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ART. XXIV.—*A Brief Survey of the Animal Communities in Danish Waters, based upon quantitative samples taken with the bottom sampler; by C. G. JOH. PETERSEN, Director of the Danish Biological Station.*

During late years I have published several works on the animal communities of the sea bottom in Danish waters, determined on the basis of quantitative investigations with my bottom samplers, which take up 0.1 sq. m. of the sea bottom in each sample. These investigations have been carried out for biological purposes, connected with the fisheries, but they have aroused the interest of the geologists both in Europe and in America, because for the first time they make it possible to point out the commonly occurring, characteristic species, by means of which an orientation becomes comparatively easy, and because they give information as to which species are living together in the different places of the sea bottom.

Professor Charles Schuchert, of Yale University, has requested me to give a short survey of these investigations, intended for paleontologists, and I therefore here make the first (and surely very deficient) attempt to give a general view of the common species of animals, important for paleontologists, which we find in communities from the shore out to a depth of about 700 m., in the waters within the Skaw and in the Skagerak. I must necessarily base the description upon the communities of the level sea bottom, while the epifaunas on plants, stones, rocks, etc., will only be mentioned to the extent they are known, as in such conditions of the sea bottom the bottom sampler gives less serviceable results.

Most of the Danish waters, especially the more shallow and land-locked, are often during the winter under a cover of ice. The difference in the level of the water

FIG. 1.

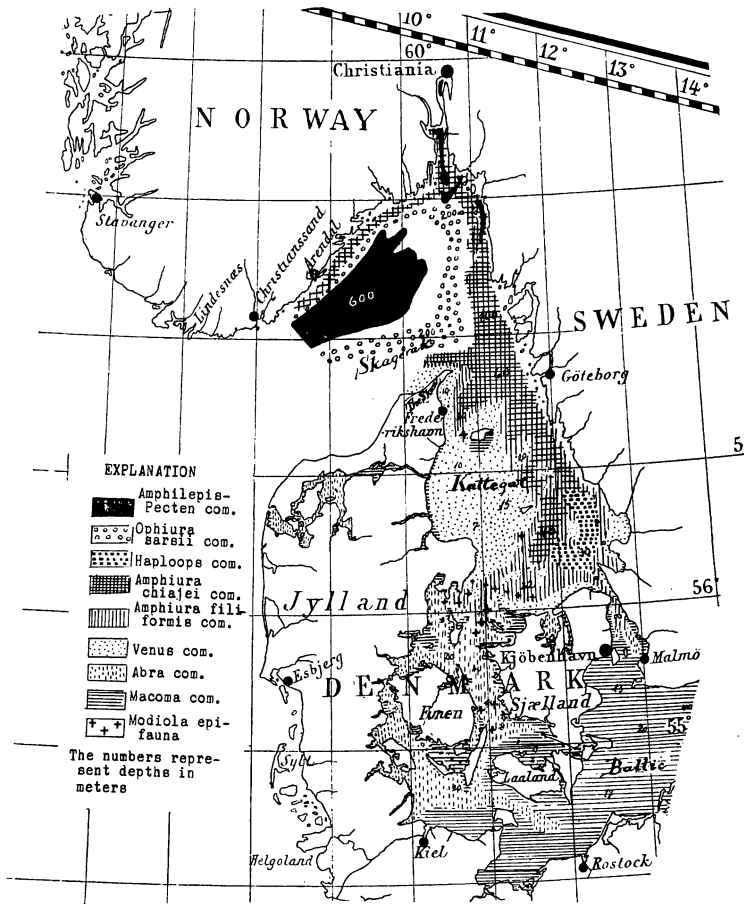


FIG. 1.—Chart showing the distribution of animal communities in Danish waters.

caused by the daily tides is as a rule less than 30 cm., and therefore rather insignificant. As a rule, the waters, the shallow parts excepted, are very transparent, i. e., little polluted by minute particles.

I. The animal community which occurs off nearly all our coasts from a water-depth of 0 m. and outward, is the *Macoma baltica* community (see the accompanying chart). Its characteristic animal is *Macoma baltica* which is found under all the very variable external conditions of this community; although other communities occur in rather homogeneous external conditions, this community ranges from a salinity of about 5 per thousand or less in the deep water of the true Baltic (more than 140 m.), to 0 m. on sand bottom at a salinity of above 30 per thousand in the North Sea, and here in temperatures varying from about 0°-20°C. However, whereas in the Baltic it occurs from the shore out to great depths, and thus at varying as well as at constant temperatures of about 5°C., in the more saline waters, such as the North Sea, it is found only close to the shore, where no other communities can thrive, because here a considerable flux and reflux of the tide is prevalent, and where it is cold during the winter. It may be found on a bottom consisting of sand or of black mud, or of all mixtures between these; it might be able to live in various other localities than those in which it actually does, if it were not that it cannot thrive together with the other communities. The *Macoma* community demands so little in the way of external, chemico-physical conditions that it can only be the competition with other animals which prevents it from living almost everywhere in our seas.

The species of the *Macoma* community on the level sea bottom which are important to paleontologists, are: *Macoma baltica*, *Cardium edule*, and *Mya arenaria*. In shallow water there is, in addition, *Hydrobia* sp.; in very muddy localities and in water not too fresh, *Scrobicularia plana*; and in more saline water, *Ostrea edulis*, *Tapes aureus*, and *T. pullastra*.

Nearly the whole of the Baltic, as has been said, belongs to this community, from the shore out to very great depths, but in the deeper parts *Macoma baltica* is the sole representative; on the other hand, huge numbers of the "arctic" isopod, *Idothea entomon*, occur in this

assemblage. In this brackish, cold sea it finds good living conditions although generally no echinoderms at all are met with.

Of epifaunas the *Macoma* community has a great number. (1) Upon stones by the shore: *Littorina littorea*, *L. rudis* (typica), *Mytilus edulis*, *Balanus* sp., and, where the water is more saline, also *Purpura lapillus*, *Patella vulgata*, Chitons, etc. (2) On *Zostera marina* and other plants, a multitude of *Rissoa inconspicua*, *R. membranacea*, *Cerithium reticulatum*, *Littorina obtusata*, *L. rudis* var. *tenebrosa*; in water of greater salinity, ca. 25 per thousand, *Trochus cinerareus*, *Rissoa striatus*, *Lacuna divaricata*, *L. pallidula*, *Modiolaria marmorata*, and *M. discors* are also met with, and of echinoderms *Echinus miliaris*. Otherwise echinoderms are rare in the domains of this community, and often they are entirely wanting; *Asterias rubens*, however, lives in several localities within the community, where the salinity allows it to do so. It preys eagerly upon *Mytilus*.

II. The community which succeeds the *Macoma* community out towards the deep in our more sheltered waters,¹ is the *Abra* community, named after *Abra alba*; the number of *Abra*, however, varies very much in the different years. This community, which includes many echinoderms, especially *Ophiura*, occurs generally in deeper water than the *Macoma* community, and evidently requires a higher salinity and a somewhat slighter variation of temperature; also a water with stronger current.

¹ Transitions between the communities are often found near the limits of their area of distribution, though not extending over so large areas as one might expect. The characterization of the communities is of course mainly based upon the areas where the communities occur in their purest condition.

Single individuals of a species belonging to one community may occur in other communities where they are not indigenous, especially when the distances are so small as in the Danish waters; young of several species, also, may be found outside their usual domain; but the eight communities named here have through many years turned out to be mainly constant, both as to content of characteristic species and distribution. The Danish waters within the Skaw seem to be very rich as compared to the open seas outside, e. g., the North Sea, where the communities are very poor in number of individuals per square meter, but the orientation becomes more difficult, as one of course cannot expect to get a characteristic animal there in each sample of 0.1 sq. m.; in such cases it is necessary either to take so many samples that a sufficient number of characteristic animals is obtained, or to orient oneself by means of the associated animal species (see page 352). It is also of considerable help in the orientation, when the succession of the various communities from low to deep water is known.

The bottom may vary from nearly pure gravel and sand to soft, light grey clay, but black mud is not liked. A sparse growth of algæ may often be found here, or no plants at all. The community has its main distribution around the whole of Funen, and in the Limfjord; in the Kattegat it practically does not occur.

Its characteristic species are, besides *Abra alba*, *Ophiura albida*, *O. texturata (ciliaris)*, and in the deeper parts *Echinocardium cordatum*. Of associated species (see page 352) a number of bivalves are met with: *Cyprina islandica*, *Cardium fasciatum*, *C. echinatum*, *Axinus flexuosus*, *Leda pernula* and *L. minuta*, *Nucula tenuis*, *N. nitida*, *Modiolaria nigra*, *Solen pellucidus*, *Corbula gibba*, *Montacuta ferruginosa*, *Mya truncata*, and *Abra nitida*; of gastropods: *Buccinum undatum*, *Fusus antiquus*, *Nassa pygmæa* and *N. reticulata*, *Natica* sp., etc.; of echinoderms: *Strongylocentrotus dröbakienensis*, *Echinocyamus pusillus*.

Furthermore, the "arctic" forms, peculiar to our waters, occur in the deeper parts within this community on gravelly or sandy bottom, viz.: *Astarte borealis*, *A. elliptica*, *A. banksii*, and *Macoma calcarea*, frequently in great numbers. These "arctic" forms are found almost exclusively south of the Kattegat and some distance into the Baltic to the south of Sweden, where the *Abra* community ceases; apparently these animals cannot stand the brackish water of the Baltic as well as can *Idothea entomon*.

The five "arctic" species mentioned are often found in huge numbers on the bottom of our waters, up to 400 specimens of the genus *Astarte* occurring per square meter; in spite of this abundance, however, they can not be regarded as of importance in the *Abra* community, being partly relicts from the glacial period. We have in other places *Abra* communities in which they are quite wanting.

In the Limfjord with its slight depth of 5-14 m., temperature 0°-18° C., the *Abra* community is characterized, in addition to *Abra alba*, by: *A. nitida*, *Corbula gibba*, *Solen pellucidus*, *Nucula nitida*, *Mya truncata*, *Cardium fasciatum*, *Pecten varius*, *Acera bullata*, *Philine aperta*, *Ophiura albida*, and *O. texturata*, rarely *Echinocardium cordatum*, frequently *Echinocyamus pusillus*. *Mya*

truncata also occurs in the *Abra* community around Funen, but in such a hard bottom that it is difficult to obtain in the bottom sampler; this species lives just outside the limit of the *Macoma* community towards the deep.

The epifauna belonging to the *Abra* community, where there are stones or other solid objects upon the bottom, does not consist of *Mytilus edulis* as in the *Macoma* community, but of *Modiola modiolus*, covered with *Ophiopholis aculeata*, *Chiton* spp., *Balanus* sp., *Psölus phantapus*, *Pomatoceros triqueter*, etc. *Saxicava rugosa*, *Ophiura robusta*, and *O. affinis* are also often encountered here.

This, as well as other epifaunas, may occur in very small patches, e. g., on a single *Modiola*; the community of the level sea bottom is therefore frequently obtained in the same sample as the epifauna.

III. In the more open Kattegat from 0 m. (or sometimes ca. 7 m.) to about 20 m. depth the *Abra* community is not met with outside the *Macoma* community, which is only sparsely represented, but we find here the so-called *Venus* community, this being probably a modification of the *Abra* community on hard sand bottom with greatly agitated water; many of the species therefore are common to both, excepting only such as demand soft bottom exclusively. In the northernmost parts of the Kattegat the *Venus* community goes right in to the shore; in more southerly or shallow, sheltered places a trail of the *Macoma* community occurs along the coast (see the chart).

The characteristic species of the *Venus* community are *Venus gallina*, *Tellina fabula*, *Mactra subtruncata*, *Ophiura albida*, and *O. texturata*, accompanied in the deeper parts by *Echinocardium cordatum*. Of frequently associated species *Cyprina islandica*, *Solen pelucidus*, *Thracia papyracea*, and *Montacuta ferruginosa* may be mentioned; of gastropods, *Buccinum undatum*, *Fusus antiquus*, *Nassa reticulata*, *Natica pulchella*, *Bela* sp., *Trophon truncatus*, and several others.

In greatly agitated, shallow water with hard sand bottom *Tellina tenuis* is often richly represented; it may,

however, also be found in the *Macoma* community under similar conditions.²

The epifauna of the *Venus* community, like that of the *Abra* community, is composed of *Modiola modiolus* with its associates.

IV. Where the bottom of the Kattegat, at depths of from ca. 15 to ca. 40 m., becomes more rich in detritus, we find a community characterized by several *Amphiura filiformis* in each square meter, and by *Echinocardium cordatum*. Associated species are, besides numerous detritus-eating *Turritella terebra*, *Aporrhais pes pelecani*, *Dentalium entalis*, *Axinus flexuosus*, and several of the bivalves occurring in the *Venus* and *Abra* communities, e. g., *Cyprina islandica*, *Abra nitida*, *Cardium fasciatum*, *Nucula nitida*, *N. tenuis*, *Leda pernula*, *L. minuta*, *Pecten septemradiatus*, *P. opercularis*. Finally, *Virgularia mirabilis* and *Pennatula phosphorea* are encountered here. Here, too, the corresponding epifauna is a *Modiola modiolus* one.

V. This community passes with even transitions into the deepest-living community of the Kattegat, on blue, soft clay bottom at depths of between 40 and 100 m., viz., the *Amphiura chiajei* community with *Brissopsis lyrifera* and *Nucula sulcata* as additional characteristic animals. Some of the molluscs from the preceding community which go deepest likewise occur here, e. g., *Abra nitida*, *Axinus flexuosus*, *Leda pernula*, *L. minuta*, and *Dentalium entalis*. The crustacean *Calocaris m'andreae* is also very characteristic of this community. Of "sea-pens," *Pennatula phosphorea* is encountered. The epifauna includes, possibly, among other species, *Crania anomala*; it is, however, as yet but little known.

VI. A more locally occurring assemblage is the *Haploops* community, living on soft, blue clay bottom which is almost covered by clay tubes of the amphipod *Haploops tubicola*, in thousands per square meter. Char-

² In the Kattegat is sparsely found a community living in deeper water outside this *Venus* community, the deep *Venus* community, with species such as *Abra prismatica*, *Psammobia feroensis*, *Thracia papyracea* and *T. prætenuis*, *Mactra elliptica*, *Tellina pusilla*, and the echinoderms *Spatangus purpureus* and *Echinocardium flavescens*,—a community which evidently has its widest distribution in other waters (the North Sea).

acteristic bivalves are *Pecten septemradiatus*, *Lima loscombi*, *L. sp.*, *Venus ovata*; in addition are found some associated bivalves from the preceding community, as *Abra nitida*, *Cardium fasciatum*, *C. minimum*, *Axinus flexuosus*, *Leda minuta*, *Nucula tenuis*; *Verruca strömii* is attached to the *Pecten* shells. *Ophiura robusta* and *Strongylocentrotus dröbakiensis* are common here.

The epifauna of this community is not very well known.

VII. At the entrance of the northern Kattegat and in the deeper parts of the Skagerak between about 150 and 200 m. depth, a community occurs on soft, blue clay bottom, characterized by *Ophiura sarsii*, accompanied by *Brissopsis lyrifera*. This may be called the *Ophiura sarsii* community.

The temperature is here fairly constant, about 7° C., during the whole year, in contradistinction to the above mentioned communities, where it may vary a good deal; the salinity always exceeds 30 per thousand.

The most common associated bivalves are: *Abra nitida*, in hundreds per square meter, *Axinus flexuosus*, *Leda pernula* and *L. minuta*, *Nucula tenuis*, *Portlandia lucida*, *Neæra obesa*, and *Cardium minimum*. The numerous *Turritella* and *Amphiura* from the nearest community, the *Amphiura chiajei* community, have disappeared.

Only a few investigations with the bottom sampler have been carried out in the area of this community.

VIII. The deepest community we know lives in the deep of the Skagerak on soft, blue clay bottom in depths from about 250 to 700 m., at a fairly constant temperature of 5°-6° C. The salinity always exceeds 30 per thousand.

In the Christianiafjord, where the salt water with a constant temperature of 6.5° C. at least rises to about 100 m. depth, this community ranges up to these lesser depths.

The community is named after its two characteristic animals: the *Amphilepis norvegica*-*Pecten vitreus* community.

Sometimes only empty shells of *P. vitreus* are found in this community, not the living animals. Bivalves such as *Abra nitida*, *Axinus flexuosus*, *Cardium minimum*, *Nucula tenuis*, *Portlandia lucida* and *Neæra obesa* go out

on this community, but *Abra longicallis*, *Axinus croulinensis* and *A. ferruginosus*, *Malletia obtusa*, and *Nucula tumidula*, together with the gastropods *Dentalium striolatum* and *Scaphander* sp., etc., are first met with here as characteristic animals.

Kophobelemnon stelliferum occurs in the deepest parts of this community, at any rate, together with certain Spongiidæ, but the amount of animals, with respect to number as well as to weight, seems to be very insignificant in about 650 m. depth in this community, and is, as a whole, much inferior to that of all the other communities.

When finally endeavoring to give a tabulated view of our animal communities and the conditions under which they live, I am conscious of the many defects in the details of this sketch; as a connected whole, however, it gives a true picture along broad lines.

The depths indicated for the single communities are applicable only to Danish conditions; in the Norwegian fjords they are different, as in the North Sea, the scale according to which bottom conditions and temperature vary being different in the different waters; but the consecutive order of the communities from the shore out to the deep is everywhere the same in the hitherto examined waters. The depth in itself, within these depths of between 0 and 700 m., does not seem to play any decisive part, *Abra nitida*, for example, occurring from a depth of ca. 4 m. to one of ca. 400 m. in Denmark.

It would be of great interest to have such examinations carried out in other waters than those of northern Europe; at present, however, I only know of such from Puget Sound on the west coast of North America, where, strange to say, in shallow water, dry at ebb, a community occurs very similar to our *Macoma* community with its characteristic species, *Macoma baltica*, *Cardium edule*, and *Mya arenaria*. At Puget Sound three *Macoma* species are found, a *Cardium corbis*, the introduced *Mya arenaria*, and, in addition, a bivalve, *Schizothærus nuttalli*, i. e., if not quite the same species, at least the same genera.

In the table below I distinguish between the following categories of animals within the communities of the level sea bottom:

(1) Animals which in some quantity are only to be found in one definite community and which occur practically everywhere within this community are called characteristic animals of the first order.

(2) Animals which are found in some quantity in one community, but only in certain parts of it, e. g., *Mya arenaria*, *Cardium edule*, and *Scrobicularia plana* in the *Macoma* community, are called characteristic animals of the second order.

(3) Animals which are found in more than one community, but in such large quantities and over such large areas that they necessarily belong to the characteristic animals of this community, e. g., *Echinocardium cordatum* and *Brissopsis lyrifera*, are called characteristic animals of the third order.

All other more common animals of a community, which are not of such great importance for the characterization of the community, are called associated animals.

We have as yet mentioned only animals which are so numerous on the bottom that they are, as a rule, found on each square meter, but of course there occur in the communities other more rare animals, such as large gastropods, large Asteridæ and other predatory forms. Of the more mobile animals I shall mention only the fishes, the occurrence of which is well known. Some fishes live almost exclusively on the *Macoma* and *Venus* communities, others go out also to the deeper *Abra* and *Amphiura filiformis* communities; on the soft, grey clay bottom other species of fishes are encountered, and the two deep communities in the Skagerak have almost exclusively peculiar species of fishes, among which may be mentioned *Pleuronectes cynoglossus*, *Coryphænoides rupestris*, *Argentina silus*, *Chimæra monstrosa*, *Spinax niger*, *Myxine glutinosa*, and still other smaller forms.

As the bottom fishes to a certain degree follow the animal communities, so also do the larger, edible, decapod crustaceans. Especially associated with the stony parts of the *Venus* community is the lobster (*Homarus vulgaris*); in the deeper communities on soft clay bottom, especially the *Amphiura chiajei* community, lives, or lived, *Nephrops norvegicus*; in the still deeper communities, especially the *Ophiura sarsii* community, numerous *Pandalus borealis* occur.

Community	I <i>Macoma</i>	II <i>Abra</i>	III <i>Venus</i>	IV <i>Amphitura</i> <i>filiformis</i>	V <i>Amphitura</i> <i>chitajei</i>	VI <i>Haploops</i>	VII <i>Ophitura</i> <i>sarsii</i>	VIII <i>Amphilepis-</i> <i>Pecten</i>
Depth in m.	0-14	ca. 10-50	0 or 7-20	15-40	40-100	30-80	150-200	300-700
Temp. in °C.	0-20	1-12	0-15	3-14	4-10	3-13	ca. 7	ca. 6
Salinity per thousand	10-25	20 to above 30	25 to above 30	30 to above 30	Above 30	Above 30	Above 30	Above 30
Bottom	Sand to black mud	Sand and clay mixed	Gravel, sand	Sand and clay mixed	Soft, grey clay bottom			
Plants	<i>Zostera</i> and algae in abundance	Sparse algae	Scattered <i>Zostera</i> , algae, <i>Coralina</i>	Sparse algae	0	0	0	0
Epifauna	<i>Littorina</i> <i>Rissoa</i> <i>Mytilus</i> <i>Balanus</i> sp.	<i>Nodiola</i>	<i>Nodiola</i>	<i>Nodiola</i>	<i>Crania</i> <i>anomala</i>	?	Deep sea corals with echinoderms	
Characteristic species	1st order <i>Macoma baltica</i>	<i>Abra alba</i>	<i>Venus gallina</i> <i>pellina</i> <i>pabula</i>	<i>Amphitura filiformis</i>	<i>Amphitura chitajei</i> <i>Nucula sulcata</i>	<i>Haploops tubicola</i>	<i>Ophitura sarsii</i>	<i>Amphilepis norvegica</i> <i>Pecten vitreus</i>
	2d order <i>Nya arenarid</i> <i>Cardium edule</i> <i>Hydrobia</i> sp. <i>Serobicularia plana</i>		<i>Nacra subtruncata</i>		<i>Lima los-combii</i> <i>Venus ovata</i>			<i>Abra longicollis</i> <i>Kalletia obtusa</i> <i>Axinus croulinensis</i> <i>Dentalium striolatum</i> <i>Scaphander</i> sp., etc.
	3d order	<i>Ophitura albidia</i> <i>O. texturata</i> <i>Echinocardium cordatum</i>	<i>Oph. texturata</i> " <i>albidia</i> <i>Echinocardium cordatum</i>	<i>Echinocardium cordatum</i>	<i>Brissoopsis lyrifera</i>	<i>Pecten septem-radiatus</i>	<i>Brissoopsis lyrifera</i>	

It is obvious that for a paleontologist in another country it would be of still more interest to know the animal communities at the shore of his own land; it is possible that they are quite different from the Danish animal communities, even if the investigations from Puget Sound, as mentioned, tend to show a certain agreement as to shallow water. With a suitable, fast-going boat and a modern bottom sampler equipment a general view of the nature and distribution of the animal communities could, I believe, be gained over large areas in the course of a comparatively short time.

In conclusion I shall only mention that more detailed information about the bottom sampler investigation in the Danish waters may be sought for in the *Reports of the Danish Biological Station*, Nos. 20-25, 1911-1918, where are to be found also illustrations of the gears employed and of the animal species of the communities, together with a chart of their distribution.

Hellerup, December, 1923.