aquatic fauna of the western half of the country is more thoroughly studied. Although a few groups are fairly well known and reasonably stabilized, such as the Cladocera, Decapoda, Odonata, Gastropoda, and Pelecypoda, the majority of American fresh-water invertebrate groups are in the process of taxonomic refinement. In expanding taxa composed mostly of non-cosmopolitan species we are lagging behind European fresh-water taxonomy by about 10 to 20 years. All taxonomic questions aside, we are seriously lacking in our understanding of geographic distribution patterns, physiology, natural history, and ecology of fresh-water invertebrates in the United States. In a few groups, however, some remarkable progress has been made since the publication of the first edition of this book.

The organization of an introductory chapter to a text such as this one is a problem because of the wide variety of major topics that might profitably be considered. However, to avoid becoming too involved, the subject matter of this chapter is restricted to brief discussions of (1) origins of the fresh-water fauna, (2) fresh-water emigrants to the sea, (3) major distinctions between fresh-water and marine invertebrates, (4) atypical fresh-water habitats, (5) dispersal and barriers, and (6) food webs. This particular selection was made only after considerable indecision. For the most part, these are important topics *not* generally discussed in other texts dealing with fresh-water biology. It also appears advisable to eliminate topics more strictly of a limnological nature.

## ORIGINS OF THE FRESH-WATER FAUNA

The generalization that most major fresh-water invertebrate groups originated from marine ancestors is firmly established. Only a few groups, such as insects, mites, and pulmonate snails, are presumed to have clearly originated from terrestrial habitats. The fresh-water fauna is therefore appropriately termed an immigrant fauna.

The fundamental problem that must be solved before any marine animal can make its way into fresh water involves major physiological readjustments. Body fluids of most marine invertebrates are roughly isotonic with sea water; that is, the internal dissolved salt concentrations are similar to or slightly higher than the 3.5 percent average salt concentration of sea water. It is further true that the majority of marine invertebrates cannot endure much dilution of sea water. Fresh waters commonly contain about 0.01 as much salts as the ocean, and the internal fluids of fresh-water invertebrates usually contain 0.03 to 0.40 as much salts as the ocean. From an osmotic standpoint, water therefore tends to pass into the hypertonic tissues of fresh-water animals.

TABLE I. A COMPARISON OF THE TOTAL DISSOLVED SALT CONTENT OF FRESH WATERS, BRACKISH WATERS, AND SEA WATER. Maximum and minimum values are merely approximations. The most abundant salts in brackish waters are chlorides, carbonates, or bicarbonates, depending on the degree of brackishness. In fresh waters the most abundant salts are usually carbonates and bicarbonates. In alkali and saline lakes they are usually carbonates, bicarbonates, chlorides, and sulphates in varying proportions.

| | Percent concentration | | Milligrams per liter | |
|---|---|---|---|---|
| | Minimum | Maximum | Minimum | Maximum |
| Sea water | 3.5 | | 35,000 | |
| Brackish waters | 0.05 | 3.2 | 500 | 32,000 |
| Fresh waters | 0.001 | 0.05 | 10 | 500 |
| Alkali and saline lakes | 0.05 | 25.0 | 500 | 250,000 |

Consequently any successful fresh-water animal must have developed physiological mechanisms for maintaining a proper salt and water balance against this strong gradient.

It is difficult to imagine the appearance of such mechanisms de novo, and it is assumed that the transitions from marine to fresh-water environments were not sudden and rapid processes, but rather series of slow evolutionary processes occurring by way of psammolittoral and phreatic waters, littoral zones, marshes, swamps, and river estuaries where there are transition zones between salt and fresh water.

It should be borne in mind, however, that a river estuary is not a constant environment. Salinities, currents, tides, food, temperatures, and other ecological factors vary widely from time to time, and these conditions are by no means favorable to the evolution and gradual development of forms suited to fresh water. Pearse (1950) has stated the problem well:

> An estuary has been called the doorway by which marine forms have populated fresh water. This statement is perhaps in part true, but an estuarine doorway is not wide open and easily passed. There are many difficulties to be surmounted. Many animals struggle long ages to get through and fail. Only a few attain fresh water by this route.

Ideal conditions for the invasion of fresh water are afforded by such places as the Baltic Sea, where there is a large area involved and where there is a permanent and very gradual transition from the sea to fresh water. Yet the Baltic has not a single endemic brackish water species of metazoan that has evolved since the most recent glaciation, although there are a very few subspecies or physiological varieties that may be endemic.

The generalization that marine invertebrates are isotonic with sea water is actually a slight exaggeration. Even pelagic, deep-sea, and the most primitive marine species maintain a dynamic steady state by which a difference in concentration of several ions commonly obtains across external membranes and which must be maintained through physiological regulatory processes. The internal concentrations of magnesium and sulfate ions are often much lower than those in sea water. Potassium concentrations may be considerably higher or lower than in sea water, and calcium and chloride are also variable. Many marine invertebrates have the remarkable ability to concentrate astonishing amounts of elements that are present in the sea water only as traces. Examples are vanadium, iodine, strontium, and bromine.

A wide range in type and degree of osmoregulatory control is found among littoral and estuarine invertebrates. Many species have limited ability to regulate the relative amounts of internal salt and water; their membranes are easily permeable so that the body fluids become more or less isotonic in diluted sea water, and death occurs rather promptly. A few stenohaline species can endure some dilution of sea water by regulating body volume and taking up more water into the tissues. A few other species can regulate their internal osmotic concentration only to a limited degree and venture into slightly brackish water; these species have a slight ability to remain hypertonic in diluted sea water. "Typical" brackish water species are euryhaline and can persist in habitats containing 30 to 85 percent fresh water. Most of these invertebrates maintain a more or less hypertonic internal salt concentration, regardless of the degree of brackishness of their surroundings. They include representatives of many groups, especially arthropods, mollusks, and various kinds of worms. The active absorption of salts is an important mechanism, and perhaps in some species there is actually physiological control of the amounts of water absorbed. Marine and brackish species transferred directly to fresh water usually live a few hours at most, but when the transition is made very slowly, over days or weeks, they may live for weeks or months in fresh water.

Figure 1 is a diagram showing the relative composition of the aquatic fauna in relation to salinity. It is one of the most striking paradoxes of fresh-water, brackish, and marine faunas that animals thrive well in either an environment that is very low in salts or one that is high in salts, but environments of intermediate salinities (brackish) have a poor fauna. From the standpoint of total number of all types of species present, it should be noted that the minimum appears at a salinity of 7‰ (7 parts per thousand), which is well toward the fresh-water end of the diagram in Fig. 1. This situation results from the fact that the number of fresh-water species drops very rapidly with a slight rise in salinity, whereas the number of marine species drops less rapidly with a decrease in salinity.

This diagram also poses a second paradox. It shows that specific brackish-water species, which occur chiefly or exclusively in such environments, are most abundant at salinities of 7 to 10‰ or about the place where the fresh-water forms decrease abruptly and where the total number of all species is smallest. This condition is not to be expected since most brackish-water species have obviously been derived from marine relatives and not from fresh-water relatives. It would be more logical to expect the maximum number of brackish species much farther toward the right in the diagram.

The invasion of fresh waters is a continuing process, and some American species are undoubtedly new arrivals or are in the process of becoming adapted to fresh waters. The colonial coelenterate *Cordylophora* and a few species in each of the following groups are all typical examples: polychaetes, grapsoid crabs, shrimps, isopods, clams, and snails. A comparable list may be cited for Europe, where a few species are known to have invaded fresh waters within historical times. The mitten crab of the Old World has taken up permanent residence in rivers and returns to the sea only to breed. With few exceptions, the new fresh-water forms are thought to be physiological varieties of their close marine relatives.

Several species of European crustaceans are marine in northern Europe and both brackish and fresh, or fresh alone, in central and southern Europe. Certain tropical areas, especially around the Bay of Bengal, Indonesia, the Malay Archipelago, Madagascar, and tropical America are relatively rich in species that have only recently made their way into fresh waters from the sea. It is presumed that constant temperatures and heavy rainfalls facilitate fresh-water invasions via estuaries. An alternate, newer theory emphasizes temperate and subarctic regions as more likely areas for entry into fresh water, chiefly because lower temperatures minimize the physiological effects of the various ions.

One other item should be discussed briefly in this section. The present writer (Pennak, 1963) has postulated a means by which micrometazoans could colonize fresh waters from the sea via the psammolittoral and phreatic habitats. As shown in Fig. 2, micrometazoans could possibly move from intertidal and subtidal zones into the marine psammolittoral and (1) thence into the phreatic ground water and thereafter inland to distant ponds or lakes via their psammolittoral, or (2) into the psammolittoral of an estuary, and thence progressively "upstream" in the river psammolittoral or deeper phreatic zone to inland fresh-water localities. Porous substrates below typical stream beds have long been known to have well-developed phreatic currents.

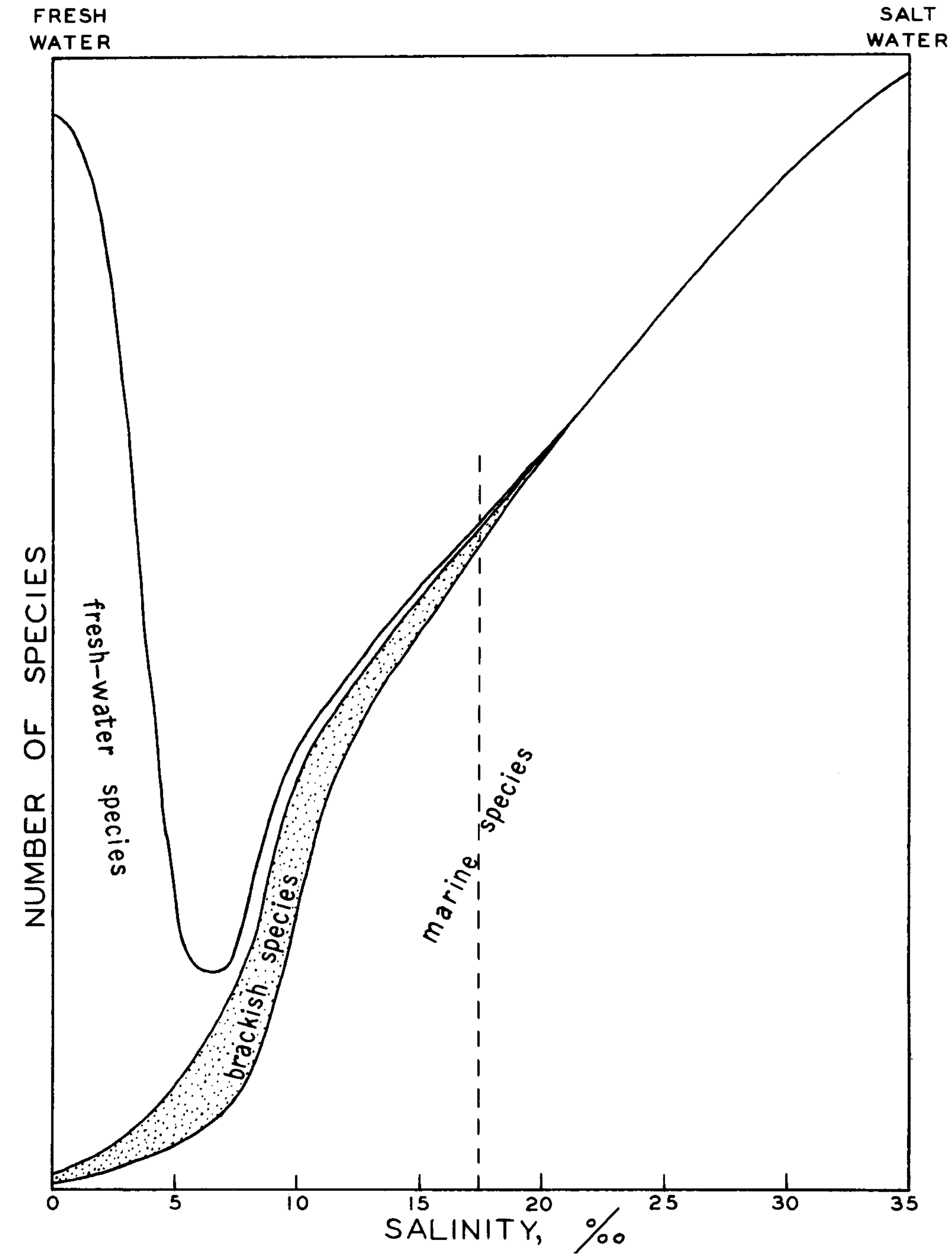


FIG. 1.–The composition of the aquatic fauna in relation to salinity of the environment. (Modified from Remane.)

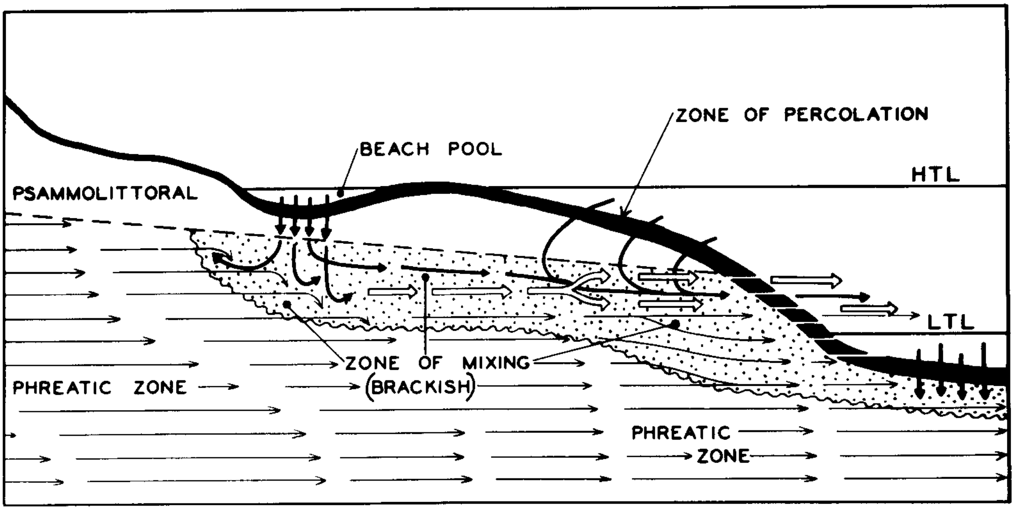


FIG. 2.–Diagrammatic section of a marine shoreline in an area where the fresh phreatic waters are seeping into the salt water. *HTL*, high tide level; *LTL*, low tide level; brackish zone of mixing shown by stippling; thick, open, and thin arrows show relative amounts of salt, brackish, and fresh waters, respectively. (From Pennak, 1963, after Delamare Deboutteville, 1960.)

The phreatic brackish interstitial zone of mixing at the edge of the sea is relatively thin, but it is also relatively constant in position, and species in this habitat are in a much less hazardous situation than those species that must swim or crawl about on the substrate of an estuarine area. Pennak (1963) also emphasizes the relative rarity of the invasion of fresh waters from the standpoint of mutations and genetics. Ax and Ax (1970) discuss other aspects of the marine–fresh-water transition.

## FRESH-WATER EMIGRANTS TO THE SEA

Once established in fresh water, few invertebrates have returned to brackish water and only rarely to undiluted sea water. Little is known about the major barriers to such migrations, but presumably they are physiological, and perhaps chiefly osmoregulatory. Potassium salts, which are abundant in the sea, are toxic to fresh-water invertebrates, but this effect may be partly neutralized by magnesium compounds. An impervious exoskeleton is advantageous for migrations into salt waters.

Only a few rotifers, hemipterans, beetle larvae and adults, dipteran larvae and pupae (especially Culicidae, Ephydridae, and Chironomidae), and several caddis larvae have successfully invaded estuaries, brackish waters, and the intertidal zone. Diptera larvae have occasionally been dredged from 10 to 15 fathoms off the coast of England. In Samoa there is a peculiar dipteran that is submarine for its entire life cycle. A few marine water striders occur regularly on the surface film of the seas far away from land.

Biologically, insects are considered a most successful group. They exhibit endless adaptations, occur in enormous numbers, and are found in almost every type of habitat. Yet they have not been successful in colonizing the seas. With the exception of some of the groups noted above, a salt content in excess of 2.5 percent appears to be toxic. However, brackish ponds with salt contents ranging up to 1.0 percent are quickly colonized by "fresh-water" insects.

Occasionally typical fresh-water mollusks are reported from brackish estuaries. A few species of *Physa* and *Goniobasis* can endure up to 50 percent sea water, *Amnicola* and *Planorbis* up to 30 percent, and *Lymnaea* up to 25 percent.