Concluding remarks

The rapidly increasing exploration of the deep-sea which has been conducted during the last few decades has resulted in a much more varied picture of the zone and its animal life. This applies to many fields of research. Thus studies of bottom topography has shown that the abyssal zone does not, as formerly assumed, consist largely of extensive, uniform plains covered with soft sediment It is now known that areas of hard bottom such as lava and manganese nodules occur. There are also topographical structures, such as ridges, guyots and sea-scarps, which are as conspicuous as the corresponding structures on land (Shepard 1963). Although the abyssal hard bottom is known to exist, it remains largely unexplored, and the fauna of these regions is known largely from photographs. The tremendous increase of the knowledge of abyssal bottom topography is illustrated very clearly by comparing the chart of bottom topography in Sverdrup *et al.* (1946), based on data obtained prior to 1940, with the charts of Dietrich & Ulrich (1968), the latter incorporating very recent data.

The movements of abyssal water masses have until now only been comparativley little studied, but may be of considerable biological importance in carrying food particles to and in dispersing eggs and larvae of benthic organisms, as well as in supplying oxygen. Knauss (1968) reviewed previous investigations on the subject, based largely on photographs, and reported on new data obtained by direct measurements and sea-bed drifters. The studies were made in the N.W. Atlantic and the E. Pacific at depths ranging from 3000 to well over 5000 m. The main conclusion from these studies was that the currents along the bottom of the deep ocean are probably not very much simpler than those at the surface of the ocean.

The diversity and complexity of the abyssal fauna has been repeatedly stressed by me. I think it can be safely concluded that the descriptive phase in the taxonomy of abyssal organisms will continue for some time in the future. It has also been stressed that as far as distributional patterns are concerned, rules generally applicable to all animal groups do not exist, a viewpoint also held by Wolff (1962). In some groups a wide horizontal and vertical distribution may be the rule, and some well-established cases of cosmopolitanism and of allopatric species seem to occur. This pattern seems to exist in the bivalves and in some groups of coelenterates and echinoderms. In other groups, holothurians for instance, there is generally a wide horizontal distribution (including several cases of cosmopolitanism), but larger systematic units are confined to definite depth zones, and have possibly developed *in situ*. Finally, some groups of smaller crustaceans seem to have a very restricted distribution, often confined to single basins. Examples are found among the Isopoda, Amphipoda and Cumacea.

The present investigation is a crude overall survey of some of the problems of the deep-sea fauna. It supports the suggestion made by Sanders *et al.* (1965) and Sanders (1968) that the abyssal fauna is greatly diverse and neither so poor in species nor so uniform as previously assumed.

However, many important problems have been left untouched in the present study. Among these are growth, egg number, reproductive cycle, life span, mortality and quantitative distribution. Detailed investigations of restricted areas will therefore be necessary to solve many problems relating to the autecology and functional morphology of the individual species.

IV. SUMMARY

The present paper deals primarily with the abyssal and hadal bivalves obtained by the Galathea Expedition, but in addition a number of samples from other sources have been included. The collection studied consists of 159 samples with about 1700 specimens and 91 species, of which 44 are considered as new. It appears to be the largest collection of deep-sea bivalves included in a single study.

At an early stage of the study it was considered necessary to examine as many samples from earlier expeditions as could be located. The reasons for this were:

1) To solve at least some of the innumerable taxonomic problems arising during the work.

2) To decide whether a species was represented by specimens alive at capture or taken only as empty valves. This is not indicated by many of the previous authors. However, even though most samples are preserved dry, in the majority of the cases it was

possible with certainty to decide whether a specimen had been alive at capture or not. This is essential to get a precise idea about the vertical and horizontal distribution of the individual species.

3) To examine previous records of shallow-water species from abyssal depths.

During this examination it was possible to study the types of most abyssal bivalves. Besides abyssal bivalves, several hundred bathyal samples were inspected for comparison with the abyssal species.

An account is given of previous expeditions, including reference to the station list of the expedition and the paper(s) dealing with the bivalves it obtained.

The systematic part describes and figures each species. Special attention has been paid to easily observable characters of the soft parts which could be considered useful specific characters. In the introductory remarks to most of the families the specific characters believed to be relevant have been briefly summarized. An examination of the soft parts (particularly the posterior mantle region) turned out to be very useful in dealing with species within the families Nuculanidae and Malletiidae, in which the shell offers less distinct specific characters.

The abyssal bivalves. An attempt has been made to give a list of all known abyssal species, i.e., occurring below a depth of 2000 m and at temperatures below 4°C (Table 1). References to the species are listed, as is the number of records of the individual species. The known horizontal and vertical distributions as well as the temperature interval of the species have been compiled. The location of the type is listed together with an indication of whether I have seen it or not. Finally, an attempt has been made to evaluate whether a given species should be considered as belonging to the abyssal fauna proper or whether it is rather a bathyal species extending its vertical distribution down in the abyssal zone.

A list is given of bathyal species found in the abyssal zone; for these the term "guest" species is used. It is evident that the "guest" species tend to occur in the upper part of the abyssal zone, and it is suggested that any bathyal species may be able, at least temporarily, to establish itself in the abyssal zone. It is not possible at present to make an absolutely clear distinction between the "endemic" abyssal fauna and the "guest" species.

The endemic abyssal fauna comprises 20 families (the recent marine fauna consists of 80 families altogether). Two of the 20 families are each represented by one record only from the upper part of the abyssal zone. With the exception of the new family Galatheavalvidae, all the families represented in the endemic abyssal fauna are well known from sublittoral and littoral waters, although in five families the majority of the species are found in the bathyal zone. In the endemic abyssal fauna the Nuculanidae and the Malletiidae are dominating (about 41 % of the total number of species), followed by the Cuspidariidae, Pectinidae, Verticordiidae, Nuculidae and Poromyidae. These seven families form nearly 80 % of the total number of species.

A comparison is made between the composition of the abyssal fauna and the bivalve faunas of other areas: N.E. Atlantic, the Antarctic, the Arctic and the bathyal faunas of the New Zealand region and that of the Indian Ocean.

The majority of the families represented in the abyssal zone extend to the deepest part.

The endemic abyssal fauna has been assigned to 45 genera, while a total of about 1330 recent marine genera are believed to exist. With the exception of the new genus *Galatheavalva,* all the genera were represented in the overlying zones, and the majority of the genera are represented in the deepest part of the abyssal zone.

It thus appears that neither at the family level nor at the generic level does the abyssal fauna exhibit any independence.

This is in contrast to the conditions found in the abyssal holothurians where HANSEN (1967) found that higher taxa evolved wholly within the deep-sea. Several families are exclusively abyssal or with few species occurring in the deeper part of the bathyal zone. The order Elasipoda is confined to the deep-sea.

Apart from the new family and genus just referred to, the abyssal bivalve fauna is at present not known to contain any endemic family or genus.

A comparison between the abyssal bivalve fauna and those of the Arctic and the Antarctic indicates that the former has relatively little in common with the two latter, both at the family and at the generic level. It is suggested that the abyssal bivalve fauna originates from the warm water bathyal or sublittoral regions.

The known endemic abyssal fauna is believed to comprise 193 species, but this number is probably likely to be considerably increased as a result of future research. It is important to note that no less than 65 % of the known species have been recorded once only, and 86 % of the species have been recorded three times or less. Less than 6 % have been recorded ten times or more. Ten per cent of the species are known as valves only.

It is evident that the abyssal zone has a much larger number of species of bivalves than is found in either the Antarctic or the Arctic.

Three species of bivalves have been shown to have a cosmopolitan distribution in the abyssal zone *(Malletia cuneata, Acar asperula,* and *Arca orbiculata)* A number of examples of invertebrates having a corresponding distribution are mentioned. Three taxa *(Limopsis pelagica pelagica, Abra profundorum* and *Poromya tornata)* are found in the Atlantic Ocean extending eastwards, and have their eastern limit in the eastern part of the Indian Ocean or the W. Pacific. It is suggested that the three species just mentioned are represented in the E. Pacific by allopatric taxa *(L. pelagica dalli, A. californica, P. perla)*. Examples of invertebrates supposed to have a similar type of distribution are mentioned.

It is evident from this that to some species the central Pacific is not a barrier to distribution. Besides the cosmopolitan species mentioned above, *Spinula calcar* is found both in the E. and W. Pacific. To other species the C. Pacific may act as a barrier. The causes for this are unknown, but poor nutritional conditions may be responsible. Another factor could be the biological properties of the water itself, the bottom water of the N. E. Pacific being "old water", which could be less favourable for the developing embryos.

A more restricted distribution has been found in several bivalves. This may, however, be due to our still very incomplete knowledge of the abyssal bivalves. Future investigations will probably demonstrate that in general the abyssal bivalves have a wide, often even cosmopolitan, or Atlantic-W. Pacific distribution. Exceptions from this are species living in special isolated habitats as, e. g. the species of *Xylophaga*, which are confined to the restricted and patchy occurrence of plant debris.

The generally wide distribution proposed to be the rule in bivalves contrasts with the restricted distribution of several groups of invertebrates (Amphipoda, Isopoda, Cumacea, Ostracoda) in the abyssal zone. In these groups there appears to be a considerable degree of "basin endemism". A wide distribution occurs in several groups of invertebrates such as Echinodermata and Tunicata.

Bipolarity has been postulated to occur in the distribution of abyssal benthic invertebrates. No examples could be found among the bivalves. A number of examples from other groups are discussed and it is concluded that bipolarity in abyssal, benthic invertebrates is non-existent.

Most endemic abyssal bivalve species have their upper limit between 2000 and 3000 m depth. The known upper limit of the individual species varies greatly (to a large extent because of insufficient investigations). There is nothing to indicate a subdivision into an upper and a lower abyssal zone, but three species *(Spinula calcar, Limopsis galatheae* and *Myonera undata)* have their upper limit at about 4500 m depth and may indicate the presence of a faunal element confined to the lower half of the abyssal zone.

Based on a consideration of more than 1000 species of abyssal benthic invertebrates of different groups (the bivalves were not included), it has been suggested that with increasing depth there is an increasing percentage of endemism, i. e., species occurring in the deeper part of the abyssal zone have a more restricted distribution than species from the upper abyssal zone. This does not appear to be the case in the bivalves.

The known number of species of abyssal bivalves decreases with increasing depth, the largest number of species, 64, being known from the 3000-3500 m interval. The decrease in the number of known species is obviously consistent with the decrease in the number of hauls made with increasing depth. Of all abyssal hauls yielding bivalves, only 29 % have been executed at depth greater than 4000 m, which is the average depth of the world ocean. Recent quantitative investigations have demonstrated that there is no general decrease of the abyssal fauna directly correlated with increasing depth. Obviously, such factors as the availability of food exert a profound influence on the quantitative distribution of the abyssal fauna.

It has been suggested that in abyssal organisms the decrease with increasing depth is not uniform, but occurs in some depths more rapidly and abruptly than in others, and that in some depths certain animal groups show a maximum number of species. Such maxima could not be observed in the bivalves.

Certain species which are classified as "endemic abyssal" may in fact penetrate into the bathyal zone under certain circumstances. One example *(Acar asperula)* is discussed in some detail. These "extra-abyssal" occurrences are apparently correlated with upwelling of abyssal bottom water. Like the occurrence of abyssal "guests" from the bathyal zone, the "extra-abyssal" distribution of endemic species makes the border zone between the bathyal and abyssal zones less clear cut.

The available data on the temperature relationships of the abyssal bivalves show that most species seem to have an upper temperature limit between 3 and 4°C, but some species showing an extra-abyssal distribution may tolerate up to 10-12°C.

If temperature alone is the controlling factor, we might expect that arctic shallow-water areas would harbour at least some abyssal species. This is, however, not the case, which strongly indicates that there must exist an efficient ecological barrier other than temperature, separating the abyssal bivalve fauna of the world ocean from the arctic shallow-water fauna living under the same temperature conditions. Perhaps the hydrostatic pressure may be the responsible factor, but nothing is, in fact, known about its effect. Obviously, many abyssal bivalves tolerate a very wide range of pressure.

The present survey has not demonstrated any relation between bottom sediment and the distribution of bivalves. This does not mean that such a relationship is non-existent, but rather that a more refined analysis is required to demonstrate it. The abyssal bivalves probably play an important role in the re-working of abyssal sediments.

It has often been maintained that the abyssal zone contains elements of an archaic relic fauna. Eight of the 20 abyssal bivalve families originated in the Palaeozoic, seven in the Mesozoic, and five in the Cenozoic. From this a great antiquity of a large part of the abyssal bivalve fauna might be deduced. However, several of these families have shown a great stability throughout their geological history, and there is nothing against assuming that during any time of the geological history abyssal species could split off, while the main stock remained in shallow water. If the 44 abyssal genera are considered, 19 are either without any record or of Recent origin. Of the remaining three of are Palaeozoic, nine are Mesozoic, while 13 are Cenozoic. Since both the Palaeozoic and the Mesozoic genera are well represented in recent shallow water there is nothing to indicate that the abyssal species originated in the Palaeozoic or Mesozoic, but the descent could have taken place at any later time. The majority of the genera are Tertiary, indicating a Recent origin of a great part of the abyssal bivalve fauna. Possibly there has been a more or less continuous descent of shallow-water organisms into the abyssal zone throughout the geological history. It could be inferred that at certain times the descent has been more intensive than at others. Simultaneously, also an extinction of abyssal organisms could have taken place, and, perhaps on a modest scale, also speciation. The relative importance of these three processes has undoubtedly changed during time in accordance with changes in the ecological conditions. I think that the present composition of the abyssal bivalve fauna reflects the ecological conditions of the present time rather than the geological history of the world ocean.

The existence of specialized forms in the abyssal zone has been suggested by a number of authors. Some examples are mentioned here, but specialized forms within the bivalves are difficult to recognize, as there are few morphological clues to genetic affinity, and parallel trends are of frequent occurrence. Possibly the Septibranchoidea might be considered as directly descendants from the Nuculoidea, being adapted to a specialized carnivorous mode of feeding, but the group is by no means confined to the abyssal zone. Among the bivalves there is at present no evidence of an abyssal family or genus as extinct from the Recent shallow-water areas.

Intraspecific variation was studied in larger samples and was found to be great in *Acar asperula* and in the two subspecies of *Limopsis pelagica.* Other species showed a lesser variation. In several individual samples the whole range of variation of shell morphology could be observed. By comparison of specimens from widely separated localities no geographical variation could be observed, neither in the horizontal direction nor in a vertical direction. It thus appears that differences in hydrostatic pressure do not seem to affect shell morphology in abyssal bivalves. In other cases future taxonomic research may demonstrate the presence of polytypic species, such as suggested for shallow-water Echinoidea by MAYR (1954). A few possible examples of this are mentioned, but the material did not permit a closer study of this.

The mode of feeding in abyssal bivalves is to a great extent inferred from shallow-water members of the same families. Deposit feeders (mainly consisting of the Nuculoidea) form about 47 % of the known endemic abyssal species. Recent observations on shallow-water Nuculanidae indicate that in several species at least some suspension feeding takes place, but the relative importance of the two feeding methods is yet unknown. In an environment in which the food supply may be marginal over vast areas, the possibility of being able to switch over from one feeding method to another may be of ecological value. Another 25 % are believed to be suspension feeders and 25 % are carnivores.

The suspension feeders comprise such important groups as the Arcidae and Limopsidae, as well as the Mytilidae, Kelliellidae and some of the Pectinidae.

The carnivores consist of the Septibranchoidea and some of the Pectinidae. The stomach contents of some of the carnivores consisted mainly of smaller crustaceans.

An investigation of the size of the prodissoconch and eggs in some abyssal species confirmed an earlier suggestion of the dominance within the abyssal bivalves of a lecithotrophic development with a short pelagic larval life. Except for the *Xylophaga* spp. and *Galatheavalva,* both adapted to life in very special habitats, no case of brood protection was observed.

Gigantism, which has been proposed for some abyssal animal groups does not seem to occur in abyssal bivalves, although within some families the abyssal species are among the largest species known. The shells of the abyssal bivalves are generally delicate and non-spinose, with weakly developed sculpture.

The present examination of empty valves of abyssal bivalves confirms an earlier observation that boreholes of predators are rare.

Some of the abyssal bivalves are attached by a byssus. Attachment of *Acar asperula* to different kinds of substrata has been examined in some detail. *Arca orbiculata* has a very delicate byssus which may be used for anchoring the animal to hard bodies. In *Galatheavalva* the byssus penetrates into the tissue of the holothurian host. No shell-attached bivalves live in the abyssal zone, the existing records referring to displaced shallow-water valves.

Most of the epifauna observed on the shells of abyssal bivalves lived on four species having coarse shells with epidermal bristles. The epifauna was poor in species and specimens compared to that of some shallow-water bivalves. Corrosion was observed in several species. It could not be ascertained that the corrosion was due to some organism; it seems more likely that it is caused by some chemical process.

A list is given of displaced shallow-water valves which have been recorded as abyssal. These valves may have been transferred to the abyssal zone by means of turbidity currents.

The hadal bivalves. Eight new species from the hadal zone are described. The 18 hadal species are listed (Table 12), and in addition taxa referred to genus only (compiled from Belyaev, 1966) are given (Table 13). The eleven families recorded from the hadal zone are all known from the abyssal zone and the more shallow zones. The same applies to the 21 genera until now known to be hadal. It has been found that except for most boring forms, which have probably been transported down with the plant material, all the taxa assigned to species appear to be endemic. At the present time bivalves are known from 16 of the approximately 25 known trenches. The deepest bivalve recorded is *Phaseolus* sp. from the Tonga Trench, at a depth of 10,400 to 10,700 m. One species only is known from more than one trench. Species of the order Nuculoidea dominate in the hadal fauna, as is also the case in the abyssal fauna where they form about half of the known taxa. There appear to be no morphological structures which may be attributed to life in the trenches. More than half of the genera are of Tertiary origin and no known hadal genus dates back to the Palaeozoic. This indicates a recent origin of the hadal fauna.