THE MARINE COMMUNITIES OF A TIDAL INLET AT CAPE ANN, MASSACHUSETTS: A STUDY IN BIO-ECOLOGY

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INTRODUCTION

An ecological study of the marine communities inhabiting a tidal inlet was made over a period of five years to determine the nature of their organization and dynamics. Field studies were conducted during the summer months of the years 1933 through 1937 over an annual period of eleven weeks. Brief visits were made in December of 1933 and March of 1934 for an examination of winter conditions, and additional observations were made during the month of August in 1938 and 1940. The problem was confined for the most part to the communities of an inlet known as the Annisquam River, located at Cape Ann, Massachusetts. The viewpoint of bio-ecology, or synecology, prevailed throughout the study. All common plants and animals were considered together as interlocking components of one natural unit. Life history studies were confined to those phases concerned directly with interrelationships.

Community composition was studied in reference to the physiographic features of the habitats and to the tidal flow and ebb. The ecological processes which received especial attention were those of interrelationships between organisms (coactions), of rhythmical changes produced by tidal fluctuations, of seasonal and annual changes, and of physiographic succession.

Many studies have been published on the marine life of the littoral region. The earlier works were taxonomic or faunistic in nature. Faunistic surveys soon gave way to problems of zonation and distribution and their correlation with physical factors of the environment. It is only within recent years that marine communities have been analyzed as biotic units having sociological properties as well as physical relationships to the environment (Gislen 1930).

The writer is deeply indebted to Prof. Victor E. Shelford, under whose direction the problem was carried out, for guidance in conducting the field studies and in preparing the manuscript. He is also indebted to Prof. C. E. Gordon and Prof. H. E. Warfel for suggestions and aid in the early part of the survey; to the family of the Rev. Dr. J. W. Beardslee for field assistance, especially to the Rev. W. A. Beardslee for aid in conducting the dredging operations and for information on birds; to Mr. F. S. Speck for field assistance; to Mr. Carl Freiburg for information on fishes; to Dr. C. L. Kanatzar for plankton examinations; to Capt. John Alvord for use of his diving helmet; to Mr. G. H. Colman for loan of scientific apparatus; to the Rev. R. M. Barker for meteorological data; to the Gloucester Station, United States Fish and Wildlife Service, for hydrographic data; to the United States Army District Engineer Office at Boston for topographic maps and information; to the Massachusetts State Bureau of Marine Fisheries for information on work of the bureau at Cape Ann; to Mr. N. W. Montgomery for boat and field-base accommodations; to the members of the departments of zoology and botany, Massachusetts State College, who assisted with the identification of organisms; and to the following who corrected the nomenclature for the revised manuscript: Dr. W. L. Schmitt, annelids and crustaceans; Dr. W. J. Clench, mollusks; Dr. C. L. Hubbs, fishes.

REGION OF STUDY

Geography and Geology

Cape Ann is a promontory which lies at the northern extremity of Massachusetts Bay. It is approximately 23 miles northeast of Boston Harbor. The narrow inlet known as the Annisquam River cuts off

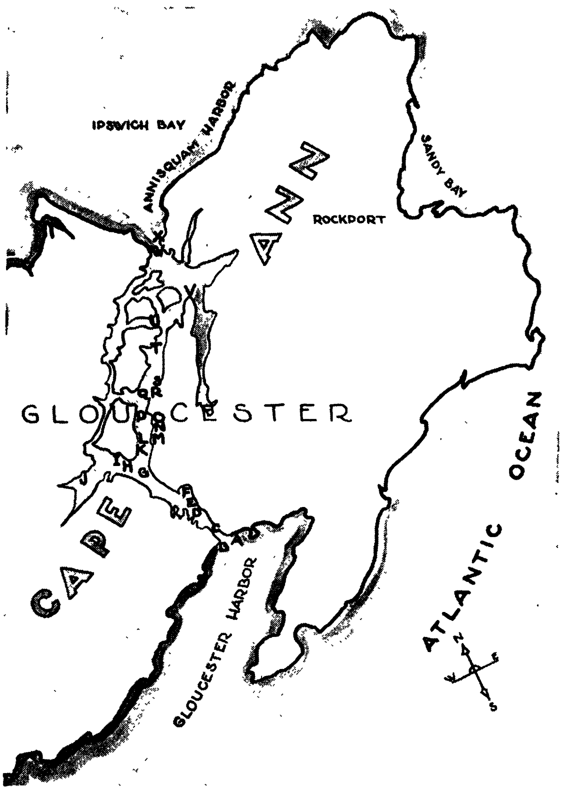


Fig. 1. Map of Cape Ann, Massachusetts. Letters indicate location of field stations.

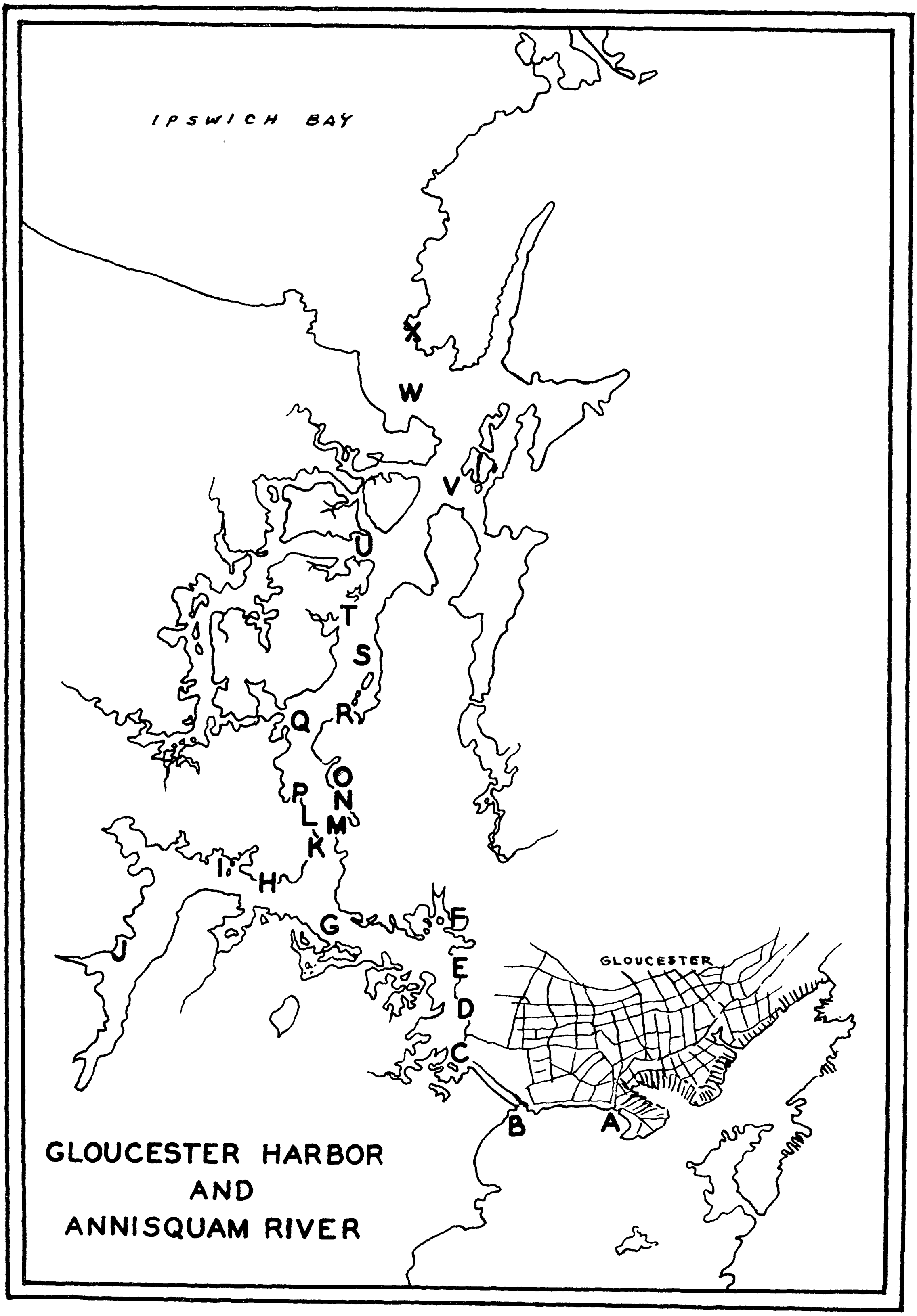


FIG. 2. Topographic map of the Annisquam Inlet. Letters indicate location of field stations. From U. S. C. and G. S. map 233.

the eastern end of the promontory, making it an island. This inlet, or strait, is 3.5 nautical miles in length (approximately 4 land miles) measured along the channel way, and has an average width of 175 yards. It connects the waters of Gloucester Harbor on the south with those of Ipswich Bay on the north. The island, on which is located the city of Gloucester and the town of Rockport, lies between longitudes 70°35′ and 70°41′ and between latitudes 42°35′ and 42°42′. (Figs. 1, 2; United States Coast and Geodetic Survey maps 233 and 243.)

Cape Ann is a massive ledge of granite and syenite rock, the surface of which has been glaciated and is now a terminal moraine covered with glacial drift. According to Shaler (1889), Cape Ann was an island at the close of the last glacial period, the dividing strait having been produced by the action of the glacier on weaker rocks. Later, deposition of sediments at the southern end of the inlet closed it at this point; subsequently, marshes developed behind this bar in the closed inlet to the northern entrance, which alone remained open. Upon the advent of colonization by the white man, an artificial canal was constructed in 1643 across the neck of land which had been deposited. This canal was blocked by deposits from violent storms in 1704 and again in 1723. Nearly a century later the inlet was reopened by the construction of a canal 600 yards long. Accumulating sediments gradually closed it once more until the state government took over the jurisdiction of the waterway in 1903 and reopened it for navigation. Thus, the island condition of the eastern end of Cape Ann was restored. More recently, a bar has been formed across the northern entrance at Annisquam, but it has not yet blocked the inlet, although it has become necessary to dig a channel through one end to allow the passage of large boats during low water.

There has been dispute in the geological literature of this region as to whether the promontory is rising or sinking. Much evidence has been presented on both sides of the question. The writer is inclined to believe that sometime after the last glacial period Cape Ann was elevated some 40 to 60 feet above the former shore level (Tarr 1903); but since that time it has come to have a sinking coastline (Shaler 1889; Penhallow 1907). Penhallow (ibid.) reported that the Atlantic coast was sinking at the rate of two feet every one hundred years, but more recently McAtee (1935) has stated that the subsidence is about one foot in a hundred years. In any event, deposition has been and is now taking place in the inlet at such a rate that it would eventually fill the inlet completely if left undisturbed. Sand and silt deposits have formed bars, beaches, flats, and marshlands. Rocky shores have been produced by glacial deposits and by weathering of adjacent ledges.

There are several small streams of fresh water that enter the strait, but nowhere does fresh water enter the waterway of Annisquam River in sufficient quantity to produce significant brackish conditions and the marine communities maintain their dominance to the limits of the high-tide level. The present study is the first of its kind to be conducted in this region.

METEOROLOGY

The general climatic conditions of Cape Ann are given in Table 1 which summarizes the temperature and rainfall records during the five years of this study. These measurements were recorded by the Rev. R. M. Barker, who operates a cooperative Weather Bureau Station at Gloucester.

Cape Ann has a temperate climate, but the winter season at times is quite rigorous. The intervening winter periods during the term of this research might be characterized as follows: 1933-34, very severe (the inlet was frozen from end to end); 1934-35, severe; 1935-36, severe; 1936-37, mild.

HYDROCLIMATE

During the summers of 1935-37, physical measurements were made on the waters of the inlet to determine in part the hydrographic environment of the marine communities. Water temperature, density, salinity, hydrogen ion concentration, and oxygen content were measured in the surface waters, for the most part those that covered the tidal zone. Additional information has been obtained from the Gloucester Station of the United States Fish and Wildlife Service located on Ten Pound Island at which has been made a record of the temperature and density of the water in Gloucester Harbor. Table 2 summarizes the hydroclimatic conditions of the inlet.

TABLE 1. Summary of Climatic Conditions, 1933-1937.

	1933		1934		1935		1936		1937	
	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.
Mean Temperature, °F.	47.3	....	45.9	....	46.7	....	47.6	....	49.1	....
Annual Rainfall, In.	....	58.8	....	43.8	....	46.0	....	54.1	....	49.1
June-August Mean, °F.	65.5	....	65.1	....	66.6	....	66.6	....	68.4	....
June-August Mean, In.	....	2.57	....	2.15	....	4.09	....	3.95	....	3.54
Monthly Maximum	66.3 Aug.	10.26 Apr.	68.3 July	7.89 Sept.	69.5 July	8.76 June	67.6 July	9.01 Dec.	72.0 Aug.	7.25 Apr.
Monthly Minimum	26.1 Dec.	1.28 Nov.	16.2 Feb.	1.07 Aug.	22.1 Jan.	0.31 Oct.	22.0 Feb.	1.53 May	28.9 Dec.	0.99 July

TABLE 2. Summary of Hydrographic Conditions, Summers of 1935-1937.

	Air Temp.	Water Temp.	pH	Density	Salinity 0/00	Oxygen cc/liter
1935						
Maximum	30.5°C.	24.0°C.	8.2	1.025	34.61	7.20
Minimum	16.0	14.5	7.6	1.021	29.69	3.54
Average	23.2	19.5	7.8	1.022	31.70	4.90
1936						
Maximum	33.0	23.5	8.3	1.023	32.94	7.94
Minimum	17.0	16.0	7.6	1.020	28.77	3.74
Average	22.5	20.4	7.8	1.022	31.03	4.96
1937						
Maximum	29.5	24.0	8.2	1.024	34.13	5.79
Minimum	17.0	17.0	7.7	1.020	28.47	3.69
Average	23.6	20.8	7.9	1.022	31.83	4.89

Water temperatures were taken at the surface. The daily water temperature fluctuates within a narrow range throughout the summer days, and the means of the three season's records agree fairly well, averaging 20° C. The water of the inlet is usually between two and three degrees warmer than the water of Gloucester Harbor. This relationship is noted by comparing daily readings as well as the monthly and seasonal averages. The shallowness of the inlet and the warming effect of the exposed tidal zone undoubtedly explain this difference in temperature. The density of the water was measured by means of a hydrometer. The samples of water were taken from the surface at those locations where temperature readings were made. The density and corresponding temperature measurements were used to compute the total salinity by an application of Knudsen's hydrographic tables. The average density each season was 1.022 while the average salinity was 31.18 $^0/_{00}$. The hydrogen ion concentration was determined with a colorimetric set employing phenol red as the indicator and a quinhydrone electrometric set. The readings show a range of 0.6 and a mean of pH 7.8. The amount of dissolved oxygen in the water was determined by the Winkler method. The samples were taken from a level approximately one foot below the surface of intertidal waters. The range in oxygen content throughout a season was considerable, but the averages of each year's samples compare very closely. The mean oxygen content of all samples analyzed was 4.92 cc. per liter.

After the restoration of the original inlet by the construction of a canal, a peculiar tidal current was produced. During the incoming tide, ocean water now enters both ends of the inlet, from Gloucester Harbor and Ipswich Bay. These currents flow toward each other converging at the channel known as Little River, into which both currents of water flow. During the outgoing tide the water of Little River runs out into both channels, and diverges at the junction into two currents that flow in opposite directions, to be emptied into Gloucester Harbor and Ipswich Bay. The velocity of the current depends on the height of tide, the direction and velocity of the wind, and the width of the inlet at various points. At times of spring tides, and with strong winds of the late summer, the waters flow quite rapidly, often with large waves and white caps. At narrow passages, especially at the canal and beneath the railroad bridge, the current is very great at times. Ordinarily the surface is quite calm, and the velocity ranges up to two miles per hour. The greater bulk of the water in the strait is changed with each tide, keeping hydroclimatic conditions fairly uniform throughout. The mean rise and fall of the tidal level at Annisquam is 8.5 feet, while at Gloucester Harbor it is 8.7 feet. The range in spring tides is 9.9 and 10.1 feet, respectively. The high water interval is 11 hours and 14 minutes. (Information from United States Engineer Office at Boston.)

FIELD STATIONS

INTERTIDAL STATIONS

Twenty-four stations were established along the inlet from the shores of Gloucester Harbor on the south to those of Annisquam Harbor on the north. These sites were selected to include all of the major types of communities and habitats, and spaced as uniformly as conditions would permit. Eleven stations were placed on either side of the inlet and two on bars in the middle of the channel. Fifteen were studied quantitatively by use of quadrats placed at certain levels, while nine were used for general and comparative observations. For the most part, a station extended from high-water to low-water line, even though several communities were often included in this range. In other cases a restricted area was set to include only one community. Reference should be made to the maps of the inlet (Figs. 1, 2) to obtain the exact location of each station. Shallow tidal pools were found only among the rocks at the extremities of the inlet (Stations B and X) and occasionally on the high marshes where holes had been dug. Consequently they did not play an important part in the community relations of these shores. Breakers and surf were also restricted to the harbor and bay shorelines (Stations A, B, X) and with these exceptions were not important factors. Table 3 gives a summary of the intertidal stations.

SUBTIDAL STATIONS

Three distinct channels were recognized in the study of subtidal bottom communities. The southern channel extends from Gloucester Harbor to Little River (Fig. 3); the northern channel extends from Ipswich Bay to Little River; and Little River itself is the third, formed at the union of the other two. Environmental conditions in the strait are quite uniform except for the character of the bottom and the varying velocities responsible for these differences. The bottom materials along Little River and the southern channel are fine mud (clay) deposits, for the most part, with occasional mixtures with sand along the lower, main channel, and a section of shelly, rocky bottom to the north of the railroad bridge at Station E, where the current is stronger as it passes through a narrow channel. Along the northern inlet the bottom is composed chiefly of local stretches of mud (particularly in the broader sections), of sand,

TABLE 3. Intertidal Field Stations.

Station	Substratum	No. of quadrat levels with horizontal distances in feet and vertical distances in inches between quadrats.
A	Sea-wall at about M.H.W.L.; Coarse sand on higher level; gravel and pebbles on lower beach	
B	Sea-wall near M.H.W.L.; Gravel bank below wall; small rocks and boulders extending to large boulders at M.L.W.L.	(1) Gravel bank; (2) 30 ft., 42 in.; (3) 20 ft., 4 in.; (4) 50 ft., 6.5 in.; (5) 21 ft., 0 in.; (6) 21 ft., 3.5 in.; (7) 21 ft., 6.5 in.; (8) 15 ft., 7 in.; (9) 15 ft., 4 in.; (10) 15 ft., 6 in. - near S.L.W.L.
C	Steep bank of rock fragments and boulders.	
D	Mud flat with black silt depression on landward side and firm, sandy-mud on channel side.	
E	Mussel bed on a bar beneath a railroad tressel.	(1) Base of sea-wall; (2) 16 ft., 28.5 in.; (3) 36 ft., 13.5 in.; (4) 36 ft., 17.5 in.; (5) 4 ft., 5 in.; (6) 2 ft., 10 in.; (7) 2 ft., 10 in. - near S.L.W.L.
F	Marsh bank and muddy creek adjoining main channel.	
G	Bar in middle of inlet; One end sandy, other muddy.	(1) Near top of bar; (2) 40 ft., 7 in.; (3) 30 ft., 5 in.; (4) 22 ft., 7 in.; (5) 22 ft., 5 in.; (6) 22 ft., 10.5 in. - near S.L.W.L.
H	Ledge of solid rock.	
I	High marsh, low marsh, and mud flat.	(1) Near M.H.W.L.; (2) 16 ft., 31.5 in.; (3) 16 ft., 37.5 in.; (4) 21 ft., 14 in.; (5) 21 ft., 14 in.; (6) 21 ft., 10 in.; (7) 16 ft., 8 in.; (8) 16 ft., 5 in.; (9) 16 ft., 4 in.; (10) 16 ft., 5 in.
J	High marsh, low marsh, and mud flat.	(1) Near S.H.W.L.; (2) 21 ft., 4 in.; (3) 21 ft., 1.5 in.; (4) 26 ft., 1.5 in.; (5) 40 ft., 4.5 in.; (6) 14 ft., 52 in.; (7) 21 ft., 25 in.; (8) 21 ft., 7 in.; (9) 21 ft., 1 in.; (10) 20 ft., 2 in.; (11) 20 ft., 3 in.
K	Ledge with weathered boulders and rocks.	(1) Near M.H.W.L.; (2) 6 ft., 14.5 in.; (3) 4 ft., 15 in.; (4) 7 ft., 17.5 in.
L	High marsh and low marsh.	(1) Near M.H.W.L.; (2) 25 ft., 18.5 in.; (3) 25 ft., 31 in.
M	Ledge and steep talus slope.	(1) S.H.W.L.; (2) 6 ft., 57.5 in.; (3) 5 ft., 19.5 in.; (4) 5 ft., 17.5 in.; (5) 5 ft., 12.5 in.
N	High marsh, low marsh, and mud flat.	(1) Near M.H.W.L.; (2) 25 ft., 30.5 in.; (3) 6 ft., 27 in.; (4) 26 ft., 11 in.; (5) 31 ft., 3.5 in.; (6) 21 ft., 1 in.; (7) 16 ft., 2 in.
O	Tidal creek with steep marsh banks and soft muddy bottom.	
P	Ledge and steep talus slope of large boulders.	(1) S.H.W.L.; (2) 6 ft., 22 in.; (3) 6 ft., 28 in.; (4) 6 ft., 36 in.; (5) 6 ft., 36 in.
Q	High marsh, low marsh, and mud flat.	(1) Near M.H.W.L.; (2) 12 ft., 35.5 in.; (3) 12 ft., 22 in.; (4) 40 ft., 8.5 in.; (5) 26 ft., 5.5 in.; (6) 16 ft., 3 in.; (7) 16 ft., 6.5 in.
R	Ledge with boulders.	(1) Near M.H.W.L.; (2) 5 ft., 24.5 in.; (3) 6 ft., 25.5 in.; (4) 4 ft., 8 in.
S	Sand bar in middle of inlet. One side is developing into a muddy lagoon.	(1) Top of bar; (2) 16 ft., 7 in.; (3) 16 ft., 4 in.; (4) 21 ft., 3 in.; (5) 21 ft., 3.5 in.; (6) 21 ft., 2 in.; (7) 21 ft., 2.5 in.; (8) 21 ft., 1 in.
T	High marsh and pile of large boulders.	(1) Just above M.H.W.L.; (2) 10 ft., 6.5 in.; (3) 16 ft., 24 in.; (4) 6 ft., 9 in.; (5) 4 ft., 9 in.; (6) 4 ft., 16.5 in.; (7) 4 ft., 13.5 in.; (8) 4 ft., 15.5 in.
U	High marsh plateau.	
V	Mussel bed over a mud flat.	
W	Extensive sandy beach.	(1) Near M.H.W.L.; (2) 20 ft., 8 in.; (3) 40 ft., 8 in.; (4) 20 ft., 6 in.; (5-18) 26 ft. apart with vertical distances of: 5.5, 4, 3.5, 2.5, 3, 1, 12.5, 6.5, 4, 6, 6, 6, 4.5, 12.5 in.
X	Ledge and pile of large boulders. Sand deposits and tidal pools among rocks.	

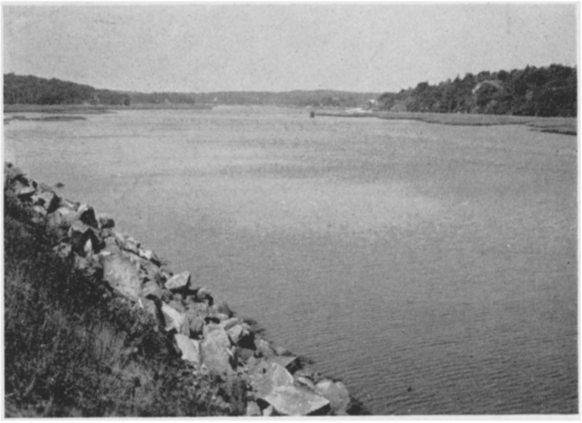


FIG. 3. Section of the inlet at mean-high-tide looking northwest from near station E.

and of mixtures of sand and mud with an occasional outcropping of rocks.

The subtidal bottom is smooth and firm except in a few regions of fine mud deposits. The central channel is narrow, winding and steepsided. Much of it has been dredged to a uniform depth of eight feet at mean-low-water, and for a width varying between 50 and 200 feet. The maximum depth is not over 34 feet at mean-low-water. (See maps of the United States Engineer Office, Boston, Mass. "Gloucester Harbor and Annisquam River." File 140, 141 Dr. 37 and "Annisquam River, Mass." File $\frac{168}{1}$, $\frac{168}{2}$ Dr. 37.)

METHODS AND TERMINOLOGY

For the most part, the field work was conducted on a quantitative basis. The intertidal communities were investigated by means of quadrat sampling. A counting frame twenty inches square was applied at selected levels at the various established stations for a sampling of the plants and animals existing at those levels. The depth of each quadrat sample varied with the substratum. In general, rocky shores were studied to the bottom of the removable rocks, while sandy and muddy habitats were dug to a depth of about ten inches. During two seasons of the field work, a quadrat ten inches square was used when it was learned that the smaller one gave as representative a sample of the common organisms and was more expedient for field use. All of the data have been adjusted to read in terms of abundance on 400 square inches or approximately one-quarter of a square meter. The square meter quadrat used by some workers was found to be altogether too large for this intertidal study because of the great density of organisms found, and the fact that it would cover too much vertical distance (Dexter 1943). A total of 432 quadrat counts was made. These were supplemented by general observations and general samplings made over the entire area.

The subtidal bottom communities were studied with the aid of a naturalist's dredge, constructed of an iron frame resting on runners and carrying a large bag of medium netting with an end base of canvas. The dredge was dragged along the bottom of the inlet from a small boat propelled by an outboard motor. Each haul was recorded separately and quantitatively. These bottom samples were supplemented by observations on the bottom communities from a diving helmet (Dexter 1942).

Plankton samples were taken with a fine bolting-cloth net. Fishes were observed from docks and collected with the dredge net and with a dip net. Additional information was secured from local fishermen. Birds were observed in the field, and information was also obtained from a number of persons who had kept records of the birds in this region.

Coactions were determined by direct observations in the field and experimentally by the use of aquaria. Movements were studied, especially of snails, by observing the progress of marked specimens.

The ecological nomenclature follows the concepts and definitions established by Shelford (1931, 1932). Because of the lack of uniformity in the use of ecological terms, and the confusion which has arisen from the use of various systems, and, in some cases, the failure to recognize ecological concepts, it becomes necessary to give briefly the terms and their definitions as used in this paper.

Biome—the largest community recognized as a unit. Consists of two or more related associations and their developmental stages.

Association—a climax community of relatively uniform taxonomic composition and physiognomy.

Faciation—a portion of an association based upon a grouping or an absence of some of the predominant species.

Sere—the sequence of successional stages from the initial to the climax condition.

Associes—a developmental community which is undergoing gradual change. Any level in a sere below the climax.

Predominants—plants and animals which are abundant and significant in the community.

Dominants—species which control and characterize the community directly or through their effects on the habitat. They are the common, large, sedentary, or slow-moving forms.

Subdominants—species having minor control of the community. They are neither as abundant nor as uniformly distributed as the dominants, but locally may take the place of dominants.

Influents—species which are significant in the community because of their importance in the food chain.

Subinfluents—less important than influents in the dynamics of the community because of less abundance, smaller size, or lack of importance in the food chain.

Permeant Influents—wide ranging, motile animals which produce significant changes, chiefly through predation.

Secondary Forms—plants and animals of minor importance.

Incidentals—species of no significance in the economy of the community.

COMMUNITIES

The earlier works on marine life of the Atlantic coast were developed from the point of view of faunal zoogeography (Sumner 1908; Murray & Hjort 1912; Sumner, Osburn, & Cole 1913). The latter publication demonstrates that Cape Cod is a faunal barrier, 55% of the fauna of the Woods Hole region being south ranging and 30% north ranging. On this basis the Woods Hole region is designated as part of the "Virginian" province while north of Cape Cod the fauna is characteristic of the "Arcadian Province." Murray & Hjort (1912) described the coast from Cape Cod to Northern Newfoundland as "Boreo-arctic." Analysis of the common macroscopic marine life at Cape Ann, so far as distribution is known, shows that 11.8% is north ranging or "Arcadian," 6.7% is south ranging or "Virginian," and 81.5% is found for considerable distances both north and south of Cape Cod. This indicates that the littoral biota of Cape Ann is within the "Arcadian" province although obviously the dividing line cannot be as sharp as formerly believed. In general, however, one can agree with Sumner et al. (1913) that "Cape Cod does have appreciable influence as a barrier."

The more recent studies have been concerned with the aggregations of marine life, and investigators are realizing more and more the necessity of a dynamic point of view on community relationships (Shelford & Towler 1925; Bigelow 1930; Shelford 1931, 1932; Allee 1934; Vaughan 1934; Taylor 1935; Rees 1939; Clements & Shelford 1939). Shelford declared succinctly (1930a) that "modern ecology may be stated to be the science of communities" and Allee (1934) has pointed out that "the distinctive contribution of ecology to biological complex has been the emphasis on the fact that organisms live in communities."

In pursuing this approach in the study of marine communities, however, an interesting difference of opinion has developed in regard to the relative importance of certain factors. Some workers have overstressed the importance of the physical environment, in some cases assigning community control to a single factor. Others have lost sight of the community in the details of life histories of the individual species. The most desirable approach seems to be a balanced point of view including consideration of environmental influences, physiological life histories, and coactions of organisms in proper perspective. As Shelford (1931) has pointed out, sometimes biotic factors control, and at other times, physical factors control. It might be added that only by a complete analysis of each situation can we come to understand the natural laws governing biotic communities.

As the best yet devised and most convenient method of designation, the system long in use of naming communities after several of the dominant or characteristic species (Peterson 1918) has been adopted here. The naming of certain ones of the following communities follows that of Newcombe (1935) as far as feasible, but because of differences in the composition of the communities between Cape Ann and the Bay of Fundy, where Newcombe did his work, it has become necessary to modify his system somewhat. Also, we are here concerned with the communities of a protected inlet which are somewhat different from those of the exposed ocean shores. It should be borne in mind that all of these designations of marine communities are provisional and subject to change with additional research on the study of community organization. The annual fluctuation of the status of some species necessitates a change in their ecological evaluation so that the naming of a fluctuating dynamic system, such as a marine coastal community, has significance only in relation to time and place. Not until an extensive ecological survey is made of the entire northeastern coast of the Atlantic Seaboard such as Shelford (1935) organized for the Pacific coast will it be possible to assign definite names and rank to the marine communities with certainty.

The writer does not agree with MacGinitie (1939) that communities should be named after the particular place where one happens to study them, or that they should be named, as by common practice, after the zones of algae. It is now known that the animal populations are not always distributed according to zones of seaweeds and a geographic name as suggested by MacGinitie would not convey any meaning in regard to the nature of the community. When one realizes that the use of generic names of the controlling and characteristic species to designate a community refers only to the organization of that community at the time of study, MacGinitie's objection on the basis of significant seasonal and annual changes is dispelled. With such changes, a new community naturally comes into existence and demands a new name as well as a new analysis. By retaining a geographic name, there would be added confusion.

The plankton-nekton of the Annisquam inlet is a portion of one biome, while over the bottom and the tidal zone of this area, according to one point of view, there exist portions of three other marine biomes. In addition, there are two major communities transitional to land conditions.

PELAGIC COMMUNITY

CLUPEA-SYNGNATHUS FACIATION

The pelagic community of the Annisquam inlet is essentially the same as that described for the shallow water of Ipswich Bay (Dexter 1944), which is a portion of the Scomber-Calanus Biome. The Clupea-Syngnathus Faciation of the inlet, however, lacks the larger animals such as the tuna *(Thunnus thunnus)*, mackerel shark *(Isurus punctatus)*, and the finback whale *(Balaenoptera physalus)*. The following organisms are known to be among the most important of the larger pelagic species of the inlet: mackerel *(Scomber scombrus)*; herring *(Clupea harengus)*; pipefish *(Syngnathus peckianus)*; pollack *(Pollachius virens)*; alewife *(Pomolobus pseudoharengus)*; butterfish *(Poronotus triacanthus)*; bluefish *(Pomatomus saltatrix)*; silver hake *(Merluccius bilinearis)*; smelt *(Osmerus mordax)*; common squid *(Loligo pealii)*; harbor seal *(Phoca vitulina)*; and jellyfishes *(Aurelia aurita, Cyanea capillata)*. The common tern *(Sterna hirundo)* and the belted kingfisher *(Megaceryle alcyon)* also became members of this community when they dive into the water for food.

The plankton was examined but not studied in detail. Diatoms, protozoans, microcrustaceans, and crustacean larvae constituted the more common organisms taken in the samples, but the bulk of the suspended material collected was detritus. The large amount of detritus and low concentration of plankton organisms in the water are accounted for by the facts that collecting was done for the most part in the shallow submerged tidal zone, and during the annual plankton minimum (July-August). A plankton sample taken on September 16, 1945, for a period of 15 minutes from a strong, outgoing current gave the following results: *Calanus finmarchicus,* abundant; fragments of green algae, common; ostracods, common; nauplius larvae, common; mysid larvae, numerous; veliger larvae, numerous; rhabdocoel turbellarian, numerous; clam seed, numerous; fragments of bryozoan and hydrozoan colonies, several; hydrozoan jellyfish, 2; detritus, abundant. The copepod *Calanus finmarchicus* is probably the most important of the plankton organisms. Large jellyfishes usually appear late in the summer in great quantities and constitute a conspicuous part of the plankton during a brief period. Within Aurelia and Cyanea there are found at times crustacean commensals of the genus Hyperia. *Aurelia aurita* was not recorded in 1933, but was carried into the inlet in great abundance in 1934, and was collected in decreasing numbers each succeeding year. *Cyanea capillata* was not seen during this study until 1935, when numerous specimens were swept in by the current. This was repeated in 1936, but in small numbers only in 1937.

SUBTIDAL BOTTOM COMMUNITY

LAMINARIA-CANCER FACIATION

General Character

The subtidal bottom community of the inlet is similar to the bottom community of Ipswich Bay (Dexter 1944). The shallow inlet is a part of the Strongylocentrotus-Buccinum Biome, but it lacks most of the large gastropods *(Buccinum undatum, Neptunea decemcostata, Colus stimpsoni)*, two of the kelps *(Agarum cribrosum,* and *Laminaria longicruris)*, the larger bottom fishes *(Melanogrammus aeglifinus, Hippoglossus hippoglossus)*, and one of the red algae *(Corallina officinalis)*. Also, some of the predominants of the bay region are less important or seldom found in the inlet.

Some of the bottom invertebrates found in the bay but not dredged in the Annisquam River are the bivalves *Arctica islandica, Modiolus modiolus;* the decapods *Libinia emarginata, Palaemonetes vulgarus;*

and the starfish *Henricia sanguinolenta*. The following predominants of the bay are present but less important in the inlet: *Echinarchnius parma, Euthora cristata, Chondrus crispus,* and *Lacuna vincta*. On the other hand, some species are more abundant and ecologically significant in the inlet than in the bay. Among these are the algae *Laminaria digitata, Chaetomorpha linum;* the mollusks *Polinices heros, Nassarius trivittata, Littorina littorea, Mytilus edulis;* the crustaceans *Cancer irroratus, Carcinides maenas, Pagurus longicarpus, Crago septemspinosus;* the arachnoidean *Limulus polyphemus;* and the fishes *Fundulus heteroclitus, Anguilla bostoniensis*. The inlet community is designated as the Laminaria-Cancer Faciation, being characterized by *Laminaria digitata, L. Saccharina* (brown algae), and *Cancer irroratus* (rock crab). Previous to 1933, there existed a Zostera (eel-grass) Faciation, which was destroyed with the virtual disappearance of this plant from the Atlantic coast in 1932. (See Dexter 1944a, 1945, and 1946 for discussion of this problem at Cape Ann.) A total of 110 dredge hauls was made in the three channels over a period of four seasons.

The evaluation of the members of this community follows the criteria as established for the study of Ipswich Bay (Dexter 1944, p. 354). The first number following each species is the maximum taken in a single dredge haul, which in most cases covered an area of about 1,610 square feet (approximately 60 square meters). The second number is the percentage of occurrence in the dredge hauls. Thus, *Asterias vulgaris*, 41/98 signifies that up to 41 specimens of this species were collected at one time, and that the species was collected in 98% of all the dredge hauls.

Dominants and Slow-Moving Influents

Dominants

Asterias vulgaris, starfish, 41/98
Polinices heros, sand-collar snail, 12/40
Strongylocentrotus drobachiensis, green sea urchin, 2/10
Ulva lactuca, sea lettuce, 13/74
Laminaria digitata, kelp, 7/38
Laminaria saccharina, kelp, 4/32
Urophycis chuss, squirrel hake, 7/30
Pseudopleuronectes americanus, winter flounder, 5/18
Myoxocephalus scorpius, shorthorn sculpin, 2/14
M. octodecemspinosus, longhorn sculpin, 1/4
M. aeneus, little sculpin

Subdominants

Chaetomorpha linum, green alga, Abun./52
Raja erinacea, little skate
R. diaphanes, big skate
Urophycis tenuis, mud hake
Lophopsetta maculata, sand flounder

Influents

Mytilus edulis, blue mussel, 25/40
Nassarius trivittata, sand snail, 80/26
Littorina littorea, periwinkle, 30/38
Gammarus locusta, amphipod, 18/44
Caprella acutifrons, amphipod, 15/30
Lepidonotus squamatus, scale worm, 4/38
L. sublevis, scale worm, 5/10
Chondrus crispus, Irish moss, 2/26
Euthora cristata, red alga, Many/20
Lumbrinereis tenuis, annelid, 4/20

Subinfluents

Lacuna vincta, snail, 15/12
Gemma gemma, bivalve, 9/20
Chalina oculata, finger sponge, 9/26
Isopods (unidentified), 10/36
Amphipods (unidentified), 8/16
Neopanope sp., mud crab, 4/12
Syngnathus peckianus, pipefish, 1/8
Crepidula fornicata, boat shell, 34/6
Sertularia pumila, hydroid, 20/26
Abietinaria abietina, hydroid, 16/38
Bugula turrita, bryozoan, 5/44

Permeant Influents

Cancer irroratus, rock crab, 51/64
Pagurus longicarpus, hermit crab, 39/30
Carcinides maenas, green crab, 37/14
Crago septemspinosus, shrimp, 40/48
P. pollicaris, hermit crab, 17/8
Limulus polyphemus, horseshoe crab, 3/20
Anguilla bostoniensis, eel, 1/2
Tautogolabrus adspersus, cunner, 1/4
Poronotus triacanthis, butterfish, 1/2
Fundulus heteroclitus, minnow
Osmerus mordax, smelt
Pholis gunnellus, rock eel
Homarus americanus, lobster

Secondary Forms

Metridium dianthus, sea anemone, 14/10
Obelia spp., hydroids, 12/20
Ophiopholis aculeata, brittle star, 4/6
Lichenophora hispida, bryozoan, 12/26
Molgula manhattensis, sea squirt, 16/10
Spirorbis spirorbis, serpulid worm, 12/6
Bryozoan (unidentified, encrusting forms), 10/30
Tubularia spectabilis, hydroid, 8/12
Crepidula plana, snail (commensal with Pagurus), 10/10
Saxicava arctica, bivalve, 3/10
Echinarchnius parma, sand dollar, 3/4
Tellina tenuis, bivalve, 5/6
Hydractinia echinata, hydroid (commensal with Pagurus), 3 sq. in./16
Botryllus schlosseri, sea quirt, 5 col./12
Balanus eburneus, barnacle, 3/6
Nereis pelagica, clam worm, 2/6
Rhodymenia palmata, red alga, 2/8
Siliqua costata, sand bar clam, 1/8
Idothea baltica, isopod, 1/6
Cerastoderma pinnulatum, bivalve, 1/6
Aeginia longicornis, isopod, 1/5
Chorda filum, sea chord, 1/5

Community Organization and Coactions

Dredging operations conducted along the entire channel-way and observations on the bottom from a diving helmet and from the surface over shallow areas as spring-low-tides have shown this Laminaria-Cancer Faciation to be as follows.

On the sandy and sandy-mud bare sediments of the channel floor are found many transient animals: Cancer, Pagurus, Carcinides (crabs); Polinices (snail); Limulus (horseshoe crab); Cargo (shrimp); and a number of ground fishes, chiefly the squirrel hake (Urophysis); flounder (Pseudopleuronectes); sculpins (Myoxocephalus); skates (Raja); and the eel (Anguilla). Also, the less rapidly moving animals, Asterias (starfish), Strongylocentrotus (sea urchin), and Echinarachnius (sand dollar) wander over the surface. In the substratum are amphipods, annelids, and bivalves (Tellina, Cerastoderma, and probably others which are not often taken in a surface dredge and for that season were not detected). The deepest portions of the channel are populated by *Laminaria digitata* and *L. saccharina.* In the holdfasts of these algae are found aggregations of small animals which occupy this microhabitat. Sea squirts (Molgula, Botryllus); mat-forming bryozoans; developing sponge colonies (Chalina, etc.); small specimens of sea anemones (Metridium); the bivalve Saxicava; and seed of the blue mussel (Mytilus) are often attached within the ramifications of the holdfast. Small motile animals, such as Gammarus and other amphipods; isopods; the worms Lepidonotus and Nereis; crabs (Neopanope, small specimens of Cancer and Carcinides); small sea urchins (Strongylocentrotus); the brittle star (Ophiopholis); developing starfishes (Asterias); a flatworm (Leptoplana); periwinkles *(L. Littorea);* and fish fry are found living within the holdfasts. Probably these are the most important microhabitats of the bottom community. On the stipe and fronds of the same algae are colonies of Sertularia, Tubularia, Obelia (hydroids), crustose bryozoans of various species, Lichenophora, Bugula (bryozoans), Ectocarpus (alga), Spirorbis (annelid), small amphipods, *Littorina littorea,* Lacuna (snails) and small specimens of Asterias. Laminaria produces important reactions by slowing the current of water, reducing light intensity, and serving to catch and hold sediment, as well as serving as a place for attachment or refuge for many animals. Andrews (1945) described the kelp bed communities of the Monterey Region of California and showed the importance of the large algae in determining the nature of the community.

Among the laminarian plants are other algae such as tufts of Chondrus, masses of Chaetomorpha, Euthora, and strings of Chorda. Chaetomorpha often harbors a number of the bivalve Gemma, shrimp (Crago), and the amphipod Caprella. Euthora is often crusted with a lacework of bryozoans and riddled with Caprella, Aeginina, Idothea and other crustaceans as well as immature annelids.

These colonies of algae with their associated animals do not form a solid mass of vegetation over the channel bottom, but occur in small groups, usually from one-half to four square feet in area, wherever anchorage of some kind is available. Laminaria is attached to rock outcrops, stones, shells, mussels, or any other solid object to which the plant can cling for support. Likewise for the other algae, except that less support is needed for them since many of them can secure a foot-hold in the sand, and once a nucleus is begun, other plants and animals adhere to it.

Colonies of Chalina (sponge) and Abietinaria (hydroid) are frequently attached to these islets of organisms and are also scattered about anchored in the sand. Chalina often harbors a number of animals which use the sponge for support, as, for example, Lepidonotus (annelid), seeds of bivalves, Caprella (amphipod), and Ophiopholis (brittle star). Shallow muddy and sandy areas often swarm with the snail *Nassarius trivittata,* while shelly, rocky bottoms have many specimens of Metridium (sea anemone), *Crepidula fornicata* (boatshell), and to a lesser extent Acmaea and Anomia (mollusks). Along spring-low-water line and somewhat below, there is found, attached to rocks, colonies of the rock seaweed *Fucus edentatus.*

On the whole, the benthos community is fairly uniform throughout the inlet with only minor differences at certain local areas where the substratum is somewhat different. The permeant influents (see list) are wide ranging and are found on all kinds of bottom. Very few species are restricted to any one of the four type bottoms, although often a greater abundance of some animal is found on one kind. Sumner, Osburn, & Cole (1913) concluded that the type of bottom was most important in explaining distribution of subtidal organisms. Thus 40% of the animal life dredged in Buzzards Bay (mud bottom) was not found in Vineyard Sound (sandy, gravelly bottom), while 35% of the latter was not found in the former. Verrill & Smith (1873) and Lee (1944) who studied in the same area also found correlations between the bottom organisms and the substratum. Shelford (1935), however, has pointed out that communities are often more closely related to physiographic forces than to bottom materials, and MacGinitie (1939) has reported different communities on similar habitats. Allee (1923, pt. 3) holds the common view that "if forced to make use of a single criterion to divide the communities of the Woods Hole littoral I should depend more on observation of the character of the sea-bottom than on any other one factor." The real influence of bottom material is apparently but little understood, although admittedly important (Petersen 1918).

The interrelationships among the major plants and animals were studied with particular reference to each individual community as a microcosm, and in the case of those of the intertidal region, to the influences of the fluctuating tidal level. These relationships are summarized in the form of food-chain diagrams which outline the most significant coactions which were found to be taking place in each community. No claim is made for completeness in this study, but rather the aim has been to determine the main lines of interactions which control the communities. In addition to the diagrams, there is a brief account which explains them.

The food habits of the fishes, birds, terrestrial arthropods, and some of the little-known marine invertebrates have been determined for the most part from published literature, although field observations were made to corroborate the findings recorded in publications. The major coactions of the marine organisms were observed at first-hand. Heavy lines in the diagrams indicate the most significant species and coactions of that community.

The interrelationships of the pelagic and subtidal communities of the shallow inlet cannot be very well separated since the dynamics of one overlaps that of the other. For that reason the two are considered together. The coactions of these two biomes are probably much the same at all times throughout the aestival season of any one year with two important variations. First, the fish population changes in composition and abundance during the summer months, and secondly the concentration of the submerged fauna is increased during low-water when the permeant and other motile animals withdraw from the tidal zone and congregate in the narrow channel. At high-water these motile animals invade the shore zone in search of food and thus decrease the food-chain activities taking place in the subtidal region at that time.

The algae (Laminaria, Chaetomorpha, Ulva, Chondrus, etc.) of the river bottom are the basic foods for many snails (Littorina, Lacuna), crustaceans (Crago, Cancer, Pagurus, Carcinides, etc.), and fishes. The herbivorous snails are devoured by carnivorous ones (Polinices, *N. trivittata*) and both types are eaten by crabs and fishes. The smaller fishes are eaten by larger ones and also by the diving birds (terns, kingfishers).

Plankton and detritus are consumed by bivalve mollusks which are attached by the carnivorous snails, the horseshoe crab or kingcrab (Limulus), decapod crabs, starfishes (Asterias), annelids (Nereis), and bottom fishes (flounders, sculpins, skates, squirrel hake, etc.), the latter consuming also all of the invertebrate enemies of the bivalves. Plankton-feeding fishes (mackerel, herring, pollock, pipefish, etc.) are devoured by the predaceous ones (bluefish, butterfish, silver hake, etc.), or by diving birds. Coelenterates, sponges, and bryozoans feed on the plankton and detritus, and they are eaten by crustaceans and fishes. Annelid worms and shrimps feed on organic matter, or "marine humus" (Waksman 1933), in the bottom sands and muds and they are dug out and eaten by the kingcrab, rock, hermit, and green crabs and by bottom-living fishes. Dead animal bodies and other organic refuse are eaten by scavenging snails, crabs, amphipods, and fishes.

As it is readily seen, the food chain is founded in algae, organic debris with its bacteria, and plankton. Detritus with adhering bacteria is probably of great importance to those organisms feeding on microscopic materials (Blegvad 1914). The importance of bacteria in the food cycles of the sea has been shown by Waksman (1934) and ZoBell (1946). Mare (1942) has studied and diagrammed the food cycle of an English subtidal community and has shown the importance of microorganisms in the cycle. The major intermediate animals are gastropods, annelids, and crustaceans, which become food for fishes, some of which at least are preyed on by the harbor seal (Phoca) and some consumed by man. (Compare these levels with the system of Lindeman 1942.) Figure 4 outlines the main coactions taking place in the pelagic and subtidal region. Bond (1933) has called attention to the importance of particulate organic matter in aquatic food cycles and has suggested the latter is probably most important for the zooplankton. Steven (1930) has pointed out that while some fishes are selective feeders, stomach content analysis indicates that most fishes eat whatever is available, and Shelford writes "each species selects the food available in greatest quantity, making selections which in a particular locality tend to give an erroneous impression as to the specific nature of food relations." In any particular community, however, the food chains are bound to be limited and more or less specific although it must be kept in mind that such a "web of life" is not the only such pattern found and will vary in each community according to its composition.

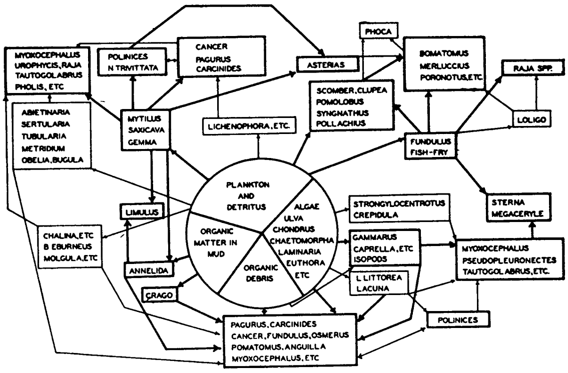


FIG. 4. Food coactions of the subtidal Laminaria-Cancer faciation.

Annuation and Succession

During the period of this study, a number of changes occurred in the marine biota of such a magnitude as to be easily detected by ordinary sampling and observation. Some of these changes can be explained by the influence of man, by disease, by extreme temperatures, by competition or predation, but for many we have no clue as to the cause. Some species increased while others decreased; some changes were extremely rapid while others were slow. Probably the operating forces in each case were different and each would have required a special study in itself, although undoubtedly many of them were related in one way or another. A study of the meteorological and hydroclimatic conditions at Cape Ann during the period of this study does not show any direct correlation between fluctuations of physical factors and the biota with the exception of the influence of low temperature on certain crabs mentioned hereafter. Moberg & Allen (1927) have shown that the properties of seawater near shore change suddenly and frequently, and only a complete and continuous analysis can detect such changes accurately. However, even without an adequate explanation, it is worth recording observed fluctuations of ecological significance. The sudden and voluminous increase in abundance of certain species which were formerly very scarce, such as a few of those recorded in this paper, raises a question as to the potential significance of some uncommon species generally overlooked by ecologists.

The eel-grass, *Zostera marina,* all but disappeared in 1932 as the result of an epidemic. During the first season of this field survey it was found persisting in a single brackish lagoon (Goose Cove). Even there it dwindled for several years. Each year after 1934 more and more patches were discovered in scattered locations of the inlet growing chiefly from old rhizomes, but in no case was a good healthy stand of this plant found until the summer of 1945. By that time, a sizeable stand had returned in Goose Cove (northeast of Station V), and to a lesser extent in the channel leading to it. These were extended considerably by the summer of 1946 but it has not yet returned in the region in sufficient quantity to be of ecological significance. Two crustaceans, the lobster *(Homarus americanus)* and a mud crab (*Neopanope* sp.), practically disappeared from the inlet with the eel-grass. How much influence can be attributed to the loss of the eel-grass cannot be stated. Both crustaceans returned in small, but in increasing numbers, after 1936. A snail, *Lacuna vincta,* formerly found on the eel-grass, moved to the brown algae *Laminaria digitata* and *L. saccarhina* when the eel-grass disappeared. This snail remained a common species until 1935, when it became very scarce for two years. In 1937 it began to return in larger numbers and was still increasing in 1940. Stauffer (1937) found that animals formerly found on eel-grass in the Woods Hole region either adapted themselves to living on the mud or disappeared.

Another snail, *Polinices heros,* on the other hand, increased in abundance each year from a small population in 1933 to a very large one by 1937. One factor concerned in this increase was the virtual elimination of the green crab, *Carcinides maenas,* which was dredged from the channel and destroyed in its hiding places on shores and marshes by the Massachusetts Bureau of Marine Fisheries in the winter of 1933-34. The severe weather of that season (as low as −20° F.) is also believed responsible for killing a large number of the crabs while wintering in the marshes. This crab was not found in significant numbers again until 1936 when it was once more reduced in abundance by the Bureau of Marine Fisheries. Allee (1919, 1923 pt. 4.) determined changes in the Woods Hole fauna after a severe winter and discussed the importance of temperature in relation to annuation. Blegvad (1929) and Caullery (1929) also described changes in abundance of marine organisms as a result of a very severe winter season.

During the absence of the green crab, the rock crab, *Cancer irroratus,* was noticeably more abundant. The common starfish, *Asterias vulgaris,* suddenly became much more abundant in 1935 than it had been previously. Dredge hauls that year from the northern channel averaged 33 specimens. This increased population was maintained, but not at such a high level, for the next two years. Galtsoff & Loosanoff (1939) found that increases in population of *A. forbesi* were caused by increased rates of reproduction and survival rather than by invasion. Burkenroad (1943) has demonstrated a 14-year cycle of abundance of this same species. *Limulus polyphemus* and *Lepidonotus squamatus* were not collected in their usual abundance in 1935.

The most important change which has taken place each year in the inlet is the annual deposition of silt and sand. This has led to the formation and extension of bars, flats, and beaches. The Annisquam River originally had a natural depth of about 6 feet at mean-low-water from Ipswich Bay to Little River, while from this point to where the railroad bridge now crosses Station E it gradually decreased in depth. Beyond, the channel was reduced to a drainage ditch, the bottom of which ranged up to 2 feet above mean-low-water level. The inlet was terminated at this point by the land bridge or bar previously discussed. The canal through the bar and the natural inlet (Annisquam River) have been dredged from time to time to widen and straighten the channel for passage of the larger fishing vessels, and to remove the accumulated deposits which have tended to obliterate the inlet, and which indeed nearly succeeded in doing so before white man appeared on the Massachusetts coast. At intervals between 1906 and 1929 the Commonwealth of Massachusetts dredged various sections of the inlet to a depth of 8 feet at mean-low-water. The last dredging in this series was completed in September of 1929 when 50,428 cubic yards of material were removed, four years before this ecological survey was begun. In 1936 the Federal Government restored the channel to its 8 foot depth and straightened and widened it in places by removing 91,773 cubic yards of bottom deposits.

As the bars and flats are rebuilt, the subtidal bottom community becomes more and more restricted, and through this process of physiographic succession becomes replaced by the intertidal communities of sediments—chiefly the Mya-Nereis pelagica Biome.

TIDAL COMMUNITIES OF SEDIMENTS

MYA-NEREIS PELAGICA BIOME

General Character

This bivalve-annelid community resembles that of the Mya-Nereis virens Biome described by Newcombe (1935). At Cape Ann the dominating annelid is of a different species. This community is probably very extensive along the New England coast, as it occupies most of the periodically exposed bars and flats of all kinds of loose sediments from about mean-low-water line to a vertical height of about 4 feet. Like that described by Newcombe (1935) this community does not descend into the subtidal region.

In the listings of the predominants of intertidal communities, the first number given is the average abundance on 400 square inches of the samples of that species taken from all levels in a particular community. The second number is the percentage of occurrence of that species in all samples taken in that community. Thus, *Mya arenaria,* soft-shell clam, 22/46 indicates that this bivalve had an average abundance of 22 specimens on 400 square inches, and that this species was found in 46 per cent of all quadrat samples taken in the Mya-Nereis pelagica Biome of the Annisquam inlet.

Dominants and Slow-Moving Influents
Dominants
Mya arenaria, soft-shell clam, 22/46
Nereis pelagica, clam worm, 16/45
Lumbrinereis tenuis, annelid, 52/50
Clymenella torquata, annelid, 609/19
Subdominants
Macoma balthica, bivalve, 6/24
Polinices heros, sand-collar snail, 1/9 (at low-water)
Influents
Glycera dibranchiata, annelid, 3/19
Gammarus locusta, amphipod, 154/6
Nassarius obsoletus, snail, 40/4
Talorchestia longicornis, amphipod, 6/14
Chaetomorpha linum, green alga, Com./15
Subinfluents
Solemya velum, bivalve, 4/13
Gemma gemma, bivalve, 51/23
Ensis directus, razor clam, 2/5
Cerebratulus lacteus, nemertean, 2/4
Onoba aculeus, snail, 61/21
Littorina littorea, periwinkle, 21/22
Anurida maritima, insect, 78/8
Ulva lactuca, sea lettuce, Num/15
Permeant Influents
Pagurus longicarpus, hermit crab
P. pollicaris, hermit crab
Cancer irroratus, rock crab
Carcinides maenas, green crab
Limulus polyphemus, horse-shoe crab
Crago septemspinosus, shrimp
Fundulus heteroclitus, minnow
Tautogolabrus adspersus, cunner
Myoxocephalus octodecemspinosus, long-horn sculpin
Pseudopleuronectes americanus, cunner
Larus argentatus, herring gull
Pisobia minutilla, least sandpiper
Ereunetes pusillus, semipalmated sandpiper
Charadrius semipalmatus, semipalmated plover
Actitis macularia, spotted sandpiper
Butorides virescens, green heron
Nycticorax nycticorax, black-crowned night heron
Corvus brachyrhynchos, crow
Secondary Forms
Mytilus edulis (seed), blue mussel, 15/9
Dolichoglossus kowalevski, acorn worm, 9/7
Balanus balanoides, barnacle, 45/3
Littorina saxatilis, snail, 29/5
Allorchestes sp., amphipod, 18/1
Mulinia sp., bivalve, 1/3
Asterias vulgaris, starfish, 1/1
Siliqua costata, sand-bar clam, 2/1
Enoplobranchus sanguineus, annelid, 2/1
Idothea baltica, isopod, 2/1
Cyathura carinata, isopod, 1/1

Faciations

Two faciations are recognized at Cape Ann as an expression of bottom effect. The Talorchestia Faciation occupies the coarse sediments (sand bars, beaches) and might be considered as a skeleton Mya-Nereis pelagica Community composed almost entirely of the dominants with a few additions, such as the characteristic sand-dwelling amphipods. The Macoma-Clymenella Faciation of the mud flats, in addition to the dominants of the biome, has many other species, and a much greater abundance of life than is found in the other faciation. This is probably explained by the fact that the silt and clay deposits contain a much higher concentration of organic detritus with favorable conditions for microorganisms, and they have a smooth, moist surface which is favorable for many motile animals. Stephen (1928, 1929, 1932-34) has studied quantitatively the bivalve-annelid communities at many points along the Scottish coast. He recognized the Tellina tenuis-Nephthys caeca Association on clean sand, the Cardium edule-Macoma balthica Association on black mud, and transitions between the two. He also determined the zonation of the predominants in each case.

Some bars and flats are composed of a mixture of sand and mud in various degrees, and here will be found a mixture of some of the animals which ordinarily prefer one or the other type of substratum and a rough correlation in abundance according to the proportion of the mixture. Bruce (1928), Pirrie, Bruce & Moore (1932), and Newcombe (1935) have all shown the importance of the texture and size of particles of sediment and their influence on the distribution of certain animals.

Fragments of another community (Balanus-Mytilus-Ascophyllum Association) occur wherever rocks or other hard surfaces are present. These spotted fragments give rise to a condition which might be compared to the savannah type of community on land (Newcombe 1935 and Shelford et al. 1935). To the rocks are attached *Balanus balanoides* over most of the exposed surface. *Fucus vesiculosus* is often draped over much of the surface, and *Mytilus edulis* is attached around the base of the rocks and in crevices. On the barnacles and mussels are Asterias and Thais, while on the Fucus are *Littorina littorea, L. obtusata*, Sertularia, and Clava. Small rocks and shells on the mud attract *L. littorea* and *L. saxatilis* into concentrated groups.

Zonation and Coactions

The communities are first described as they are organized at the time of spring-low-water. Changes in composition and the resulting interactions brought about by the incoming tide will be explained as the water level gradually rises. This plan will be followed throughout the description of the intertidal communities.

Between the lowest water level reached during the spring tides and the mean-low-water line is a transition zone which might be considered an ecotone. It contains organisms of both the subtidal and intertidal regions. Lepidonotus (annelid), Aeolis, Onchidoris (nudibranchs) are found under small stones while *Nassarius trivittata* (snail), Mulinia, Siliqua (bivalves), Strongylocentrotus and Echinarachnius (echinoderms) are occasionally found on or in the sand along this lowest zone where they have been exposed by the extreme low tide. Lumbrinereis, Clymenella, Nereis, Glycera (annelids), Ensis, and Solemya (bivalves) of the intertidal group penetrate to this level and intermingle with the fringes of the subtidal community. Clymenella is generally restricted to the lower part of the shore and the greatest concentration of Glycera and Solemya is also found there.

Ensis extends back to about midpoint on the shore. Lumbrinereis and Nereis range back to the highest point on the bars, and for a considerable distance up the beaches, declining in abundance toward the higher portions of the strand. The distribution of Mya (clam) begins several inches above spring-low-water line and extends to the top of bars and to the level of the marshland on the beaches and flats. Macoma has much the same limits but is found in smaller numbers. Gemma is often spotted over the entire bar or flat, but reaches greatest concentration under and among the fronds of Chaetomorpha which often coat large areas of the flats, after being dropped there by a retreating tide. On some shores *Littorina littorea* may be found at any level, especially around pebbles or fragments of seaweed cast upon the beach. Polinices also is located at all levels on the sandy bars and beaches. Usually this snail moves off the tidal zone with the retreating tide, but when exposed on the shore it buries itself below the surface. It can then be detected by a low mound of sand directly over it. Talorchestia (amphipod) might be found anywhere from the middle to the highest point of the shore, but it is generally in greatest numbers along the highest level. The same distribution of this crustacean was noted by Davenport (1903).

This typical community as just described is found on the sandy bars and wet, firm, sandy beaches. A broad beach such as Wingersheek Beach at Station W (Table 4, Fig. 5) extending as it does to spring-high-water line, has a high margin of dry, clean sand which is not very densely populated by plants or animals. The composition of the community is much the same, but the concentration of organisms is not as great, especially in the high, dry sand. Marsh communities are gradually invading this area, with pioneer low marsh and high marsh organisms already present over a considerable portion of the upper level at one end of the beach. The Talorchestia Faciation was studied at Stations A, S, and W, with a total of 84 quadrat counts.

The Macoma-Clymenella Faciation was studied at stations D, F, I, J, N, O, Q, while a mictium of the two was found at station G (Table 5). One hundred and five quadrat counts were made in all. Additional members of the mud flat assemblage not found in or on the sand included the following: *Nassarius obsoletus* was found in varying quantities on the flats, being most abundant on the soft, black muds which had a jelly-like consistency, and which were protected in small bays and inlets. It extended from low-water level to the junction of the flats with *Spartina glabra* marshland. Cerebratulus was centered chiefly in the lower portion of the shore while Dolichoglossus centered in the middle of the shore. Talorchestia was not found on the muddy shore, while no case was found where the exposed flats

TABLE 4. Station W. Sandy beach. Top number sample of 7-23-35; bottom number sample of 7-23-36.
Key to Tables 4 to 10 That Show Composition and Zonation of Intertidal Communities.

Each column represents a quadrat level. Distances between quadrats are recorded as follows: D=number of feet down-shore measured along the ground; L=number of inches lower measured vertically. Numbers indicate abundance on 400 square inches. Each group of numbers gives the abundance for each year reported. Abun.=abundant; Com.=common; Num.=numerous; Sm. Amt.=small amount; S=seed or juvenile individuals. In those tables in which more than one community is represented, each community is separated by double vertical lines.

Only a few of the stations studied by quadrat sampling are represented by the selected tables presented in this paper and in some cases not all quadrat counts taken at the stations included here are listed. No one station and no one series of samples may be regarded as typical of the community composition and organization as described in the text. The evaluations and descriptions are based upon an over-all study of all of the shores and samples taken over a period of five years.

	1 Near M.H.W.L.	2 20D; 8L	3 40D; 8L	4 20D; 6L	5 26D; 5.5L	6 26D; 4L	7 26D; 3.5L	8 26D; 2.5L	9 26D; 3L	10 26D; 1L	11 26D; 12.5L	12 26D; 6.5L	13 26D; 4L	14 26D; 6L	15 26D; 6L	16 26D; 6L	17 26D; 4.5L
Orchestia platensis	400 4																
Terrestrial arthropods	4 0	0 8	1 0	....	2 0	8 0	3 0										
Talorchestia longicornis	0 4	0 8	7 20	1 0	....	....	....	1 0	....	....	5 12	2 0	2 0	....	....	0 2	
Littorina littorea	....	0 4	....	....	0 2	2 60	1 12	0 2	0 2								
Littorina saxatilis	....	0 1	....	2 4	1 28	1 28	0 16	....	0 6	0 92							
Spartina patens	....	....	Com. Com.														
Spartina glabra	....	....	....	....	Com. Com.	....	....	....	....	Com. Com.							
Mat of algae	....	....	....	....	....	Abun. Abun.	Com. Sm. Amt.	0 Sm. Amt.	0 Sm. Amt.								
Nereis pelagica	....	....	....	....	....	0 2	....	....	....	....	0 2	....	....	0 2			
Mya arenaria	....	....	....	....	....	0 2	3 6	2 16	1 8		0 10	7 8	5 4	10 8	12 4	9 0	
Lumbrinereis tenuis	....	....	....	....	....	....	....	....	....	....	....	....	....	....	0 4	....	30 12

FIG. 5. Sandy beach at station W occupied by the Talorchestia faciation of the Mya-Nereis pelagica biome. Notice invasion of marsh grasses on higher beach level.

reach a level high enough to have a deposit of seawrack with its attendent fauna of Orchestia and its associates, as was found on the sandy beaches. Cerebratulus, Clymenella, Gammarus, Dolichoglossus, Anurida, *L. littorea,* Ensis, and Solemya were much more numerous in this faciation, while some others were practically restricted to it (Nassarius, Onoba, and a number of less significant species). Table 6 and Figure 6 portray typical mud flat conditions at Cape Ann. Verrill & Smith (1873) described animal communities in the mud and sand sediments of the intertidal region of Vineyard Sound. Appellöf in Murray & Hjort (1912) described similar communities for various sections of the Atlantic coast. The papers of Allee (1923) include collecting records from sediments of the Woods Hole region analyzed from a community point of view. Pearse, Humm, and Wharton (1942) studied in detail the inhabitants of the sand beaches at Beaufort, N. C. In the British Isles studies on communities of marine sediments have been made by Bassindale (1938), Beanland (1940), C. B. Rees (1940), Spooner and Moore (1940), and Brady (1943).

During low-tide there is a minimum of activity. The marine invertebrates which remain on the exposed shore cease movement almost entirely, and what feeding activities take place are, for the most part, those of land animals, particularly birds, which feed on the exposed shores. *L. littorea* and Onoba continue to feed to some extent on Ulva, Chaetomorpha, Laminaria, etc., which have been washed ashore, and on microscopic algae on the shore, although for the most part they remain idle at this time. Haseman (1911) found there was no rhythm in the movements of *L. littorea* in the absence of a tidal flow, and the writer has found that often a number of specimens will continue activities even though exposed. Stranded starfishes (Asterias) are not very active, but do feed on the tiny bivalve, Gemma, which they can easily pick up from the surface. Anurida (insect) is the exceptional surface invertebrate which is at its peak of activity at this time, hunting dead bodies of fishes, mollusks, crustaceans, etc. on which it feeds. A special report on the scavenging activities of this marine insect has been published earlier (Dexter 1943c). *Nassarius obsoletus* and Gammarus also are somewhat active if a carcass is near at hand or if the substratum is moist and smooth. In the sand or mud, activity is normal. Nereis, Glycera, and other carnivorous annelids feed on the bivalves. Clymenella, Lumbrinereis, etc. feed on the bacteria (MacGinitie 1932, 1935) and organic matter in the mud, while Polinices bores into the bivalves.

The shore birds, herons, gulls, and crows use the uncovered shoreline for a hunting ground. They feed on annelids, snails, bivalves, crustaceans, starfishes, and debris. This is essentially the same as the food chain reported by MacGinitie (1935) for Elkhorn Slough: "Plants → Detritus and bacteria → Detritus feeders → Animal feeders → Birds." ZoBell & Feltham (1942) have shown the importance of bacteria in the food cycle of such mud flat communities.

As the tide returns, the bivalves of the lower beach, Ensis, Solemya, Gemma, and Siliqua, extend their siphons and again strain the water of its plankton

TABLE 5. Station G. Sandy-mud bar. Top number sample of 7-4-35, middle number sample of 7-4-36, bottom number sample of 7-5-37. The dominants only are shown. Legend as on Table 4.

	1	2	3	4	5	6
	Near top of bar	40D;7L	30D;5L	22D;7L	22D;5L	22D;10.5L
Mya arenaria	120;368S 60;88S 0	160;420S 36;136S 8	200;744S 32;72S 104;412S	32;488S 12 108;388S	12 4 48;812S	1 0 56;676S
Nereis pelagica	18 8 24	17 0 12	17 12 4	14 16 0	27 24 0	5 8 4
Macoma balthica	5 0 0	6 8 0	10 4 4	1 0 4	....	0 0 8
Clymenella torquata	0 0 4	....	....	....	600 0 0	1200 0 0

TABLE 6. Station Q. High marsh, low marsh, and mud flat. Top number sample of 7-13-35, bottom number sample of 7-13-36. Legend as on Table 4.

	1 Near M.H.W.L.	2 12D;35.5L	3 12D;22L	4 40D;8.5L	5 26D;5.5L	6 16D;3L	7 16D;6.5L
Spartina patens..........	Abun. Abun.						
Orchestia platensis	0 68						
Anurida maritima	25 0	25 40					
Littorina saxatilis.......	1 4	0 16					
Littorina littorea........	42 112	96 296	3 100	1 0			
Spartina glabra.........	....	Abun. Com.					
Fucus vesiculosis........	....	Com. 0					
Balanus balanoides......	....	2000 0					
Littorina obtusata.......	....	8 0					
Mytilus edulis..........	....	1 1	50 0				
Lumbrinereis tenuis......	....	....	20 0	60 16	24 0		
Nereis pelagica.........	....	....	8 0	12 12	13 0	6 24	0 4
Mya arenaria...........	....	....	20;140S 20;40S	3;788S 100;360S	2;580S 4	512S 8 S	5S 0
Macoma balthica........	....	....	20 4	44 12	10 4	6 0	1 0
Glycera dibranchiata.....	....	....	1 0	....	1 0	1 4	4 12
Clymenella torquata......	....	....	....	0 48	12 400	12 800	3600 1200
Solemya velum..........	....	....	....	1 0	....	....	1 2
Polinices heros..........	....	....	....	....	1 0		
Chaetomorpha linum.....	....	....	....	....	....	0 Sm.Amt.	
Onoba aculeus..........	....	....	....	....	....	0 4	
Gemma gemma..........	....	....	....	....	....	0 24	
Cerebratulus lacteus......	....	....	....	....	....	2 0	0 2

FIG. 6. Mud flat at station N occupied by the Macoma-Clymenella faciation of the Mya-Nereis pelagica biome.

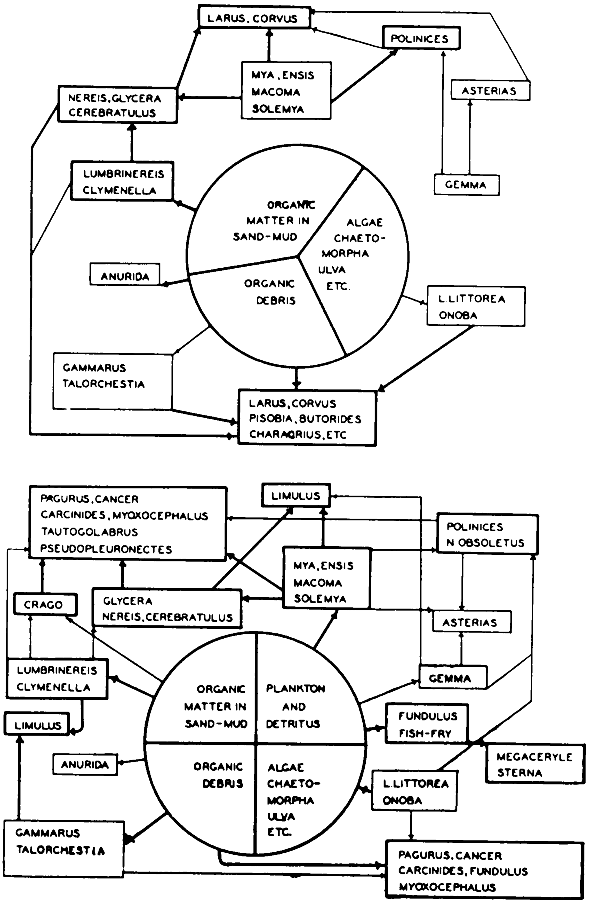


FIG. 7. Food coactions of the Mya-Nereis pelagica biome of intertidal sediments.

and bacteria-laden detritus. As the water level rises and reaches other bivalves (Mya, Macoma), they do likewise. The inflowing waters give the annelids and nemerteans an opportunity to escape and swim off to another location. With the advance of the water, the birds are gradually forced back until they are no longer able to feed on the shore. Replacing the shore birds is a constant stream of shrimps (Crago), minnows (Fundulus), and crabs (Carcinides, Cancer, Pagurus) which come upon the shore as rapidly as the water advances and feed upon the worms (Nereis, Glycera, Lumbrinereis, Cerebratulus, Clymenella), snails (*L. littorea,* Onoba, Nassarius), and bivalves (Gemma, Ensis, Solemya, Mya, Macoma), as well as upon organic debris. As the water deepens, bottom fishes (flounders, sculpins, skates), kingcrabs (Limulus), sand-collar snails (Polinices), and starfishes (Asterias) invade the shore to feed on the worms and mollusks.

When the water floats the stranded masses of Chaetomorpha, the animals *L. littorea,* Onoba, Caprella, and Gammarus become more active in their feeding and locomotion. Anurida retreats up the shore. hides in air bubbles in the mud, or is floated upon the incoming water. By the time the tide has come in three feet above spring-low-water-line, all of the communities inhabiting the bars have been covered, and with an additional foot of water all of the communities inhabiting the mud flats and sandy beaches (except at Station W) have been inundated. These rhythms of activity are associated with rhythms of oxygen consumption by the tidal invertebrates, being greatest during submergence (Gompel 1938). See Figure 7 for diagrams of food coactions of this community at low tide and at high tide.

Annuation and Succession

Mya arenaria was declining in abundance seriously at the beginning of this study. Over-taking of clams by the clam industry, natural enemies, covering of the flats by blue mussels, and the absence of eel-grass to hold the clam seed were causes contributing to the decline. In 1934, the Massachusetts Bureau of Marine Fisheries planted hundreds of bushels of clam seed in flats north of Cape Ann, and without doubt some of the spawn drifted into the Annisquam inlet. In the absence of *Carcinides maenas,* mentioned earlier, and with the removal of blue mussels from many of the flats, a good set of clam seed was established. Natural reseeding also played some part in this reestablishment. Between 1936 and 1937, the Bureau of Marine Fisheries placed 400 bushels of seed clams into the flats of the Annisquam waterway. By 1940, *Mya arenaria* was again a very common species, although for the most part still small in size. Newcombe (1935, 1936) observed annual fluctuations in soft-shell clam populations in the Bay of Fundy region and has shown that the rate of growth during the first four years of life is rapid for this species.

Nereis pelagica increased in abundance in 1934, maintained its numbers until 1936, when it declined to about the 1933 level. It then decreased still further the following season. *Nereis virens* was collected in 1932, the season preceding the beginning of this survey, but was never found again in subsequent years. *Lumbrinereis tenuis* was not found in the same abundance in 1936 as in other years. *Clymenella torquata* increased during the first two years, decreased in 1936, and remained about the same the following year. Phyllodoce catenula was collected during the summer of 1933 only. *Macoma balthica* increased for two years while *Mya arenaria* was decreasing, and then decreased while Mya was being reestablished. *Ensis directus* was found in less abundance each year, declining from a common species to one collected only rarely. *Nassarius obsoletus,* on the other hand, was collected in greater quantity each year after 1933 and extended its range considerably over the flats and marsh channels of the inlet. *Onoba aculeus* was less abundant in 1937 than previously.

As the accumulation of sediments continues, the bars and flats are extended and elevated with a resulting expansion of the Mya-Nereis pelagica Biome. Soon, however, the blue mussel *Mytilus edulis* begins to cover the sediments. At first this bivalve becomes attached to small rocks or shells lying on the surface. As clumps of mussels develop they attach to each other and eventually form a solid carpet over the bars and flats. By blanketing out the inhabitants of the sediments and providing a solid surface for attachment of other organisms, a new community comes into existence—the Balanus-Mytilus Faciation. At the higher level of the flats and beaches, within five feet of mean-high-water line, the thatch grass *Spartina glabra* invades the sediments as they are elevated to that level and extend the low marsh community (Spartina glabra-Littorina saxatilis—Brachidontes Associes).

TIDAL COMMUNITIES OF HARD SURFACES

BALANUS-MYTILUS-LITTORINA BIOME

General Character

The Balanus-Mytilus-Littorina Biome (barnacle-mollusk) is represented along the inlet by fragments of two faciations: Balanus-Mytilus and Balanus-Littorina-Ascophyllum Faciations. Together they form the communities on hard surfaces, particularly on rocks and over flats and beaches where they themselves produce a solid foundation. This biome is similar to the one described by Newcombe (1935) as Balanus-Littorina-Fucus, but here two separate faciations are recognized, and Mytilus is believed to be of greater significance than Fucus. This community is flooded and uncovered twice daily through a mean vertical height of 8.6 feet.

Studies on hard surface communities, particularly those of rocky shores, have been published by Verrill & Smith (1873), King & Russell (1909), Pearse (1913), Huntsman (1918), Allee (1923), Shelford & Towler (1925), Fischer (1928, 1929), Shelford (1930, 1935), Coleman (1933, 1940), Newcombe (1935a), Kitching (1935), Hewatt (1937), and T. K. Rees (1939).

Dominants and Slow-Moving Influents

Dominants

Balanus balanoides, rock barnacle, 740/81
Mytilus edulis, blue mussel, 72/60
Littorina littorea, periwinkle, 111/85
Ascophyllum nodosum, rock seaweed, Abun./47

Subdominant

Fucus vesiculosus, rock seaweed, Com./16

Influents

Littorina obtusata, seaweed snail, 51/47
L. saxatilis, snail, 77/34
Gammarus locusta, amphipod, 15/17
Thais lapillus, rock snail, 13/32
Asterias vulgaris, starfish, 2/11

Subinfluents

Anurida maritima, insect, 155/56
Orchestia platensis, amphipod, 41/11
Spirorbis spirorbis, annelid, 324/4
Neopanope sp., crab
Fucellia sp., seaweed fly
Coelopa frigida, seaweed fly

Permeant Influents

Carcinides maenas, green crab
Cancer irroratus, rock crab
Pagurus longicarpus, hermit crab
P. pollicaris, hermit crab
Tautogolabrus adspersus, cunner
Myoxocephalus octodecemspinosus, sculpin
Fundulus heteroclitus, minnow
Larus argentatus, herring gull
Corvus brachyrhynchos, crow

Secondary Forms

Acmaea testudinalis, limpet, 6/2
Crepidula fornicata, boat shell, 4/1
Obelia spp., hydroids, Com./11
Metridium dianthus, sea anemone, 3/7
Sertularia pumila, hydroid, Abun./3
Gemellaria loricata, bryozoan, Com./3
Schizoporella unicornis, bryozoan, Com./3
Tubularia spectabilis, hydroid, Com./1
Clava leptostyla, hydroid, 16/1
Fucus edentatus, kelp

Faciations

The Balanus-Mytilus Faciation (barnacle-mussel) develops on all kinds of bottom material—sand, mud, and rock. Mytilus forms extensive beds from spring-low-water line to a height of about 5 feet. Below the lowest tidal level the mussels are found in small groups only. Newcombe (1935a) found that while the growth of *M. edulis* in complete submergence is equal to that on the intertidal region, it was not present in the subtidal area of New Brunswick because of echinoderm predators, although it was present on the subtidal shores of Nova Scotia. Warren (1936) found the growth of *M. edulis* better when submerged, but again found the mussels absent below the low-water line in Passamaquoddy Bay because of predation. Without doubt the same factor is responsible for the smaller population of the blue mussels in the subtidal community of the Annisquam inlet. Above the 5 foot vertical limit of solid beds they are likewise scattered, usually small, and few in number. Seldom do they live for long because of the extended period of exposure. Upon the mussels are attached *Balanus balanoides* (rock barnacles), and upon these dominants as a substratum are found the other predominants.

The Balanus-Littorina-Ascophyllum Faciation (barnacle-snail-rock seaweed) is found on hard surfaces. Balanus and Ascophyllum attach to flat surfaces, while Mytilus occurs in crevices and among the rocks. Over all is *Littorina littorea,* the most universally distributed organism in the marine communities of Cape Ann.

Zonation and Coactions

Balanus-Mytilus Faciation

Along the lowest margin of the mussel beds, at about spring-low-water line and somewhat above, there is an ecotone consisting of many sedentary animals which cling to the mussels for support. Sponges, hydroids (Tubularia, Obelia), bryozoans (Celaria, Electra, Lichenophora), sea anemones (Metridium) and the ivory barnacle *(Balanus eburneus)* are somewhat common, although spotted in distribution. In favorable locations they form a carpet over the mussels, but often are scarce or entirely absent. Beneath the railroad trestle at Station E a protection is afforded which makes possible a very abundant, sedentary fauna; but on the margin of the exposed beds these animals are less frequent. Among the mussels at this level are occasional specimens of Cancer, Carcinides, Pagurus, and Asterias waiting the return of the tide.

Scattered over the shore at any point, but more often along the lower portion, fragments of algae are found. Ulva, Chaetomorpha, Ascophyllum, Fucus are often left strewn about by the receding tide and on some beds Fucus grows attached to the shells. The mussel bed is a solid mass of the bivalve *Mytilus edulis* (including the var. *pellucidus*) firmly held together by byssal threads. It extends from spring-low-water line to the top of the bars and to within 4 or 5 feet of the spring-high-water line along the strand. *Littorina littorea* is numerous all over the beds while much of the exposed surface of the bivalves is coated with the rock barnacle *(Balanus balanoides)* from about mean-low-water line to the upper limit of the mussels. *Anurida maritima* is common along the upper half of the beds.

During exposure, activity is reduced to a small amount of feeding on algae by *Littorina littorea,* on barnacles and mussels by *Thais lapillus* (rock snail), and to the scavenging activities of *Anurida maritima,* the herring gull, and crow. The scavengers feed on dead animals that have been exposed or washed in upon the beds.

Beginning again at the spring-low-water level, the incoming water allows the sponges, hydroid colonies, anemones, and ivory barnacles to feed on the microscopic organisms and bacteria-laden detritus. As the water continually rises, the mussels open their shells tier after tier and resume the straining of water. From the mean-low-water line to the top of the bed, or to the highest level reached by the water if rocks continue above the bed, the rock barnacles *(Balanus balanoides)* likewise resume their feeding activity. *Littorina littorea* and *Thais lapillus,* when present, continue their wandering and feeding after being stationary since exposure. Thais was found to feed largely on Mytilus, but also to some extent on Balanus. Fischer-Piette (1934) reported observations to the contrary. In some instances the writer found that both organisms were being attacked rather equally, but on the whole more borings were found taking place in *Mytilus edulis.* Newcombe (1935, and personal communication) claims that *L. littorea* also feeds on *B. balanoides,* although the writer failed to corroborate this after careful and extended observations in the field. The evidence seems to rest chiefly on the destruction of barnacle seed by *L. littorea,* probably incidentally as it scrapes off algae from hard surfaces. In any case, such a coaction could not be demonstrated on these shores to justify listing it as an item of importance. *Asterias vulgaris* invades the beds to open the mussels and barnacles, and fishes and crabs invade to scavenge about. *Anurida maritima* is forced off the shore again, and the birds take leave. The Balanus-Mytilus Faciation was found at Stations C, E, and V (Table 7, Figure 8). Thirty-eight quadrat counts were made.

Balanus-Littorina-Ascophyllum Faciation

Along the lowest zone of the rocky shores laid bare by the spring tides is an ecotone, which is found best developed at Station B (Table 8, Figure 9) at the junction of the inlet with Gloucester Harbor. There the rocks are exposed to the spring-low-water line while along the inlet the lower levels of the rocky shores are for the most part covered with sediments. *Chondrus crispus* is the dominant alga, with scattered tufts of *Ulva lactuca.* Spirorbis (annelid) and bryozoans (Gemellaria, Schizoporella) encrust many of the rocks. Crepidula, Acmaea, *L. littorea* (snails), and Asterias (starfish) constitute the motile animals, but they remain stationary during exposure. Wilson (1929) has called attention to the fact that *L. littorea* fastens itself to the rocks with a mucus secretion and withdraws into its shell.

Over the shore from mean-low-water line to about mean-high-water line are strewn masses of *Ascophyllum nodosum* and to a lesser extent *Fucus vesiculosus.* Coating nearly all hard, exposed surfaces are the barnacles, *Balanus balanoides,* and dotting the rocks and seaweeds are the periwinkles, *Littorina littorea.* On the algae in large numbers is the seaweed snail, *L. obtusata,* which is practically restricted to such a habitat. Mytilus often forms a floor between the rocks and fills most of the crevices in them, especially around their bases. Crawling over all—rocks, barnacles, mussels, seaweed—is the ubiquitous insect *Anurida maritima.*

Thais (rock snail) occupies the lower third of the shore on the barnacles and mussels. In this zone Gammarus (amphipod) is most numerous, living under the seaweed (often in pairs); and Sertularia and Clava are attached to the algae in large colonies. Asterias at times remains on the exposed shore. Acmaea and *Crepidula fornicata* (snails) are rarely present.

Carcinides is common, hiding under seaweed and in crevices during the exposure of the shore, while Neopanope and occasionally Cancer (crabs) hide beneath loose rocks and bunches of seaweeds. All of

TABLE 7. Station E. Mussel bed. Top number sample of 8-16-35, bottom number sample of 8-12-36. Legend as on Table 4.

	1 Base of seawall	2 16D;28.5L	3 36D;13.5L	4 36D;17.5L	5 4D;5L	6 2D;10L	7 2D;10L
Anurida maritima	0 24	....	0 32				
Balanus balanoides	4000 2400	800 40	1000 20	200 4	160 20	80 0	40 —
Littorina littorea	72 56	72 28	120 24	60 56	20 12	4 0	16 —
Mytilus edulis		80;2000S 16;740S	1200 16;660S	200 24;340S	100 24;240S	96 28	32 —
Nassarius trivittata	....	....	....	0 6			
Obelia sp.	....	....	....	Com. Num.	Abun. Num.	Abun. Abun.	Sm.Amt. —
Asterias vulgaris	....	....	....	1 1	1 6	....	1 —
Metridium dianthus	....	....	....	0 1	0 4	4 4;12S	4 —
Cancer irroratus	....	....	....	0 1	1 2	0 6	1 —
Balanus eburneus	....	....	....	....	....	25 0	
Chondrus crispus	....	....	....	....	....	....	6 —
Sponge	....	....	....	....	....	....	50 sq.in. —
Tubularia spectabilis	....	....	....	....	....	....	25 —

FIG. 8. Mussel bed at station V. The Balanus-Mytilus faciation has developed over sediments. Notice the invasion of low marsh on the highest level of the mussel bed.

these are commonly found paired during the latter part of the summer and remain paired even when disturbed.

Over the upper half of the shore *Littorina saxatilis* is common, especially among the smaller, loose rocks, around mean-high-water line. Orchestia (amphipod) is often abundant among the algae, and at times Tabanus, Culicoides, and other flies take refuge there. The highest reaches of the community consist chiefly of *Balanus balanoides, Littorina saxatilis, L. littorea,* and *Anurida maritima.* The vertical distribution of the three species of Littorina is believed to be correlated with the varying resistance of these species to adverse conditions (Gowenlock & Hayes 1926). Some of the larger groups of rocks near high-water-line and above are used by the herring gulls for dropping hard shelled animals to break them open prior to eating the soft parts. On certain rocks regularly used for that purpose shell heaps accumulate (Dexter 1943b).

Not all of these communities occupy the full breadth of the intertidal zone; but where they are found they contain the species characteristic of that level. The Balanus-Mytilus-Ascophyllum Faciation was studied at Stations B, H, K, M, P, R, T, and X, with a total of 141 quadrat counts (Tables 8, 9; Figs. 9-12).

TABLE 8. Station B. Rocky shore. Top number sample of 9-3-35; bottom number sample of 9-7-36. Quadrat No. 10 for 1936 only. Legend as on Table 4.

	1 Gravel bank	2 30D;42L	3 20D;4L	4 50D;6.5L	5 21D;0L	6 21D;3.5L	7 21D;6.5L	8 15D;7L	9 15D;4L	10 15D;6L
Anurida maritima	1 4	20 56	0 24							
Littorina saxatilis	1 0	....	112 0	48 0	....	16 0				
L. littorea	1 0	40 16	900 432	640 128	244 376	100 56	124 100	272 480	180 340	— 144
Balanus balanoides	....	8 4	800 108	520 28	720 20	3600 800	40 28			
L. obtusata	....	0 8	....	0 60	200 32	24 40	96 64	44 100	16 8	
Cancer irroratus	....	....	0 1							
Fucus vesiculosis	....	....	4 0	0 Com.	Com. 4	0 8				
Mytilus edulis	....	....	12 292S	32 464S	20 8	4 28	16 8			
Mya arenaria	....	....	40S 8S	20S 0	12S 20S	....	4S 0			
Thais lapillus	....	....	0 100	0 64	28 32	0 8	4 8	12 36	8 0	
Lumbrinereis tenuis	....	....	50 28	....	0 40	....	4 0	20 0	0 12	
Gammarus locusta	....	....	....	0 4	12 40	....	....	8 Com.	8 8	
Neopanope sp.	....	....	....	....	0 1	....	0 1			
Ascophyllum nodosum	....	....	....	....	Abun. Abun.	Abun. Abun.	Abun. Abun.	Abun. Abun.	Abun. Abun.	
Sertularia pumila	....	....	....	....	....	Com. 0	0 Com.			
Carcinides maenas	....	....	....	....	....	....	0 1	1 1		
Spirorobis spirorbis	....	....	....	....	....	....	100 0	400 400	600 400	— 48
Asterias vulgaris	....	....	....	....	....	....	1 1	0 1	0 1	— 1
Schizoporella unicornis	....	....	....	....	....	....	....	12 sq. in. 5 sq. in.	16 sq. in. Abun.	— 4 sq.in.
Gemellaria loricata	....	....	....	....	....	....	....	8 0	20 Com.	— 1
Acmaea testudinalis	....	....	....	....	....	....	....	4 0	8 0	— 8
Anomia simplex	....	....	....	....	....	....	....	....	0 2	
Strongylocentrotus drobachiensis	....	....	....	....	....	....	....	....	0 1	
Crepidula fornicata	....	....	....	....	....	....	....	....	0 4	— 4
Chondrus crispus	....	....	....	....	....	....	....	....	....	— Com.
Lichenophora hispida	....	....	....	....	....	....	....	....	....	— 1 sq.in.

TABLE 9. Station P. Rocky shore. Top number sample of 7-31-35, middle number sample of 7-31-36, and bottom number sample of 8-3-37. Legend as on Table 4.

	1 S.H.W.L.	2 6D;22L	3 6D;28L	4 6D;36L	5 6D;36L
Orchestia platensis	0				
	12				
	4				
Terrestrial arthropods	84				
	56				
	52				
Littorina saxatilis	....	0			
	....	124			
	....	12			
Isopod	....	0	4		
	....	0	0		
	....	8	0		
Mytilus edulis	....	0	16	24	40
	....	2S	2	4	0
	....	0	0	0	0
Anurida maritima	....	20	400	1200	0
	....	0	32	20	0
	....	0	12	0	12
Balanus balanoides	....	80	2800	3000	4800,
	....	1600	1200	0	16
	....	108	1480	1108	1400
Littorina littorea	....	28	84	40	180
	....	104	0	0	160;210S
	....	4	16	48	496
Littorina obtusata	....	....	84	100	
	....	....	24	48	
	....	....	60	60	
Ascophyllum nodosum	....	....	Abun.	Abun.	
	....	....	Abun.	Abun.	
	....	....	Abun.	Abun.	
Sertularia pumila	....	....	0	Abun.	
	....	....	Com.	Abun.	
	....	....	0	Abun.	
Thais lapillus	....	....	0	4	8
	....	....	2	32	8
	....	....	0	20	12
Gammarus locusta	....	....	....	4	
	....	....	....	8	
	....	....	....	0	
Bryozoan	....	....	....	0	
	....	....	....	1 sq.in.	
	....	....	....	3 sq.in.	
Clava leptostyla	....	....	....	0	
	....	....	....	0	
	....	....	....	8	
Chondrus crispus	....	....	....	0	
	....	....	....	0	
	....	....	....	Sm.Amt.	
Cancer irroratus	....	....	....	....	0
	....	....	....	....	0
	....	....	....	....	1

Activity in this community when exposed is much the same as that of the Balanus-Mytilus Faciation. The snails *L. littorea* and *L. obtusata* continue to feed on algae, especially under the moist heaps of Ascophyllum; scavenging arthropods (Gammarus, Orchestia, Anurida) are active, but all under cover except Anurida. The strewn masses of brown seaweeds serve as a haven for the motile animals and the stranded subtidal animals for protection against predators and desiccation. Shallow tidal pools, when present, allow some of the intertidal organisms to continue their activities as though there were no tidal rhythm. The herring gull and crow comb the shores for food.

As the water covers the lowest zone, the bryozoans (Lichenophora, Schizoporella, etc.), sedentary snails (Acmaea, Crepidula), Spirorbis, and Anomia resume their feedings. Strongylocentrotus (sea urchin), when present, continues its movements.

Upon reaching the mean-low-water line, the water

FIG. 9. Rocky shore at station B inhabited by the Balanus-Mytilus-Ascophyllum faciation. This type is found on the shores of Gloucester Harbor at the extremity of the inlet. Stakes indicate certain quadrat levels.

FIG. 10. Rocky shore at station P inhabited by the Balanus-Mytilus-Ascophyllum faciation. This type is found along exposed ledges bordering the inlet. Stakes indicate quadrat levels.

Fig. 11. The Balanus-Mytilus-Ascophyllum faciation on glacial boulders at station T. Stakes indicate quadrat levels.

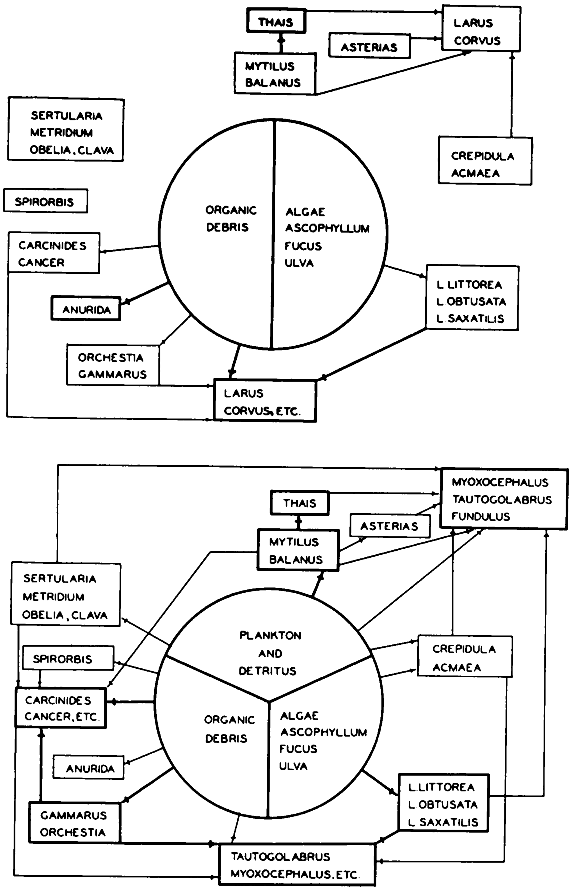


Fig. 12. Food coactions of the Balanus-Mytilus-Littorina biome.

begins to float the brown algae (Ascophyllum, Fucus) which remain attached to the rocks at one end and float freely at the other. On the seaweeds, Sertularia and Clava once again have access to the plankton, and *L. littorea* and *L. obtusata* crawl about, scraping away the plant tissue. Mytilus and Balanus resume feeding from this point back to the upper limit of their distribution, and Thais and Asterias continue their predation on them.

Gammarus and other amphipods often take to swimming when submerged while the insects (Tabanus, Culicoides, etc.) leave the shore.

Crabs (Carcinides, Cancer, Pagurus) and fishes (sculpins, minnows, cunner) come upon the shore to feed on the wealth of the invertebrates present. About middle shore and higher, Neopanope and Tanais, which hide under loose stones during low tide, become active again; likewise for *Littorina saxatilis* on the rock surfaces where they remain dormant until submerged.

Anurida is driven into air bubbles under loose stones and among gravel or else onto higher ground. Above mean-high-water line the seaweeds and their associated animals are not present. *L. saxatilis,* Orchestia, and terrestrial arthropods compose the community at this level. Orchestia is driven into the seawrack, and at flood tide the terrestrial spiders, isopods, mites, and insects are driven out to the water line or floated upon the flood waters. Terns and kingfishers take the place of gulls and crows as the community becomes inundated.

Annuation and Succession

Mytilus edulis was very abundant everywhere in 1933 and was increasing and spreading the following season. In 1935, however, this mussel was removed from certain flats to prevent its encroachment upon the clam flats. In 1936 abundant seed mussels invaded the uncovered sediments; but in 1937 the Bureau of Marine Fisheries removed thousands of bushels of blue mussels in its campaign to restore the soft-shell clam. By 1940, this prolific mussel was successfully invading many of the areas which had been cleared.

Littorina saxatilis underwent a most remarkable fluctuation in abundance during the period of this study. In 1933 no living specimen was found although the presence of numerous shells indicated that it had been abundant in recent years. In 1934, less than a dozen living snails of this species could be found. The following summer, however, this snail was exceedingly abundant on all shores of the inlet, and in many cases was found out of its normal vertical range and habitat. Mud, rocks, seaweeds, and marshes were peppered with it. In 1936 it was still more abundant at certain levels, but was restricted more to the higher tidal levels and for the most part confined to solid surfaces—rocks, blades of thatch grass, and the firm marsh banks. An average of two snails per square inch was found over a wide area. By the next summer the population density had dropped to about the 1935 level and this snail remained on the higher shore levels.

Littorina obtusata, the seaweed snail, was more common in 1934 than during the previous year, in many places being as abundant as the introduced periwinkle, *L. littorea.* In 1935 it was often more abundant than *L. littorea* on some shores. During the following two years, *L. obtusata* gradually decline in numbers. *L. littorea* withstood the low temperatures (−20° F.) of the winter of 1933-34 very well, large populations being found in December and March, with an unusually large number of young snails found in March, but the following year this species declined somewhat in abundance, and on many shores was overshadowed by the expanding populations of *L. saxatilis* and *L. obtusata*. In 1936 it returned to its usual abundance. Orton & Lewis (1931) reported on changes in snail populations after a severe winter in an English estuary. *L. littorea,* introduced from the British Isles, was first observed in this section of North America in Salem Harbor in 1872, and by 1880 was one of the most abundant snails along the Massachusetts coast (Morse 1880).

In years preceding this survey, the writer had observed *Thais lapillus,* the rock snail, on many rocky shores of the inlet. In 1933, however, very few specimens could be collected, and those that were found were taken at the extremities of the inlet bordering Gloucester Harbor and Ipswich Bay. Empty shells along the inlet reminded one of its former range and abundance. In 1934 it began to return, increased to a noticeable degree the following year when many young snails were observed and at that time as many as 24 could be collected in a 400-square-inch quadrat. The next year collections quadrupled. In 1937 the species was once again an abundant member of the hard surface communities, and by 1940 it was as common as ever observed in the inlet.

Acmaea testudinalis was collected in greater quantity in 1934 than during other years. A crab of the genus Neopanope, found in abundance under rocks in 1933, disappeared from the collections in 1934, possibly because of the low temperatures of the intervening winter. It returned in 1935 in small numbers and gradually increased in abundance each year. *Metridium dianthus* suffered a severe set back in the season of 1936 because of fresh coats of tar which were applied to the pilings of the railroad trestle. These pilings had been one of the principal habitats of this sea anemone. Shelford et al. (1935) described changes in barnacle populations between 1928 and 1930 on the Pacific coast and called attention to the importance of annuation in the study of marine communities. Rice (1930) and Towler (1930) made studies on these same barnacle communities.

With the continuation of sedimentation, silt and sand cover the lower margins of the rocky shores. Pockets of sediment among the rocks lead to the establishment of the bivalve-annelid biome as isolated outposts within the hard-surface community. The mussel beds can keep up with the accumulating sediments by constructing layer upon layer of new sets of mussels. Eventually, however, when the elevation reaches the level of the thatch grass marshes, *Spartina glabra* invades the mussel beds and the pockets of sediments among the rocks as well as the higher levels of sand beaches and mud flats (Figs. 5, 8, 13). In time, the low marsh community S. glabra-L. saxatilis-Brachidontes Associes becomes established.

COMMUNITIES OF SUCCESSION TO LAND

Bordering the Mya-Nereis pelagica and Balanus-Mytilus-Littorina Biomes are two marsh communities which are transitional between them and land communities. These are designated as the Spartina glabra-Littorina saxatilis-Brachidontes Associes and the Spartina patens-Melampus-Orchestia Associes. It is well known that marshes are extensively developed along shores that are gradually subsiding (Ganong 1903, McAtee 1935). The entire inlet at Cape Ann is bordered by the two marsh communities mentioned, commonly referred to as the low marsh (mid-littoral marsh of Johnson & York 1915) and the high marsh. Observations show that these marsh communities develop on all kinds of bottom materials. Along the inlet they are found on sand, mud, old mussel beds, and among rocks. Ganong (1903) made an extensive study of the Bay of Fundy marshes and mapped out their distribution. Johnson & York (1915) correlated marsh types and vegetation zones with tidal levels at Cold Spring Harbor. Johnson & Skutch (1928, pt. III) described marsh zones and traced marsh succession to a spruce climax on Mt. Dessert Island. Prat (1933) discussed the relation of marsh lands to mud flats and sand beaches. McAtee (1935) outlined the general features of the marshes on the east coast of North America with an annotated list of the vertebrate fauna. Chapman (1938-1940), in a series of studies on salt marshes in the British Isles and the eastern coast of North America, described them and their algal communities in detail. A thorough analysis was made of the tides, water table, drainage, aeration, and salinity, and comparisons made between British marshes, and between those at Long Island, N. Y., Lynn, Mass., and the Scott marshes of England. In another paper (Chapman 1940a) he outlined the successions of east coast North American marshes.

SPARTINA GLABRA-LITTORINA SAXATILIS-BRACHIDONTES ASSOCIES

General Character

The Spartina glabra-Littorina saxatilis-Brachidontes Associes occupies the marsh banks between the lower shores and the high marshlands. These banks are for the most part steep and narrow and have a vertical height of about five feet, ranging up to the mean-high-water line. Johnson & York (1915) found this marsh at Cold Spring Harbor between 1.5 and 6.5 above mean-low-water line. With the exception of breaks caused by the rocky shores and ledges, the low marshes at Cape Ann form a continuous line along either side of the channel from end to end. This associes was studied at Stations F, I, J, L, N, O, and Q, (Tables 6, 10; Figs. 13-17). Thirty-six quadrat counts were made.

Dominants and Slow-Moving Influents

Dominants

Spartina glabra, thatch grass, Abun./100
Littorina littorea, periwinkle, 80/97
L. saxatilis, snail, 75/84
Ascophyllum nodosum f. scorpioides, marsh seaweed, Com./40

TABLE 10. Station J. High marsh, low marsh, and edge of mud flat. Top number sample of 8-24-35; bottom number sample of 8-26-36. Legend as on Table 4.

	1 Near S.H.W.L.	2 21D;4L.	3 21D;1.5L.	4 26D;1.5L.	5 40D;4.5L.	6 14D;52L.	7 21D;25L.	8 21D;7L.
Spartina patens	Abun. Com.	Abun. Abun.	Abun. Abun.	Abun. Abun.				
Isopod	20 12	8 4	....	4 0				
Orchestia platensis	16 24	20 12	28 12	0 16	10 4	1 0		
Melampus bidentatus		48 16	116 36	72 56	0 32			
Talorchestia longicornis	....	8 0	....	....	1 0			
Littorina saxatilis	....	....	....	8 0	400 124	50 24		
Littorina obtusata	....	....	....	....	1 0			
Spartina glabra	....	....	....	....	Com. Com.	Com. Com.		
Anurida maritima	....	....	....	....	10 0	7 20		
Littorina littorea	....	....	....	....	35 52	300 48		
Mytilus edulis	....	....	....	....	....	4S 12S		
Brachidontes demissus	....	....	....	....	....	17 1;25S		
Nassarius obsoletus	....	....	....	....	....	3 0	25 28	— 56
Cyathura carinata	....	....	....	....	....	....	1 1	
Nereis pelagica	....	....	....	....	....	....	4 0	— 4
Mya arenaria	....	....	....	....	....	....	2 4	— 8
Lumbrinereis tenuis	....	....	....	....	....	....	4 0	— 4
Macoma balthica	....	....	....	....	....	....	1 0	— 8

Subdominant

Brachidontes demissus, ribbed mussel, 8/25

Influents

Gammarus locusta, amphipod, 109/33
Anurida maritima, insect, 68/77
Littorina obtusata, seaweed snail, 37/37
Fucus vesiculosis, brown alga, Com./20
Coelopa frigida, kelp fly
Culicoides sp., midge
Tabanus nigrovittatus, horse fly
Aedes sollicitans, salt marsh mosquito
Fucellia sp., kelp fly

Subinfluents

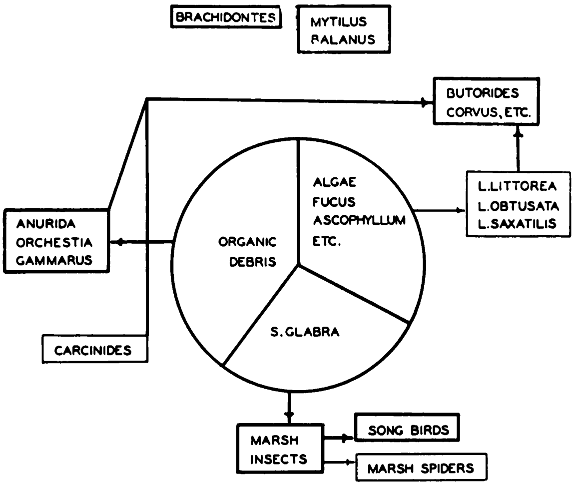
Mytilus edulis (seed), blue mussel, 29/57
Orchestia platensis, amphipod, 10/27
Balanus balanoides, barnacle, 94/30
Fucus vesiculosis v. spiralis, brown alga, Num./10

Permeant Influents

Carcinides maenas, green crab
Cancer irroratus, rock crab
Fundulus heteroclitus, minnow
Butorides virescens, green heron
Nycticorax nycticorax, night heron
Corvus brachyrhynchos, crow
Charadrius semipalmatus, semipalmated plover
Actitis macularia, spotted sandpiper
Pisobia minutilla, least sandpiper
Tyrannus tyrannus, kingbird

Iridoprocne bicolor, tree swallow
Hirundo erythrogaster, barn swallow
Dumetella carolinensis, catbird
Sturnus vulgaris, starling
Sturnella magna, meadowlark
Agelaius phoeniceus, red-wing
Quiscalus quiscula, bronzed grackle
Ammospiza caudacuta, sharp-tailed sparrow

FIG. 13. Low marsh community, Spartina glabra-Littorina saxatilis-Brachidontes associes, invading upper level of mud flat at station J. Notice Nassarius obsoletus scattered over surface of mud.



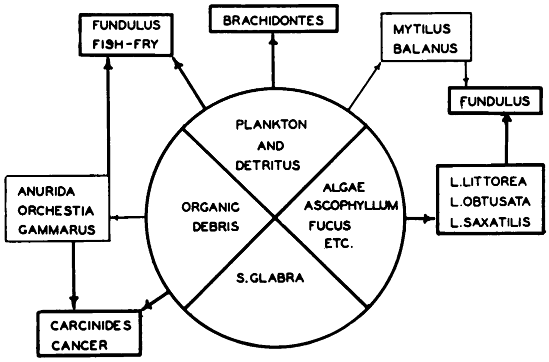


FIG. 14. Food coactions of the Spartina glabra-Littorina saxatilis-Brachidontes associes of low marshes.

Melospiza melodia, song sparrow

Secondary Forms

Melampus bidentatus, marsh snail
Anas rubripes, black duck

Organization and Coactions

This low marsh is dominated by a tall, solid stand (4-5 feet high) of thatch grass *(Spartina glabra)*. *L. saxatilis* is common on the stems and lower leaves of Spartina, usually attached by mucus during exposure. Intermingled at the base of the stems is a mass of *Fucus vesiculosus*, including *var. spiralis*, or *Ascophyllum nodosum f. scorpioides* or both. Abundant on these algae are *Littorina littorea* and *L. obtusata*, while *Gammarus locusta* remains under them or in tunnels in the bank. Crawling everywhere over the ground and algae is *Anurida maritima*, while Tabanus, Culicoides, and other dipterous insects are found throughout the marsh.

Brachidontes demissus (ribbed mussel) occupies the ground, being half embedded in the bank and half exposed, with the center of its population on the lower bank level. A number of blue mussels (Mytilus) usually become attached here to some convenient anchorage, and *Balanus balanoides* seed is often

FIG. 15. Junction of the low marsh and high marsh communities at mean-high-water line at station J.

FIG. 16. Tidal creek at station F with marsh banks of low marsh Spartina glabra-Littorina saxatilis-Brachidontes associes and with high marsh plateau of S. patens-Melampus-Orchestia associes.

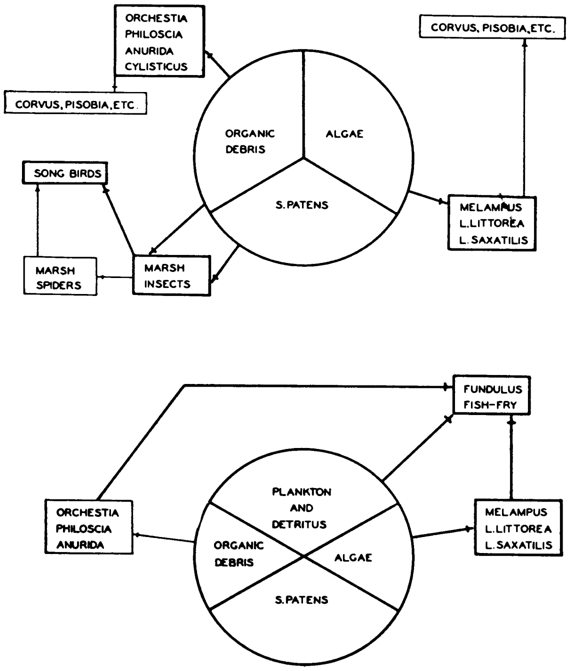


FIG. 17. Food coactions of the Spartina patens-Melampus-Orchestia associes of high marshes.

abundant, adhering to the mussels, to small rocks, old plant stems, and occasionally to algae or the marsh bank itself. *Nassarius obsoletus* on the muddy sediments often penetrates the lower edge of this marsh community. On the higher level small numbers of mites, spiders, and insects are present while on the top ridge, Orchestia, Philoscia (crustaceans), and Melampus (marsh snail) overlap from the high marsh community.

During exposure snails of the genus Littorina are generally quiescent, as elsewhere at time of low-water, although a small number of the seaweed snail (*L. obtusata*) may be active. Anurida, and to a less extent some of the amphipods, are feeding at this time.

The typical marsh insects (Tabanus, Culicoides, Aedes, etc.) are feeding on debris and marsh plants, while they are fed on by the marsh spiders, both groups falling prey to the passerine birds (kingbird, swallows, meadowlark, redwing blackbird, sparrows, etc.) which visit here. Shore birds and herons pick up various invertebrates among the thatch grass.

About one foot below half-tide level, the water begins to contact the low marsh community. The scattered mussels and barnacles begin to take in plankton and detritus again after several hours of inactivity. As the water continues to rise the three Littorina snails become more active and feed on the algae. Gammarus is able to swim about and Brachidontes opens its shells and extends its siphons. Anurida is driven back up the shore or into air pockets in the marsh. The marsh spiders and insects also retreat. *L. saxatilis* migrates up the shore to a certain extent, especially during the days of spring tides when the shore is flooded to a maximum and the marsh is covered to a greater depth than usual. The common crabs (Carcinides, Cancer), minnows (Fundulus), and fish fry invade the low marsh zone and feed on debris and various invertebrate animals.

Annuation and Succession

On some shorelines the low marsh retreated each year because of wave action which cut into the marsh banks, undermined the growth of *Spartina glabra*, and caused fragments of the marsh banks to break away. Another contributing cause was the action of ice in winter time which broke down the edges of the marsh banks and pushed fragments of the thatch grass community and its sod out onto the mud flats (see right hand corner of Figure 6.). On the other hand, where wave action was not severe, the banks were not undermined and consequently there was no abrupt edge which could be torn down by ice action. In these protected marshes the junction between them and mud flats, beaches, mussel beds, or rocky shores was sharply defined but on a gradual slope. As sedimentation continues, the low marsh community invades these other communities of the tidal zone (Fig. 13) as discussed earlier.

The sudden and pronounced increase of *Littorina saxatilis* is discussed in the section on annuation of hard-surface communities, and the drastic decline and eventual return of *Carcinides maenas* are accounted for in the discussion of the subtidal community. *Brachidontes demissus* was collected in greater abundance in 1936 than in other years. This was a successful year for the seeding-in of this ribbed mussel, which accounted for the greater density that year.

As the S. glabra-L. saxatilis-Brachidontes Associes is slowly elevated to the mean-high-water line, it is replaced by the high marsh community, the Spartina patens-Melampus-Orchestia Associes. The junction between the two is usually abrupt and follows the mean-high-water contour (Fig. 15, 16). Above this level, broad and extensive marshes of the fox grass (*Spartina patens*) predominate to the spring-high-water line.

SPARTINA PATENS-MELAMPUS-ORCHESTIA ASSOCIES

General Character

The high marsh is a very gently sloping, almost level expanse of soggy, peaty ground built up by deposition and peat formation between mean-high-water line, where the low marsh ends, and spring-high-water line. It is populated by an almost solid stand of *Spartina patens*. Johnson & York (1915) believed that this species is held at this level by competition with *S. glabra* that occupies the next lower zone, and they found *S. patens* at lower levels in the absence of *S. glabra*. Along the Annisquam River, however, the two are nearly always found adjacent at their respective levels, even on newly developing marshes. Both species, according to Chapman (1940), reproduce chiefly by rhizomes. He found very few viable seeds on the marshes at Lynn. Wherever *S. patens* has been removed for one reason or another, there is a patch of *Salicornia europaea.* This plant is slowly replaced by the fox grass.

Dominants and Slow-Moving Influents

Dominants
Spartina patens, fox grass, Abun./100
Orchestia platensis, beach flea, 23/90
Melampus bidentatus, marsh snail, 47/50
Subdominants
Littorina littorea, periwinkle, 53/40
Philoscia vittata, isopod, 7/50
Influents
Littorina saxatilis, snail, 5/40
Terrestrial arthropods (insects, sowbugs, spiders, mites)
Anurida maritima, insect, 20/10
Culicoides sp., midge
Tabanus nigrovittatus, horsefly
Aedes sollicitans, salt marsh mosquito
Subinfluents
Salicornia europaea, saltwort
Limonium carolinianum, marsh rosemary

Permeant Influents

Pisobia minutilla, least sandpiper
Charadrius semipalmatus, semipalmated plover
Corvus brachyrhynchos, crow
Buteo lineatus, red-shouldered hawk
Circus hudsonius, marsh hawk
Actitis macularia, spotted sandpiper
Tyrannus tyrannus, kingbird
Iridoprocne bicolor, tree swallow
Hirundo erythrogaster, barn swallow
Dumetella carolinensis, catbird
Sturnus vulgaris, starling
Sturnella magna, meadowlark
Agelaius phoeniceus, red-wing
Quiscalus quiscula, bronzed grackle
Ammospiza caudacuta, sharp-tailed sparrow
Melospiza melodia, song sparrow
Microtus pennsylvanicus, field mouse
Sylvilagus transitionalis, cottontail
Thamnophis sirtalis, garter snake
Fundulus heteroclitus, minnow

Secondary Forms

Distichlis spicata, spike grass
Puccinellia maritima, sea spear
Juncus gerardi, black grass
Gerardia maritima, seaside gerardia
Plantago decipiens, seaside plantain
Solidago sempervirens, seaside goldenrod
Anas rubripes, black duck

Organization and Coactions

In these marshes shore and song birds are common everywhere flying over the marsh and walking among the grass. Among the matted stems of Spartina are the snails, Melampus, *Littorina littorea,* and *L. saxatilis,* a beach flea (Orchestia), an isopod (Philoscia), and marsh spiders, mites, and insects. These species are scattered about more or less evenly throughout. Either among the grass or in the air will be found the horsefly (Tabanus), midge (Culicoides), black fly (Coelops) and similar insects which inhabit these marsh communities.

Along spring-high-water line there is an ecotone or transition belt between the fox grass marsh community proper and the terrestrial communities. Near the upper limit of *S. patens,* the marsh rosemary *(Limonium carolinianum)* and seaside goldenrod *(Solidago sempervirens)* dominate, while along the highest ridge black grass *(Juncus gerardi)* and its associates *(Distichlis spicata, Puccinellia maritima, Plantago decipens, Gerardia maritima)* dominate. The animal population of this ecotone consists chiefly of terrestrial insects, spiders, mites, isopods, snails, song birds, and small mammals.

Even during the long exposure Melampus, Orchestia, and Philoscia are found scattered about rather generally under the fox grass or marsh hay *(S. patens)* and are quite active. *L. littorea* and *L. saxatilis* are more dormant. Marsh and terrestrial insects are abundant, flying in the air or living among the grass where they fall prey to spiders. The song birds feed on them while shore birds search the high marshes for snails and crustaceans. Davenport (1903) has shown the typical chain on the high marshes at Cold Spring Harbor to be: "debris feeders → predaceous spiders, robber flies, tiger beetles → swallows."

Each fortnight as the spring tides (equinoctial tides) spread over the high marsh communities, the spiders and insects are floated or driven off. Melampus and *L. saxatilis* are driven back to a higher level or climb to the top of the grass, and the birds go elsewhere for a time. As the seawrack along the highwater line is submerged, the isopods, spiders, and insects are driven out. Fundulus (minnow) and fish-fry swim over the flooded marsh and pick up the various small snails and crustaceans.

A number of crabs (Carcinides), king crabs (Limulus) and shrimps (Crago) likewise invade the high marsh at this time, and the motile animals in general move to a higher level. After the retreat of the water, snails, especially of the genus Littorina, are found in large numbers along the highest margin of the shoreline with the center of the population of each some two feet above the normal distribution. The S. patens-Melampus-Orchestia Associes was studied at Stations F, I, J, L, O, Q, T, and U, including 28 quadrat counts (Tables 6, 10; Figs. 15-17).

Annuation and Succession

Spartina patens with its associated animals is slowly but definitely filling in the marsh creeks, coves, and the margins of the inlet. This process is proceeding more slowly than the succession taking place in communities of lower levels since the high marshes are inundated only at times of spring tides. During the interval of this study no significant change could be observed.

One of the characteristic marsh snails, *Melampus bidentatus,* was observed to increase to a noticeable degree. In 1933 it was found locally in the marshes, but numerous shells in the seawrack along the entire shoreline indicated a greater abundance in past years. In 1935 it was more abundant and widely distributed. It had increased to as many as 113 in a 400 square inch quadrat.

CLIMAX. BEECH-MAPLE ASSOCIATION

The climax land community of Cape Ann is the Beech-Maple Association of the Temperate Deciduous Forest Biome. Some of the principal dominants are beech, sugar maple, red oak, black oak, white oak, elm, white pine, pitch pine, and hemlock. Cape Ann is within the Transition Zone, possessing both deciduous and coniferous trees, but with a decided majority of hard woods. The conifers may be regarded as forming a mictium with the deciduous trees, or they may be regarded as persistent relics from the last post glacial period.

Most of the original land vegetation bordering the inlet has been destroyed, but in places, climax or subclimax trees are still found. Much of the riparian zone contains a poor, gravelly soil, and probably had not developed a climax community before disturbance took place. Above station R there is a small area of climax beech woods with the characteristic red backed salamander *(Plethodon cinereus)* and at Ravenswood Park, a nearby preserve area, is found a tract of climax Beech-Maple-Hemlock forest.

SUMMARY AND CONCLUSIONS

An ecological study of the organization and dynamics of the marine communities of a tidal inlet (Annisquam River) at Cape Ann, Massachusetts, carried out principally during the summer seasons of 1933-1937 inclusive, has brought forth the following conclusions.

1. The marine communities are divisible into the following:
   a. Scomber-Calanus Biome of the pelagic realm. This community within the inlet is recognized as the Clupea-Syngnathus Faciation.
   b. Strongylocentrotus-Buccinum Biome of the subtidal bottom. The inlet portion of this community is designated as the Laminaria-Cancer Faciation.
   c. Mya-Nereis pelagica Biome occupies intertidal, loose bottom sediments.
      1. Talorchestia Faciation occupies coarse sediments.
      2. Macoma-Clymenella Faciation occupies fine sediments.
   d. Balanus-Mytilus-Littorina Biome occupies hard surfaces.
      1. Balanus-Mytilus Faciation, found primarily over sediments.
      2. Balanus-Littorina-Ascophyllum Faciation, found primarily on rocks.
   e. Communities of succession to land.
      1. Spartina glabra-Littorina saxatilis-Brachidontes Associes occupies the low marshes, particularly marsh banks.
      2. Spartina patens-Melampus-Orchestia Associes occupies the high marshes.
2. Narrow ecotones exist between the major communities resulting from an overlapping of characteristic species along the spring-tide levels. Ecotones were found between the following communities:
   a. Laminaria-Cancer Faciation and Mya-Nereis pelagica Biome along the spring-low-water margin.
   b. Laminaria-Cancer Faciation and Balanus-Mytilus-Littorina Biome along the spring-low-water margin.
   c. Spartina patens-Melampus-Orchestia Associes and terrestrial communities along the spring-high-water margin.
3. An intermingling of communities results from a mixture of sediments and hard bottom materials, and developments in physiographic succession. Fragments of the Balanus-Mytilus-Littorina Biome are found scattered in the Mya-Nereis pelagica Biome and vice versa, giving rise to a condition comparable to the terrestrial savanna or parkland community.
4. The precise zonation of intertidal communities and their components (which has been demonstrated by many investigators), is the only method by which these communities can be studied. Quadrat sampling is of significance in the study of tidal communities only in so far as the level of examination is known, with consequent relationship to exposure and submergence.
5. There is a rhythmical change in the composition and dynamics of the communities associated directly with the tidal flow and ebb. The organization and coactions of intertidal communities are markedly different at low-tide and at high-tide, the transformation taking place gradually and uniformly during fluctuation of the tide. Terrestrial and marsh animals feed on the intertidal zone when it is exposed. They invade the shore during ebb tide following down the water line as it retreats, and are forced back from the feeding grounds gradually as the tide returns. Subtidal permeant animals feed on the intertidal zone when it is submerged. They advance upon the shore with the incoming tide, some species being immediately behind the front wave of water. Intertidal animals for the most part remain inactive during exposure, resuming locomotion and feeding when submerged.
6. Each year significant differences were found in the major communities as a result of the fluctuation of abundance of certain species. Some of the most striking and important changes observed involved the following species: *Zostera marina, Lacuna vincta, Polinices heros, Carcinides maenas, Asterias vulgaris, Mya arenaria, Nereis pelagica, Nassarius obsoletus, Mytilus edulis, Littorina saxatilis, L. obtusata, Thais lapillus,* and *Melampus bidentatus.*
7. While the marine communities inhabiting the Annisquam inlet are similar to climax communities found elsewhere, within the inlet they are undergoing successional changes as the result of sedimentation which is gradually filling the inlet and which has several times in the past nearly obliterated it as an open inlet from the ocean. Periodic dredging is necessary to maintain the waterway. The Mya-Nereis pelagica Biome of marine sediments is extended as the bars and flats are enlarged

TABLE 11. Systematic Arrangement and Ecological Evaluation of the Common Macroscopic Organisms of the Marine Communities at Cape Ann, Massachusetts.

1. Clupea-Syngnathus Faciation of the Scomber-Calanus pelagic biome. * indicates presence in Ipswich Bay but not in the Annisquam River.
2. Strongylocentrotus-Buccinum Biome of the Ipswich Bay bottom.
3. Laminaria-Cancer Faciation of the Annisquam River bottom.
4. Mya-Nereis pelagica Biome of tidal sediments.
5. Balanus-Mytilus-Littorina Biome of tidal hard surfaces.
6. Spartina glabra-Littorina saxatilis-Brachidontes Associes of the low marshes.
7. Spartina patens-Melampus-Orchestia Associes of the high marshes.

D = Dominants
SD = Subdominants
IF = Influents
SI = Subinfluents
PI = Permeant influents
SF = Secondary forms
IC = Incidentals

	1	2	3	4	5	6	7
ALGAE							
Chlorophyceae							
Enteromorpha intestinalis (L.)		SI	SF				
Ulva lactuca L.		D	D	SI	IC	IC	
Chactomorpha linum (Muller)		SF	SD	IF			
Chaetomorpha spp.		SI					
Cladophora rupestris (L.)					SF		
Phaeophyceae							
Chordaria flagelliformis (Muller)		SI					
Chorda filum (L.)		SI	SF				
Agarum cribrosum (Mert.)		D					
Laminaria longicruris De la Pylaie		D					
Laminaria saccharina (L.)		D	D				
Laminaria digitata (L.)		SD	D				
Fucus edentatus De la Pylaie			IC		SF		
Fucus vesiculosus L.					SD	IF	
Fucus vesiculosus V. spiralis						SI	
Ascophyllum nodosum (L.)					D		
A. nodosum f. scorpioides (Hornemann)						D	
Ectocarpus sp.		SF	SF				
Rhodophyceae							
Porphyra umbilicalis (L.)		SI	SF				
Euthora cristata (L.)		D	IF				
Chondrus crispus (L.)		D	IF				
Gigartina stellata (Stackhouse)		SI	IC				
Rhodymenia palmata (L.)		SI	SF				
Plumaria pectinata (Gunner)		SF	IC				
Ceramium rubrum (Hudson)		SF	IC				
Polysiphonia lanosa (L.)					SF		
Lomentaria baileyana (Harv.)		SI	SF				
Callithamnion sp.		SD	SF				
Corallina officinalis L.		SI					
Angiospermae							
Zostera marina L.		IC	IC				
Spartina glabra Muhl.						D	
Spartina patens (Ait.)							D
Distichlis spicata (L.)							SF
Puccinellia maritima (Huds.)							SF
Juncus gerardi Loisel							SF
Salicornia europaea L.							SI
Limonium carolinianum (Walt.)							SI
Gerardia maritima Raf.							SF
Plantago decipiens Barneoud							SF
Solidago sempervirens L.							SF
Porifera							
Leucosolenia sp.		IC					
Sycon ciliatum (Fahr.)		IC					
Suberites compacta Verrill		SF	IC				
Chalina oculata (Pallas)		SF	SI				
Chalina arbuscula Verrill		SF	SI				
Coelenterata							
Clava leptostyla Agassiz					SF		
Hydractinia echinata (Fleming)		IC	SF				
Corymorpha pendula Ag.		SF					
Tubularia spectabilis (Ag.)		SF	SF		SF		
Sertularia pumila L.		SI	SI		SF		
Abietinaria abietina (L.)		SF	SI				
Campanularia flexuosa (Hincks)							
Obelia spp.		SF	SF		SF		
Cyanea capillata (L.)	IF						
Aurelia aurita (L.)	IF						
Metridium dianthus (Ellis)		SF	SF		SF		
Platyhelminthes							
Bdelloura propinqua (Wheeler)			IC				
Leptoplana variabilis (Girard)		SF	SF				
Cerebratulus lacteus (Leidy)		SF	SF	SI			
Bryozoa							
Lichenophora hispida Fleming		IC	SF				
Gemellaria loricata (L.)			SF		SF		
Electra pilosa (L.)		SF	SF				
Cellaria fistulosa (L.)		SF	SF				
Bugula turrita (Desor)		SI	SI				
Bugula flabellata (Thompson)		SI					
Schizoporella unicornis (Johnston)		IC	IC		SF		
Flustrella hispida (Fabricius)			SF		IC		
Membranipora sp.		SF	SF				
Annelida							
Lepidonotus squamatus (L.)		IF	IF				

TABLE 11. (Continued)

	1	2	3	4	5	6	7
Lepidonotus sublevis Verrill		IF	IF				
Phyllodoce catenula Verrill				IC			
Nereis pelagica L.		SF	SF	D			
Lumbrinereis tenuis (Verrill)		IF	IF	D			
Glycera dibranchiata Ehlers				IF			
Enoplobranchus sanguineus Verrill				SF			
Clymenella torquata (Leidy)			SF	D			
Spirorobis spirorbis (L.)		IF	SF		SI		
Hydroides sp.		SI					
ARTHROPODA							
Crustacea							
Balanus balanoides (L.)				SF	D	SI	
Balanus eburneus Gould		IC	SF				
Balanus crenatus Bruguiere		IC	SF				
Hyperia galba (Montague)	IC						
Orchestia platensis Kryer					SI	SI	D
Talorchestia longicornis (Say)				IF			
Allorchestes sp.				SF			
Gammarus locusta (L.)		IF	IF	IF	IF	IF	
Carinogammarus sp.		IF					
Caprella acutifrons Latreille		IF	IF	SF			
Aeginia longicornis Kryer		IF	SF				
Amphipoda (unidentified)		SI	SI				
Cyathura carinata (Kryer)				SF			
Idothea baltica (Pallas)		IF	SF	SF			
Philoscia vittata Say							SD
Isopoda (unidentified)		IF	SI				
Crago septemspinosus (Say)		PI	PI	PI			
Palaemonetes vulgaris (Say)		PI					
Homarus americanus Milne-Edw.		PI	PI				
Pagurus longicarpus Say		PI	PI	PI	PI		
Pagurus pollicaris Say		PI	PI	PI	PI		
Libinia emarginata Leach		PI					
Cancer irroratus Say		PI	PI	PI	PI	PI	
Cancer borealis Stimpson		PI	SF	IC			
Neopanope sp.			SI		SI		
Carcinides maenas (L.)		SF	PI	PI	PI	PI	
Arachnoidea							
Limulus polyphemus L.			PI	PI			
Insecta							
Anurida maritima Lab.				SI	SI	IF	IF
Coelopa frigida Hald.					SI	IF	
Culicoides sp.						IF	IF
Tabanus nigrovittatus Macq.						IF	IF
Aedes sollicitans (Walker)						IF	IF
Fucellia sp.					SI	IF	
MOLLUSCA							
Amphineura							
Neomenia sp.		SI					
Chaetopleura apiculata (Say)		SF					
Gastropoda							
Onchidoris bilamellata (L.)			SF				
Aeolis sp.			SF				
Melampus bidentatus Say						SF	D
Acmaea testudinalis (L.)		IC	IC		SF		
Polinices heros (Say)		SD	D	SD			
Crepidula fornicata (L.)		SI	SI		SF		
Crepidula plana Say		SF	SF	SF			
Littorina littorea (L.)		IC	IF	SI	D	D	SD
Littorina saxatilis Olivi				SF	IF	D	IF
Littorina obtusata L.					IF	IF	
Lacuna vincta (Montague)		IF	SI				
Onoba aculeus Gould				SI			
Thais lapillus (L.)					IF		
Nassarius trivittata Say		SF	IF				
Nassarius obsoletus Say				IF			
Buccinum undatum L.		D					
Neptunea decemcostata (Say)		SD					
Colus stimpsoni Morch		SD					
Pelecypoda							
Solemya velum Say				SI			
Anomia aculeata L.		IC	IC		IC		
Anomia simplex D'Orbigny		SF	SF				
Mytilus edulis L.		IC	IF	SF	D	SI	
Modiolus modiolus (L.)		IF					
Arctica islandica L.		IF					
Brachidontes demissus Lam.						SD	
Cerastoderma pinnulatum Conrad			SF				
Mulinia lateralis Say				SF			
Gemma gemma (Totten)			SI	SI			
Petricola pholadiformis (Lam.)				IC			
Tellina tenera Say			SF				
Macoma balthica (L.)				SD			
Ensis directus Conrad				SI			
Siliqua costata (Say)		IF	SF	SF			
Mya arenaria L.			SF	D	IC		
Saxicava arctica		SF	SF				
Lyonsia hyalina (Conrad)			IC	IC			
Cephalopoda							
Loligo pealei Lesueur	IF						
Echinodermata							
Henricia sanguinolenta (O. F. Muller)		IF					
Asterias vulgaris Verrill		D	D	SF	IF		
Ophiopholis aculeata (L.)		SF	SF				

TABLE 11. *(Continued)*

	1	2	3	4	5	6	7
Strongylocentrotus drobachiensis (O. F. Muller)		D	D				
Echinarachnius parma (Lamarck)		D	SF				
CHORDATA							
Protochordata							
Dolichoglossus kowalevski (A. Ag.)				SF			
Botryllus schlosseri (Pallas)		SF	SF				
Cynthia carnea Verrill		SF					
Molgula manhattensis (DeKay)		SF	SF				
Boltenia ovifera (L.)		SF					
VERTEBRATA							
Pisces							
Caracharias taurus Raf.	PI*	SD					
Isurus punctatus Storer	SD*	PI					
Raja erinacea Mitchill		D	SD				
Raja diaphanes Mitchill		SD	SD				
Anguilla bostoniensis (LeSueur)			PI				
Clupea harengus L.	D						
Salmo salar L.	SD*						
Pomolobus pseudoharengus (Wilson)	PI						
Osmerus mordax Mitchill	SD	PI	PI				
Fundulus heteroclitus (L.)			PI	PI	PI	PI	PI
Syngnathus peckianus Storer	D	SF	SI				
Ammodytes americanus DeKay		PI					
Scomber scombrus L.	D						
Thunnus thynnus L.	SD*						
Pomatomus saltatrix (L.)	PI						
Poronotus triacanthus Peck	D	PI	PI				
Tautogolabrus adspersus Waibaum	PI	PI	PI	PI	PI		
Tautoga onitis L.	PI*	PI					
Myoxocephalus scorpius (L.)		SD	D	PI			
M. aeneus Mitchill		SD	D	PI			
M. octodecemspinosus Mitchill		D	D	PI			
Pholis gunnellus L.		PI	PI				
Pollachius virens L.	D						
Merluccius bilinearis (Mitchill)	PI	PI					
Gadus morhua L.	SD	SD					
Melanogrammus aeglifinus L.		PI					
Urophycis tenuis (Mitchill)		SD	SD				
Urophycis chuss Walbaum		D	D				
Hippoglossus hippoglossus L.		PI					
Paralichthys dentatus L.		SD					
Pseudopleuronectes americanus Walbaum		D	D	PI			
Lophosetta aquosa (Mitchill)			SD				
Reptilia							
Chelonia mydas (L.)		PI	IC				
Thamnophis sirtalis (L.)							PI
Aves							
Phalacrocorax auritus auritus (Lesson)	PI						
Butorides virescens virescens (L.)				PI		PI	
Nycticorax nycticorax hoacti (Gmelin)				PI		PI	
Anas rubripes tristis Brewster				SF		SF	SF
Buteo lineatus lineatus (Gmelin)							PI
Circus hudsonius (L.)							PI
Charadrius semipalmatus Bonaparte				PI		PI	PI
Actitis macularia (L.)				PI		PI	PI
Pisobia minutilla (Vieillot)				PI		PI	PI
Larus argentatus smithsonianus Coues				PI	PI		
Sterna hirundo hirundo L.	PI						
Megaceryle alcyon alcyon (L.)	PI						
Tyrannus tyrannus (L.)						PI	PI
Iridoprocne bicolor (Vieillot)						PI	PI
Hirundo erythrogaster Boddaert						PI	PI
Corvus brachyrhynchos brachyrhynchos Brehm				PI	PI	PI	PI
Dumetella carolinensis (L.)						PI	PI
Sturnus vulgaris vulgaris L.						PI	PI
Sturnella magna magna (L.)						PI	PI
Agelaius phoeniceus phoeniceus (L.)						PI	PI
Quiscalus quiscula aeneus Ridgway						PI	PI
Ammospiza caudacuta caudacuta (Gmelin)						PI	PI
Melospiza melodia melodia (Wilson)						PI	PI
Mammalia							
Microtus pennsylvanicus (Ord.)							PI
Sylvilagus transitionalis (Bangs)							PI
Phoca vitulina L.	SD						
Balaenoptera physalus (L.)	SD*						

and encrouch upon the Laminaria-Cancer Faciation of the subtidal bottom. These bars and flats in time become covered over by the Balanus-Mytilus Faciation. With the elevation of both this mussel bed community and the communities of the uncovered sediments up to a height of 4 feet within the mean-high-tide level, they are captured by the low marsh Spartina glabra-Littorina saxatilis-Brachidontes Associes. Accumulation of sediments among the rocks of the Balanus-Mytilus-Ascophyllum Faciation also leads to its replacement by the low marsh community. As this community is elevated to the mean-high-water line it is succeeded by the Spartina patens-Melampus-Orchestia Associes of the high marshes. At spring-high-water line the marine communities pass through a narrow ecotone to an upland terrestrial climax, the Beech-Maple Association of the Temperate Deciduous Forest Biome. Table 11 summarizes the ecological evaluation of the predominant species which compose these marine communities.

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