STUDIES IN MARINE ECOLOGY: I. THE DISTRIBUTION OF COMMON LITTORAL INVERTEBRATES OF THE WOODS HOLE REGION.

W. C. ALLEE,

MARINE BIOLOGICAL LABORATORY AND THE UNIVERSITY OF CHICAGO.

The distribution of animals within the Woods Hole region has been well studied by men interested in individual species and by those concerned with general faunistic problems. Some aspects of the ecology of the region are thoroughly set forth by Verrill and Smith in their "Report on the Invertebrate Animals of Vineyard Sound" made fifty years ago. This classic study remains the best account of the ecology of littoral species available.

The extensive "Biological Survey of the Waters of Woods Hole and Vicinity" [1] completed about ten years ago by Sumner, Osburn and Cole, while a mine of information concerning the animals of the region, was directly concerned with dredging operations and has little to say at first hand concerning the animals of the intertidal region or those found just below the tidal zone. Among other suggestions they recommend (p. 25) that the intertidal fauna should receive the same detailed attention that they have given to the bottom dwelling species.

In the absence of a report by the person best qualified to write on the subject, Mr. George M. Gray, the present series of papers has been prepared to make available information accumulated in nine consecutive summers' experience with the inshore invertebrates of the region.

The work has been done in connection with a teaching appointment in the course of Invertebrate Zoölogy of the Marine Biological Laboratory. It represents the collaboration of eighteen staff members and of about four hundred students. Many of the present collecting methods were installed in conjunction with Professor Caswell Grave, my predecessor in charge of the

[1] This report will be referred to hereafter as the *Biological Survey*.

course, but the records here used have been kept from the beginning by myself with the occasional help of other staff members.[1]

The records are based on the bi-weekly collecting trips of the Invertebrate Class and cover most thoroughly the period from about June 20 to August 15. These trips have been supplemented by expeditions made by instructors and by special trips for particular observations.

The organization of field work for eight years has been to divide the class into as many collecting teams as there were instructors. One person from each team was appointed recorder for the day and was supplied with a list of all the animals previously taken from the locality under consideration. The animals found were recorded according to habitats. The complete list for the year was made up from these combined records.[2]

[1] The following people have been at one time or another members of the instructing staff of the Invertebrate Course and have contributed to the data on which this series of papers is based. Without their coöperation this work could not have been done. Caswell Grave, Raymond Binford, E. J. Lund, George A. Baitsell, T. S. Painter, F. M. Root, W. J. Kostir, Robert H. Bowen, C. L. Parmenter, G. S. Dodds, Robert Chambers, Jr., Ann H. Morgan, W. J. Crozier, Donnell B. Young, J. P. Visscher, J. A. Dawson, Christianna Smith and E. A. Adolph.

I am indebted also to Mr. G. M. Gray for much valuable aid and friendly assistance; to Dr. Mary J. Rathbun for identification of the Brachyura; to Mr. Waldo L. Schmitt for similar service with the Anomura and Macrura; to Mr. Clarence R. Shoemaker for similar service with the amphipods and isopods; to Professor E. S. Morse for assistance with some of the molluscs and to Professor Raymond Osburn for assistance with the Bryozoa.

[2] The formal record of collecting experience has been recorded in abbreviated form on library cards which are deposited in the Library of the Marine Biological Laboratory. An annotated catalog of the distribution has been prepared as Study II. of this series and deposited with the library of the U. S. Fish Commission who have kindly agreed to furnish copies to the libraries of the Marine Biological Laboratory at Woods Hole; the Museum of Comparative Zoölogy at Cambridge, Scripps Institution at LaJolla; the United States National Museum at Washington and to the Harpswell Laboratory at Mount Desert Island, Maine.

The catalog shows the littoral invertebrates collected during the years 1915–1921 inclusive. Each locality in which an animal has been taken is recorded. The number of years which it has been found in a given locality is shown and an index figure of comparative abundance is also given. Where possible and desirable the location of particularly favorable collecting grounds is given with some exactness. This elaborated catalog forms the basis from which the facts presented here are drawn and together with the present report gives the background for the two following studies.

So far as possible, identification was done in the field. Doubtful specimens were referred from one instructor to another. Specimens new to the locality or difficult to identify were brought into the laboratory for further study. With the exception of the arthropods, few of the specimens have been referred to experts although we have gradually accumulated a type collection of animals found. The identification of animals has been made on the conservative basis that when doubt existed, the specimen was referred to the more common species. Wild identifications have been eliminated as far as possible, even to the extent of throwing out the entire reports of inexperienced instructors.

In spite of this care, mistaken identifications have probably been turned in and accepted. The list here given is substantially correct since the animals have either been reported by qualified collectors or placed on the list from demonstrated specimens. The imperfections lie largely in failing to distinguish closely related species and in possible errors in distribution records.

II.

The collections upon which this series of reports are based have been made largely in the littoral zone as defined by Edward Forbes; that is, between high water and a depth of two fathoms. This is not the littoral zone of modern zoölogists, but the term has been used with so great a variety of meanings that the extent of the study can be more easily and definitely located as being in the intertidal and ad- or sub-tidal regions.[1]

The intertidal zone is much restricted in the Woods Hole region on account of the slight rise and fall of the tides. The

[1] Murray and Hjort use the term "littoral zone" to include the region near the shore down to a depth of 30 or 40 meters: "almost as far as there are sea-weeds." It is frequently used as by Petersen to include the entire continental shelf. The botanists tend to be more exact. Kjellman limits the term to the region between extreme low and extreme high tide. Davis regards the littoral zone as extending from about mean low water to the highest point at which algæ can grow. Flattely and Walton ('22) follow Cotton ('12) and define the littoral region as extending from the level of highest marine vegetation, to low water at neap tide.

I prefer to use littoral in its original meaning of "pertaining to the shore"; intertidal or tidal zone adequately and exactly describes the region between the tide lines, and sub-tidal or adtidal are exact terms, if not the most correct etymologically, for the region below low tide. The question is discussed in the *Biological Survey*, p. 179.

tide tables of the U. S. Bureau of Commerce show a spring tide range of about five feet for this section of Buzzards Bay and only about two feet for Vineyard Sound stations.

Studies have been made in the following localities:[1]

Wharf Pilings.

Crane's Wharf Pilings.—This is a comparatively new wharf located near the public steamboat wharf in Great Harbor at Woods Hole. At the shore end the water at low tide comes close to the retaining wall and some collecting has been done annually in the crevices of the wall. The water at the outer end is over twelve feet deep. The number of species and of animals on these pilings has increased noticeably during the period of observation.

Vineyard Haven Wharf Pilings.—The old New York and Portland Wharf on the south side of Vineyard Haven is located well out toward the Sound. The water here comes up on a sandy beach which at low tide is bare for a considerable distance under the wharf. At the outer end the Government Chart shows 11 feet of water. In my experience the water is deeper. This is an old wharf with many pilings rotted off below water level. Some of the pilings are reproduced in the American Museum of Natural History in New York. Collections from both wharfs were made from boats by means of the usual scrape nets.

Marine Biological Laboratory Pier on Glass Slides.—For a number of years, glass slides have been placed under the M. B. L. pier in connection with other studies. In 1921 the slides were carefully examined by Dr. D. B. Young and myself after they had been suspended in water under the pier from July 1 to August 9 at a depth of about six feet. The M. B. L. supply float containing animals from all parts of the region was only a few feet away and accordingly more species were attached than might normally be found.

Rocks and Flats.

Hadley Harbor, Southwest and Southeast Gutters.—These naturally narrow rocky gutters have been further narrowed artificially

[1] Consult map.

so that they can be bridged. Strong tidal currents run through them the greater part of the day. They are relatively shallow, rock-walled channels, containing about six feet of water and are connected with open water by creeks which are also rock edged. Small patches of mud and sand occur frequently and the whole system of protected waterways supports many plants, *Ascophyllum*, *Fucus* and *Sargassum filipendula*.

Hadley Harbor Flats, Northwest Gutter.—Northwest Gutter separates Uncatena Island from Naushon. Before opening into Buzzards Bay it enlarges to form an approximately square expanse of shallow water about 250 yards along the south and west sides and about 400 yards in greatest diagonal. In most places the water is so shallow that it is difficult to push a boat along at low water. The sand bar over the channel of the gutter is fully bare at extreme low tide often to the extent of an acre or more.

The wide channel is kept scoured clean by the current, but behind the protecting sand and gravel spits, organic debris has accumulated to the depth of several feet and supports a rank plant growth composed chiefly of eel grass. At the Bay entrance there is the usual accumulation of rocks which extend off to a sand bottom some four feet below the lowest tide. The mud flats are bordered by rocks partially buried by mud.

Gansett.—Gansett is an offshoot of Quamquissett Harbor and has the same opening into Buzzards Bay. The main axis extends at an angle from the opening so that the back portion is usually protected from the direct drive of the waves. The opening is about 200 yards wide and the bay is approximately twice that length. At mid-mouth at mean low tide the water is 18 feet deep. The sides slope in rapidly near the shore so that there are only narrow strips of the different habitat zones. At the sides are the customary rocks and the outer corners are guarded by rock piles. At the head of the bay the shore is sand mixed first with gravel and lower with mud. Eel grass comes within two rods of the water's edge at low tide and thickly covers the bottom throughout its extent.

North Falmouth.—The collecting grounds here are scattered. They are located at the head of Cataumet Harbor and extend

over Squeteague Harbor which opens from the former by a winding narrow passage. Except for the dredged passage, most of the region can be waded at low tide. Much of the ground in Cataumet and almost all in Squeteague Harbor is left bare by the spring tides. The collecting is over a wide range of bottom: sand, mud, scattered rocks and gravel with and without eel grass and other sea-weeds. There is a somewhat sparse collection of rocks along the shore line.

Lackey's Bay.—Lackey's Bay belongs to the Hadley Harbor complex. It is located on the Vineyard Sound side between Naushon and Nonamasset. The part studied forms an expanded entrance to Middle Gutter which, by the construction of a causeway, has become Blind Gutter. The current is much diminished by the causeway and the inner part of the bay is deeply overlaid with muck. Eel grass is abundant. The region most studied is about 400 yards long by 200 yards wide and is separated from the Sound by a sand bar which is left bare at low tide.

Dredging.

The dredging has been largely in three localities in Vineyard Sound. These are the sand dollar bed (Map, No. 8) near the east side of the entrance to Tarpaulin Cove in about 20–30 feet of water. The bottom material brought up by the coarse dredge used is largely composed of shells. The starfish hole (Map, No. 7) is further east and still off Naushon, has about 90 feet of water. The *Chætopleura* grounds (Map, No. 3) off Nobska have about sixty feet of water. The bottom is decidedly pebbly. Some dredging has been done further east on or near the planted oyster bed (Map, No. 2) in Falmouth Harbor. The bottom here is sand and gravel in about 60 feet of water. In 1921 we dredged off the west entrance from Vineyard Sound to Great Harbor (Map, No. 4) in about 80 feet of water. This is over an *Amarœcium pellucidum* bed.

In 1920 we dredged in Great Harbor (Map, No. 5): at the east end of Nonamasset in 10–12 feet of water; in the Fish Commission Hole at a depth of 50 feet and at the West end of the passage in Woods Hole in about 20 feet of water.

The dredging work has been largely incidental and the results are given chiefly as a means of comparing the more extensive

results obtained by the dredgings of the *Biological Survey* with our main work further inshore.

A Habitat Check List of the Common Invertebrate Animals of the Woods Hole Littoral with Distribution Records for 1920 and 1921.

The appended list of animals is based on all the collecting done since 1912. The distribution records are based on the reports from operations in 1920 and 1921. The statistics given are from team records. Thus in these two years, two teams collected *Chalina* from the mud, eight teams have recorded it from rocks, ten from wharf pilings and nine from dredging. The figures given show no indication of the number of specimens taken other than that suggested by the fact that the more animals present, the greater the probability that all teams would find them. Anyone interested in the abundance of these animals in particular localities is referred to the second study in the present series.

The tabulation is from the reports of 30 collecting teams operating on wharf pilings; 52 from sand, mud, gravel and eel grass; 56 teams from rocks and 42 from dredging. The records of plankton have been kept in a different way and the presence of recognized animals in late July or early August is merely checked.

The classification of habitats in the field has sometimes been left to the judgment of the student recorder and it is entirely probable that some of the 52 recorders thought a given habitat was best recorded as "sand" while others regarded animals from a similar place as "mud" dwelling. All gradations between the two exist and the conditions under which the collecting was done do not permit a more refined grading. The error arising from this source is somewhat compensated by the fact that no dragnet collections were made as it was desired to find where individual animals live as well as to collect different species.

Unidentified animals have not been included in the habitat list unless the genus, at least, could be determined with some assurance. All the records are for living animals since for ecological purposes the recording of dead shells can only be worthless and confusing in a region where tidal currents run strongly and where the shore birds distribute shells even over the land.

The nomenclature follows Pratt wherever the species are listed in his *Manual*. Other species have the name given them in the catalog of the *Biological Survey*. No attempt has been made to give synonyms since these can usually be found in the *Survey* catalog.

The arrangement of species within the major divisions is alphabetical. While this does violence to all principles of taxonomy, the taxonomic sense is not strongly developed at present, and this method renders the material more easily available to the average zoölogist than would be the case if a strictly taxonomic system were followed.

The records given in the habitat list are necessarily abbreviated. Thus, *Hydractinia* is recorded as taken from "sand" when the whole record should read: "on shells inhabited by hermit crabs taken on sandy bottom"; or other animals, as *Sagartia luciæ*, recorded from "mud" which does not mean that the anemone was growing on the mud but that it was found attached to a bit of board or rock surrounded by typical mud conditions.

The classification headed "eel grass" includes records of animals living free among the eel grass, as *Pecten;* attached to eel grass, as *Pennaria;* crawling over it, as *Ophioderma;* on the substratum at its base, as *Microcione;* or burrowing in the substratum at its roots, as *Cumingia*. In addition the lumping is still greater for one must remember that eel grass begins to grow on fairly pure sand and extends back to the pure muck of the flats.

A number of animals are recorded under "rocks and rockweeds" which were taken only from the substratum under or among the rocks. Whenever all the records are for an animal so found, the entry has been appropriately labeled.

Under "range" is listed the information at hand showing the distribution of the animal along the Atlantic Coast. The abbreviations are: N., north ranging; S., south ranging; M., approximately mid-range; L., local; C., cosmopolitan. Whenever an animal is known to extend twice as far north of Woods Hole as south, it is listed as north ranging and *vice versa*. (Cf. Hoyle, 1889). Some relations between the local and geographical distribution will be discussed in a later paper.

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
PROTOZOA.										
List not given.										
PORIFERA.										
Chalina arbuscula	S.		2				8	10	9	
Cliona celata (?)	S.			2		1	33	25	16	
Grantia ciliata	N.			1			11	30	13	
Leucosolenia botryoides	N.						13	24	1	
Microciona prolifera	S.		1			4	43	30		
Tethya gravida	L.		1						1	
CŒLENTERATA.										
Hydrozoa										
Abietinaria abietina	N.								12	
Bougainvillia carolinensis	S.					1	2	1		✓ sp.?
Campanularia calceolifera								1		
Campanularia sp.?							1	5		
Clava leptostyla	N.						1			
Clytia grayi	L.						2			
Clytia bicophora	N.					1	1	1		✓ sp.?
Clytia cylindrica						1				
Eucheilota sp.? *medusæ*										✓
Eudendrium album						2	4	6		
Endendrium ramosum	M.						7	22	7	
Eudendrium tenue								1		
Gemmaria gemmosa	S.			1			1	1		✓
Gonionemus murbachii	L.									
Hydractinia echinata	N.		9	18	3	5	12		11	
Obelia bicuspidata	S.					1		1		
Obelia commissuralis	S.		1			12	8	11	2	✓ sp.?
Obelia geniculata	N.					5	6	7		
Pennaria tiarella	S.					14	4	10	4	✓ ✓
Phialidium sp.? *medusæ*										✓
Podocoryne carnea	N.			2		1				
Schizotricha tenella	S.						1	11	2	
Sertularia pumila	N.					11	30	12	10	✓ ✓
Stylactis hooperi	S.									
Tubularia crocea	S.							30	7	✓
Scyphozoa.										
Aurelia flavidula	M.									
Cyanea capillata arctica	N.									
Dactylometra quinquecirrha	S.									
Haliclystus auricula	N.									

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
Anthozoa.										
Astrangia danæ.....	S.						11		7	
Alcyonium carneum.....	N.									
Edwardsia elegans.....	N.		1	5		1				
Eloactis producta.....	S.			3						
Metridium dianthus.....	N.						29	24		
Sagartia leucolena.....	S.		3	3		2	37	11	4	
Sargartia luciæ.....	S.		2	2		6	38	6	2	
Sagartia modesta.....	S.					4	12 under			
PLATYHELMINTHES.										
Turbellaria.										
Bdelloura candida.....	S.	3	5	2		7				
Bdelloura propinqua.....		1								
Polychærus caudatus.....	N.		1	3		5	2	1	1	
Procerodes wheatlandi.....	N.						1			
Stylochus ellipticus.....	N.		3	2	1	1	6	3		
Stylochus zebra.....	L.						1		1	
Syncælidium pellucidum.....						2				
Nemertini.										
Amphiporus ochraceus.....	S.								5	
Cerebratulus lacteus.....	S.		7	11		2	2 under			✓
Cephalothrix linearis.....	N.						1 under			
Lineus sp.?.....			2	6		5	1		2	
Lineus bicolor.....	S.		1	1			1	2		
Micrura leidyi.....	M.		6	15		8	3 under			
Tetrastemma vermiculum.....	S.							5	3	
NEMATHELMINTHES.										
Pontonema marinum.....	S.		1	1		5	6	19	6	
ECHINODERMA.										
Asteroidea.										
Asterias forbesi.....	S.		1	8		4	28	14	29	✓
Asterias vulgaris.....	N.							1	4	
Henricia sanguinolenta.....	N.						6	4	11	

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
Ophiuroidea.										
Amphipholus squamata.....	N.						2		12	
Ophioderma brevispina.....	S.					5				
Echinoidea.										
Arbacia punctulata.....	S.			6			18	2	17	✓
Echinarachnius parma.....	N.						1		12	
Strongylocentrotus drœbachiensis.....	N.									
Holothuroidea.										
Leptosynapta inhærens.....	S.		11	24		10				
Thyone briareus.....	S.		25			6			2	
ANNELIDA.										
Archiannelida.										
Dinophilus sp.?.....										✓
Polychæta										
Ampharete setosa.....	S.									
Amphitrite attenuata.....							1	9		
Amphitrite brunnea.....	N.							1		
Amphitrite ornata.....	S.		19	8		3	3		2	
Arabella opalina.....	S.		8	17	2	5	under 1	1	7	
Arenicola cristata.....	S.		3	6			under 1			
Autolytus cornutus.....	N.					1	under	9		
Autolytus varians.....	S.							1		
Chætopterus pergamentaceus..	S.					1				
Cirratulus grandis.....	S.		11	6	1		5		1	
Cirratulus tenuis.....							under		1	
Capitella sp.?.....										
Clymenella torquata.....	M.		17	25		6	6			
Diopatra cuprea.....	S.		6	14		2	under 1		2	
Drilonereis longa.....			1	7	1		under			
Enoplobranchus sanguineus..	M.		3							
Glycera americana or dibranchiata.....	S. M.	}	20	53	1	12	1 under			
Harmothœ imbricata.....	N.		2	5	1	3	26	27	11	

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
Polychæta Con't.										
Hydroides hexagonus	S.	5	2	3	1	3	39	17	22	
Laonice viridis	S.	3	3	1						
Lepidametria commensalis	S.						1 among			
Lepidonotus squamatus	N.	1	3	5	2	2	37	29	22	
Lepræa rubra	S.				1		4 under			
Lumbrinereis hebes										
Lumbrinereis tenuis	S.		7	19	2	1	3 under		14	
Maldane urceolata	S.		3	9		2				
Marphysa leidyi			1						3	
Nereis limbata	S.		12	9	2	3	8	3		sp.?
Nereis pelagica	N.		4	6			9	29	22	sp.?
Nereis virens	N.		17	20		9	3 under	1		
Nicolea simplex			1	3		2	7	13	7	
Pectinaria gouldi	S.		9	18	1	5				
Potamilla sp.?									1	
Pholoë sp.?										
Phyllodoce catenula	N.	1	3	6		3	5	17	13	
Pista palmata	S.		3	1		1				
Platynereis megalops	S.					1		1		
Podarka obscura	S.		2			4	4	7	6	
Polycirrus eximeus	S.		10	14		4	15	6	12	
Polydora sp								2		
Sabella microphthalmia	S.		1	1	2		3	7	1	
Sabellaria vulgaris	S.	1	2	2		5	6	2	4	
Scoloplos acutus			12	1		6				
Scoloplos fragilis	S.		8	19		9	1 under			
Scoloplos robustus	S.		8	10		3	1 under			
Spio (setosa?)				1						
Spirorbis spirorbis	N.		3	4	2	11	26	19		
Spirorbis tubæformis	S.						1		1	
Sthenelais leidyi	S.		6	5		4	3	4	6	
Terebellides stræmi	N.									
Thelepus cincinnatus	N.						1	3		
Trophonia affinis	S.		4	1					6	
Chætognatha and Sipunculoidea										
Phascolosoma gouldii	M.		13	22		3	2 under			
Sagitta sp.?										✓

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
BRYOZOA.										
Ætea anguina	N.					5	10	12		
Alcyonidium sp.?							3			
Bicellaria ciliata	M.							3	3	
Bowerbankia gracilis	N.						3	1		
Bugula cucullifera	N.							1		
Bugula flabellata	N.						1	1		
Bugula turrita	S.		1	2		17	17	31	14	✓
Cribrillina punctata	N.								1	
Crisia eburnea	N.		1	1		4	21	18	12	
Flustrella hispida	N.					1	22			
Hippothoa divaricata	C.							1		
Hippothoa hyalina	C.							1		
Lepralia pallasiana	N.									
Lepralia pertusa	S.	1		1		10	14	6	6	
Lepralia serrata	M.							1		
Lichenopora verrucaria	N.							2		
Membranipora monostachys								1		
Membranipora pilosa	N.			1	1	6	21	13	5	
Membranipora tenuis									6	
Microporella ciliata	C.						1	2	3	
Schizoporella biaperta									5	
Schizoporella unicornis	S.		2	3	1	8	32	25	11	
Smittia trispinosa nitida	M.					1	3		15	
ARTHROPODA.										
Phyllopoda.										
Evadne nordmanni	M.									✓
Podon leuckarti	M.									✓
Cirripedia.										
Balanus balanoides	M.		5	4	3	2	48		2	✓
Balanus eburneus	S.		1	3	1	6	18	19	17	✓
Lepas anatifera	C.	1					1			
Arthrostraca.										
Amphithæ rubricata	N.		1	1			6	6	8	
Autonœ (Lembos) smithi	L.			1			5	5	9	
Æginella longicornis	N.						1	4		
**Caprella geometrica*	S.			1		6	13	26	1	✓
Chiridotea cæca	S.		2	2		2	2			
Corophium cylindricum								2		
Cyathura carinata	N.			1		1				
Edotea triloba	M.	1	3			2	2			

* In part *Æginella*

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
Arthrostraca Con't.										
Erichsonella filiformis	N.			1		2	2	2	4	
Gammarus (Sev. sp.)		2	8	11	3	15	10	28	18	✓
Haustorius arenarius	S.			2						
Idothea baltica	M.		5	4		20	9	15		✓
Idothea metallica	S.		3		2	5				✓
Idothea phosphorea	N.						1			
Jæra marina	N.	2		2	1	4	3			
Ligyda oceanica	N.						3			
Orchestia agilis	S.	10	1	33			8	2		
Sphæroma quadridentatum	S.						5			
Talorchestia longicornis	S.		2	14	6	1				
Tanais cavolinii	N.							1		
Unicola irrorata	N.								1	
Thoracostraca.										
Callianassa stimpsoni	S.		1				1 among			
Callinectes sapidus	S.		1	1						
Cancer borealis	N.					3				
Cancer irroratus	M.		5	7	2	4	6	2 near	2	
Crangon vulgaris (*Crago septemspinosus*)	M.		3	4	4	16	3		1	
Carcinides mænas	S.		16	4	4	4	8		5	
Heterocrypta granulata	S.								1	
Heteromysis formosa	N.	1	3	3		1	1		12	✓
Hippa (*Emerita*) *talpoida*	S.									
Hyas coarctatus	N.									
Libinia dubia	S.		14	8	1	10	3	20	16	
Libinia emarginata	S.		14	4	1	7	1	10	9	
Lysiosquilla armata										
Mysis stenolepis	M.									
Michtheimysis mixta										
Ovalipes ocellatus	S.		1	3		3	2		1	
Pagurus acadianus	M.			1					2	
Pagurus longicarpus	S.	3	19	16	5	10	7	2	22	
Pagurus pollicaris	S.	1	4	10	4	7	1	1	10	
Palæmonetes vulgaris	S.		9	7		16	8			
Panopeus sayi or *Neopanope texana sayi*	S.	2	17	12	3	12	7	27	16	
Pelia mutica	S.			1						
Pinnixa chætopterana			2			2	1 among			
Pinnixa sayana (*cylindrica*)										
Pinnotheres maculatus	S.		3					6		
Portunus sayi	S.									
Squilla empusa	S.									

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
Thoracostraca Con't.										
Uca pugilator	S.		21	4	3	2	8			
Uca pugnax	S.			2						
Virbius (Hippolyte) zostericola	S.	1	4	2		25	1			
Arachnoidea.										
Anoplodactylus lentus	N.	2					4	10	2	
Pallene empusa	S.					2	1	5		✓
Limulus polyphemus	S.	1	12	10	2	6	1			
Tanystylum orbiculare	S.							10	1	
Mollusca.										
Amphineura.										
Chætopleura apiculata	S.	3					19		16	
Gasteropoda.										
Acmæa testudinalis	N.	2	1	2		1	26	1	3	
Bittium alternatum	M.	1	6	6	2	20	17	11	8	
Busycon canaliculatum	S.			7	1		2			
Busycon carica	S.			1	1		1	1		
Cæcum pulchellum							2			
Cerithiopsis emersonii	S.	1				2	3		6	
Cerithiopsis greenii	S.					2	1 sp.?		2	
Cerithiopsis terebralis									2	
Columbella avara	S.	1	3	5	1	9	13	14	19	
Columbella lunata	S.	1	3	7		12	20	30	21	
Coryphella gymnota	N.	1			1	1	2	15		
Crepidula convexa	S.	4	12	10	1	6	20	4	7	
Crepidula fornicata	S.	2	6	15	1	2	21	12	9	
Crepidula plana	S.	3	7	16	2	2	15	14	15	
Doris bifida	N.							1	1	
Elysia chlorotica	M.					4	1			
Eupleura caudata	S.		1	3	1		4		5	
Lacuna vincta	S.		4	4	2	14	13	21	9	
Littorina irrorata	S.						2			
Littorina litorea	N.	1	15	8	6	18	29	27		
Littorina palliata	N.		4	5	3	11	24	7	1	
Littorina rudis	N.		8	4	2	12	32	6	1	
Melampus lineatus	S.		14	4	2					
Nassa obsoleta	S.		35	14		3	9			
Nassa trivittata	S.		13	16	1	3	8	11	3	
Nassa vibex	S.		1							
Natica duplicata	S.		2	6	1	3	1 among			
Natica heros	M.		2	1	1		2			

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
Gasteropoda Con't.										
Natica immaculata	N.								2	
Natica pusilla	S.		1			1				
Odostomia sp.?		1	2	1		7	24	2		
Rissoa minuta	N.		3							
Rissoa sp.?										
Scalaria sp.?			1	1						
Purpura lapillus	N.			1			10			
Urosalpinx cinerews	S.	4	5	8	1	5	31	22	5	
Pelecypoda.										
Anomia aculeata	N.					1	12	4	5	
Anomia ephippium	S.		2			1	22	10	7	
Arca pexata	S.			1			5	1	7	
Arca ponderosa	S.									
Arca transversa	S.		1	1			1		4	
Astarte castanea	M.								3	
Astarte undata	N.								5	
Cardium pinnulatum	N.								5	
Clidiophora trilineata	S.								3	
Corbula contracta	S.			2						
Cumingia tellinoides	S.		10	11		6	1			
Ensis directus	M.		9	9		2	5 among			
Gastranella tumida	S.							1		
Gemma gemma	N.			3			1			
Lævicardium mortoni	S.		11	5	2	4	1 among			
Lyonsia hyalina	S.	1		2						
Macoma tenta	S.		2	2		1			1	
Mactra lateralis	S.			1						
Mactra solidissima	N.			3			2		2	
Modiolus demissus	S.		22	15	3	6	8			
Modiolus modiolus	N.		10	7		4	6	3	3	
Mya arenaria	N.		23	21	3	6	5 among			
Mytilus edulis	N.		11	11	5	4	24	28	7	
Nucula delphinodonta	N.								1	
Nucula proxima	M.		3	3	1	4	4 among		3	
Ostrea virginica	S.		10	5			9			
Pecten irradians	S.		9	9		11	4		4	
Petricola pholadiformis	S.		3	2	3		1			
Saxicava arctica	N.						2			
Solemya velum	M.		10	20		4	4 among			
Tellina tenera	S.		5	16	3	4	1			
Teredo navalis	N.	19		2	1	1	1	7		

Species.	Range.	Unclassified.	Mud.	Sand.	Gravel.	Eel Grass.	Rocks and Rockweed.	Pilings.	Dredging.	Plankton.
			No. Teams Reporting.							
			52	52	52	52	56	30	42	
Pelecypoda Con't.										
Venus mercenaria	S.	1	19	14	2	1	4 among		2	
Yoldia limatula	N.									
Zirphæa crispata	N.		1							
Cephalopoda.										
Loligo pealii	S.			3						✓
CHORDATA.										
Appendicularia longicauda	M.									✓
Amaræcium constellatum	N.	3			2	3	19	29	14	
Amaræcium pellucidum	S.								12	
Amaræcium stellatum	S.									
Botryllus schlosseri	N.	1				13	7	5		✓
Didemnum lutarium	N.	2				6	13		30	
Dolichoglossus kowalevskyi	S.		12	14	6	2	3 under			
Molgula manhattensis	S.	2	3		1	6	8	24	1	
Molgula papillosa	N.							1		
Molgula arenata	S.							1		
Perophora viridis	S.	2		1		5	16	28	4	
Styela partita	S.		1	1		6	17	29	9	

IV.

The entire mass of data available was analyzed in 1917 and again in 1920 in an attempt to discover the relationships existing between animal associations from the different types of environments. The first type of analysis was planned to discover the number of species common to different combinations of these habitats and conversely to find the number of animals peculiar to each type of habitat. The analysis was not repeated after the 1921 records were available because it was not considered that these records would materially change conclusions already arrived at by the preceding work.

The analysis of the records from 1915–1920 inclusive follows:

Habitats.	Number of Species.
Flats, rocks, pilings and dredgings	54
Flats, rocks and pilings	16
Rocks, pilings and dredging	10
Flats, pilings and dredging	3
Flats, rocks and dredging	9
Flats and under or on rocks	26
Wharfs and rocks	8
Flats and rocks	11
Dredging and rocks	5
Flats and pilings	2
Pilings and dredging	2
Flats and dredging	9
Flats, under rocks and dredging	4
On or under rocks	10
Pilings	7
Dredging	13
Only under rocks	1
Flats	41

The analysis shows that at the close of the 1920 season 54 species had been recorded from all four types of habitats studied while only 16 species were limited to and found in all of the three habitats excluding dredging. The flats have the greatest number of peculiar species, with 41, and but few forms are limited to any one of the other habitats.

The same material analyzed in another fashion is shown in Table 1. Here the attempt is to show the total numbers of

TABLE I.

	Wharfs.	Flats.	Rocks.		Dredging.
Wharfs	110 100%	83 74%	80 73%	76 69%	(26 only in Harbor)
Flats	83 44%	187 100%	80[1] 43%	87 46%	(28 only in Harbor)
Rocks	80 72%	80 72%	111 100%	81 73%	(22 only in Harbor)
Dredging	76 64%	87 73%	81 69%	119 100%	(32 only in Harbor)

animals found in each of the four major divisions of the littoral zones of the region in comparison with each of the other divisions.

[1] 30 more dug occasionally among or under rocks.

Again the analysis follows the records through the season of 1920. The comparison is based on total distribution records as was the last. That is, for the purposes of this table the finding of a given animal once in a given type of habitat is as significant as though it were abundant there. There were 242 species in the catalogue when this study was made.

It is immediately apparent that this type of analysis serves only to call attention to the larger number of animals taken from the flats and beyond indicating the higher specificity of the flats, shows no evidence of relationships that may exist between different habitats. The species taken from any given type of habitat are found to be approximately equally distributed in the other habitats of the region. Such experience has led casual observers to conclude that relationships between different animal associations can not be analyzed.

In order to make such an analysis, the records were studied from another angle. Species approximately equally distributed through the different associations and those reported for one season only were eliminated. Then the remaining species were listed according to the habitat in which they are most abundant. When a species was found equally abundant in two habitats it was listed from both. The association in which the animal was next most abundant was also estimated. Unfortunately these records are based on "experience" cards that seldom give specific figures and on the number of collecting teams that have reported the species from the different associations, as in the data given in the check list, rather than on strictly quantitative grounds and while substantially correct, they lack the finality that statistical treatment would give.

This type of analysis gives a real basis for comparisons of the relationship between the different associations. It is of interest that the relationships shown by Table II. are practically the same as given by an analysis of the entire catalog in 1917. In other words, the early collecting gave the typical forms characteristic of the environment while much of the later work has yielded in addition to these characteristic species, a number of accidental or incidental records.

TABLE II.

RELATION OF DIFFERENT HABITATS BASED ON DISTRIBUTION OF CHARACTERISTIC ANIMALS.

Name of Association.	No. Species.	Peculiar Species.		Species Found Next Most Abundant in:									
				Pilings.		Rocks.		Flats.		Dredging.		Under or Among Rocks.	
		No.	%.	No.	%.	No.	%.	No.	%.	No.	%.	No.	%.
Wharf pilings.....	32	2	6	—	—	24.5[1]	77	2.5	8	2.0	6	0	0
Rocks and rockweed	32	3	9	14.5	45	—	—	13	41	1.5	5	0	0
Dredging.....	20	3	15	3	15	9	45	3	15	—	—	0	0
Flats.....	40	22	25	2.5	3	15	17	—	—	17.5	20	30	33

The association of the wharf pilings is found to be closely related with that of the rocks; 77 per cent. of the animals common in the former are next most abundant in the latter. This fits with one's general impression that the two sets of animals are much the same but with the emphasis placed on different species so far as numbers are concerned.

The animals common on the rocks are next most abundant on the pilings but almost as many are nearly as abundant on the flats. The latter is to be expected from the fact that the rocks extend up from the flats, often forming a belt only a few feet wide in the intertidal portion of the flats, and that single rocks frequently occur surrounded by typical mud or sand flats, and from the further consideration that the eel grass offers almost as good a place of attachment for many animals as do the rocks.

The animals taken commonly in dredging are more closely related to the rock association than to the others. This is because our dredging operations have been done on clean hard bottom where the water conditions are similar to those found among rocks. Dredging in mud as in Buzzards Bay would give different results and transition bottom associations are indicated from the dredging work in Great Harbor.

Again the marked independence of the flats as a special habitat is shown by the larger number of animals frequently taken there

[1] Where animals are approximately equally distributed between two different associations they are summarized by fractional representation.

in some abunbance and by the larger number of peculiar species. They are not closely related to other habitats if one excepts the conditions under the rocks which scarcely form a different association. Its main difference is that burrowing and exposure are more limited than on the open flats. The animals common on the flats are particularly absent from wharf pilings showing, as would be expected, that these habitats have little in common.

If quantitative data were available, the distinctions here found would doubtless stand forth more plainly. The fact that a beginning can be made in indicating relationships by the methods used when no relationships appeared from an analysis of bare check lists emphasizes the need of quantitative studies in animal ecology.

This need was first recognized by Forbes (1907) who devised a mathematical formula for determining the existence of an association. In 1911, as the result of studying seasonal succession in ponds, I concluded that qualitative work gives insufficient basis for exact conclusions. Shelford in 1915 repeats the formula of Forbes, and Michael (16, 21) has done more than anyone else in America in showing the fundamental need of quantitative investigations in ecology and in developing formulæ to enable one to study associations on a quantitative basis.

The work here presented is of course only quasi-quantitative in character but the greater clearness obtained indicates that much of the muddle of animal ecology may be cleared by the further development and the application of quantitative methods in field researches. The problem of the ecologist studying littoral distribution is not so hard as that of the plankton student where as Michael says (1921): "Granting the equivalent of the oak tree or pine tree association, the marine ecologist finds difficulty not only in describing it but even in finding it. Since he cannot directly witness such an association, he is compelled to rely on indirect evidence furnished by tow-net or similar apparatus. In other words his only recourse is to measured magnitudes and application of mathematical logic thereto." For the exact determination of such relations the methods here used are almost as gross as are the ordinary qualitative observations in trying to solve the relationships existing between littoral associations.

It is true that analysis of the results of preliminary collecting showed the same relations as the quasi-quantitative analysis of more complete records in the Woods Hole region. Unfortunately one cannot be sure that the animals found in such preliminary work are really the typical animals since they may obviously contain many incidental forms. In other words in a random sample one is more apt to collect animals typical of the habitat than incidental forms but he can never be sure of this without further work.

V. The Effect of Continued Collecting on Distribution Records.

In 1917 when the collecting records were first studied seriously there were 181 species in the catalog. In 1920 when a similar study was made, the catalog listed 242 species. In the interim the Sound Gutters, Lackey's Bay and Great Harbor had been added to the localities visited.

In 1917, 11 species were recorded only from the wharf pilings. The later lists show 7 species so limited but this includes only one (*Tetrastemma*) of the previous list. In 1917 two species were recorded only from rocks or rockweeds, while on the later list there were 10 such species including only *Clava leptostyla* from the preceding list. In the first comparison there were 10 animals recorded only from dredging; in the later one, 13, which includes four of those on the preceding list: *Arca ponderosa*, *Strongylocentrotus droebachiensis*, *Heterocrypta granulata*, and *Amaroecium stellatum*.

On the 1917 list, 71 species were recorded from the flats only. After four more years' work this had shrunk to 41 providing animals found in the sand under and among rocks are excluded. Of these only 17 appear on both lists. They are: *Edwardsia elegans*, *Eloactis producta*, *Bdelloura candida*, *Syncoelidium pellucidium*, *Ophioderma brevispina*, *Chaetopterus pergamentaceous*, *Platynereis megalops*, *Scoloplos acutus*, *S. robustus*, *Spio* (*setosa?*), *Callianassa stimpsoni*, *Mysis stenolepis*, *Squilla empusa*, *Melampus lineatus*, *Clidiophora trilineata*, *Pecten irradians*, and *Tellina tenera*.

On the earlier lists, fifteen species were recorded from some place in each of the four main types of habitats: wharf pilings, rocks, flats, and dredging. In 1920 this list had increased to 54. These results mean, as has already been suggested, that as collecting has proceeded, animals have been picked up in habitats in which they are not abundant. The scarcity of many of these is shown by the number of single specimen records on the lists. There is little doubt but that if the present type of collecting were continued long enough, there would finally be stray records of many of the animals found in the region from each type of habitat. Even dredging, which we have usually carried on in deep water in Vineyard Sound, yields a different type of animals and becomes more closely related to other habitats as a result of dredging records taken in Great Harbor. In some one or more of their dredging operations, the *Biological Survey* found most of the animals we have taken from inshore digging. This result might be expected from the fact that some of their dredgings are recorded from less than 10 feet of water. If made at high tide, these would be almost as close inshore as our deepest collecting on wading and digging expeditions when we often collect out to four feet of water at low spring tides.

In other words, in such a small region as we are now considering, provided with strong tidal currents which aid in distribution, the animals tend to become widely distributed and occasional specimens will be found that can tolerate for a time conditions that are essentially unfavorable. Under these conditions the mere record of the presence of a species in a given habitat means very little unless there is due consideration of its abundance and duration in that locality. One is thus driven again to the conclusion of the last section, that quantitative work is necessary before final judgment can be passed in the matter of the constitution of animal associations.

We have found no evidence that the long continued collecting over the same grounds by the Invertebrate Class, nor the commercial collecting of the Supply Department of the M. B. L. has affected the number of animals present within the past nine years sufficiently for the effect to be noticeable by the collecting methods we have used. With growing experience in collecting

each year we have broken previous records with monotonous regularity, for numbers of species from most of the localities we visit. This could not have continued so long had the animals been becoming less abundant.

The number of animals present in a given locality must depend more on the availability of suitable breeding places and abundance of food than upon such disturbing influences as summer collecting, particularly when the collecting does not reach all the breeding habitats of a region and there is adequate means of distributing young stages. This conclusion is emphasized by the rapid recovery in numbers of *Arbacia* after their almost complete disappearance following the winter of 1917–18 (Allee, '19) and in the face of their destruction by the thousands in the research work carried on in the Woods Hole laboratories.

VI. Summary.

1. Analysis of distribution records in the four major types of habitats of the Woods Hole littoral, viz., wharf pilings, rocks and rockweeds, flats, and the sea bottom in deeper water show that mere records of species present in the different habitats fail to indicate any relationship between the different types of associations.

2. By eliminating species known to be approximately equally distributed throughout and records for one year, only, and classifying the remaining species in terms of places where they are most abundant and next most abundant one finds:

(*a*) The association of the wharf pilings is closely related to that of the rocks.

(*b*) Species taken in dredging on clean hard bottom are found in next abundance on the rocks.

(*c*) The associations of the flats are highly independent of the others in the region but continue in the mud and sand under and around rocks.

(*d*) That some degree of quantitative work is necessary in order to determine the relationships of animal associations.

3. Preliminary collecting in a region tends to give the obvious forms and gives similar results in analysis to the type of quasi-qualitative work described in this report.

4. The number of animals present in the Woods Hole region has not been noticeably affected by the intensive collecting carried on there during the nine years covered by these studies.

LITERATURE CITED.

Allee.

'11 Ill. State Acad. Sci., 4, pp. 126–131.

'19 BIOL. BULL., 36, pp. 96–104.

'22 *Ibid.*, 41, pp. 99–131.

'23 Studies in Marine Ecology: II. An annotated catalog showing the distribution of common invertebrates of the Woods Hole littoral. MS. deposited in the following libraries: U. S. Fish Commission at Washington; Marine Biological Laboratory; Museum of Comparative Zoology; U. S. National Museum; Scripps Institution at LaJolla; Harpswell Laboratory.

Cotton, A. D.

'12 Proc. Roy. Irish Acad., Sect. I, Pt. 15.

Davis.

'11 Bull. U. S. Bur. Fisheries, 31, Pt. I, pp. 443–544; Pt. II, pp. 795–833.

Flattely and Walton.

'22 The Biology of the Sea-Shore. Macmillan, 336 pp.

Forbes.

'51 Edinburgh New Philos. Journ., pp. 192–263.

'59 The Natural History of European Seas. 306 pp.

Forbes, S. A.

'07 Bull. Ill. Lab. Nat. Hist. 7, pp. 273–303.

Hoyle.

'89 J. Linn. Soc. 20, pp. 442–472.

Klugh.

'18 Journ. of Ecol., 6, p. 230.

Kjellman.

'77 Nova Acta Regiae Societatis Scientiarum, Ser. III. Jubelbana, Upsala. (Read in abstract.)

Michael.

'16 Univ. of Calif. Publ. in Zoology, 15, pp. i–xxiii.

'20 Journ. of Ecol., 8, pp. 54–60.

Murray and Hjort.

'12 Depths of the Ocean. Macmillan, 821 pp.

Petersen.

'93 Det Videnskabelige Udbytte af Kononbaaden "Hauchs" togter. Copenhagen, 464 pp. Summary in English.

Pratt.

'16 A manual of the common invertebrate animals. McClurg, 737 pp.

Shelford.

'15 Journ. of Ecol., 3, pp. 1–23.

Sumner, Osburn and Cole.

'11 Bull. U. S. Fisheries, 31, Pt. I, pp. 1–443; Pt. II, pp. 547–795.

Verrill and Smith.

71–72 Rep. U. S. Fish Comm., pp. 295–778.