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THE HYPERBENTHOS

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Abstract The hyperbenthos is a term applied to the association of small animals living in the water layer close to the sea bed. The species composition of the hyperbenthos is distinctly different from that of other benthic and planktonic groupings, and includes endemic species, planktonic species derived from their downward extensions (often with seasonal periodicity) and endo- or epibenthic species as they emerge into the water column (usually in diel cycles). In nearly all marine ecosystems investigated to date, there is a general increase in the biomass at the benthic boundary layer (hyperbenthon) relative to the water column immediately above it, yet the zone and its fauna remain relatively poorly studied. Sampling these often highly mobile animals is not easy as they are not collected efficiently by conventional benthic or pelagic samplers. A plethora of hyperbenthic sampling devices has been constructed and used with varying success. Typically, soft-bottom communities are sampled with sledges and hard substrata (including coral reefs) with traps. In recent years, there have been considerable developments in hyperbenthic research in the tropics (mostly coral reef lagoons), in temperate to cold-water coastal and shelf regions, and in the deep sea. Unfortunately, there is little or no mutual acknowledgement of results due partly to differences in terminology. For example, "hyperbenthos" and "suprabenthos" are used mainly in temperate and northern areas, whereas "demersal zooplankton" and "benthopelagic plankton" are preferred to designate the same fauna in tropical areas and the deep sea respectively. Semantic agreement is needed to enable more progress in understanding the role played by this group of animals in ecosystem functioning. The aims of this review are to summarize the disparate literature on the hyperbenthos, to bring some order to the terminology associated with this group and to stimulate more interest for this fauna.

Introduction

Throughout modern times, the macrofauna occupying the water layer adjacent to the bottom of the sea has been a focus for commercial exploitation, yet relatively little attention has been paid to the smaller animals inhabiting the same biotope (i.e. the potential prey species of the exploited fish and crustacean stocks and/or their pre-recruits). This association of small animals is referred to here as the hyperbenthos. Recently, there has been increased interest in the hyperbenthos and questions are now being asked to identify the role of this group in the functioning of marine ecosystems. This increased interest has been led by fisheries biologists who report that many demersal fish and epibenthic crustaceans feed, for at least part of their life, on the hyperbenthos (as observed from stomach content analyses). Furthermore, there is renewed interest in pre-recruit studies (e.g. Simard et al. 1990, McCall & Fleeger 1995) and many larval and early post-larval fish and crustaceans have a hyperbenthic life style. There is also growing interest in benthic–pelagic coupling (for the development of carbon-flux models) and studies of energy fluxes through marine environments rarely include samples taken within a few centimetres of the sea bed and may, therefore, underestimate significantly the flux of particulate material. Finally, mysids, a major component of the hyperbenthos, are used increasingly in aquaculture, and in ecotoxicology and pollution studies (e.g. Laughlin & Linden 1983, Brandt et al. 1993).

Some studies of the hyperbenthos of tropical, temperate to cold-water and deep-sea environments have been reported, however, there is little or no mutual acknowledgement of these respective efforts (Sainte-Marie & Brunel 1985). This lack of synthesis may be attributed partly to differences in terminology. For example, the same group of animals is referred to as "demersal zooplankton" in the tropics, and as "hyperbenthos" or "suprabenthos" at higher latitudes; deep-sea workers prefer the term "benthopelagic plankton" and refer to the zone as the "benthic boundary layer". Vast geographical regions and habitats where hyperbenthic animals may be expected to occur abundantly, and thus play an important role in benthic–pelagic coupling, have not been sampled. This review synthesizes the disparate literature on the hyperbenthos, and summarizes the main structural features of hyperbenthic communities, the history of hyperbenthic research and the sampling methodologies used. Since most published information relates to temperate and cold-water environments, there is an unavoidable bias to these areas, however, selected recent key studies of tropical and deep-sea hyperbenthic research are included. Further information on the early research, sampling methodology and the structure of the hyperbenthic communities in these latter environments may be found in the cited papers. Functional relationships of the hyperbenthos are also touched upon briefly, although no attempt to review the extensive literature on the biology of the constituent taxa was made; no unpublished theses or reports are included in the review. For ease of comparison, all densities are, where possible, expressed as numbers of individuals per 100 m^3.

Terminology and definitions

Generally, the term "benthos" is used as a descriptive term for the entire bottom community and the "benthic boundary layer" relates to the immediate physical environment of the benthos (McCave 1976). The marine benthos may be divided, however, on size (into macro-, meio-, and microbenthos) and on position relative to the sediment/water interface (into endobenthic and epibenthic) (Pearson & Rosenberg 1987). Following the principles behind this terminology, the group of animals occupying the uppermost benthic layer should be called the hyperbenthos and the zone they occupy the hyperbenthon. There are two arguments in favour of using the term hyperbenthos in preference to the frequently used term suprabenthos. The first is etymological; a noun derived from Greek (benthos) should be preceded by a Greek prefix (hyper-) rather than by its Latin equivalents (supra-, super-). The second argument is historical. Beyer (1958) was the first to use the term hyperbenthos to describe those animals that occupied the lower layers of the water column during different periods of their life or at different times of day, but which retained some contact with the substratum. Boysen (1975a) defined the transitional zone between the zones occupied by the benthos and the plankton as the hyperbenthal, and identified that the hyperbenthos was not delimited clearly in space but represented a meeting of animals from two neighbouring "Lebensräume" (the plankton reaches the sea bed during its diurnal migration and the endobenthos rises to this or an even higher level in the water column). Planktonic organisms (mostly mysids) that lived within one metre of the bottom were referred to as "hypoplankton" by Fager et al. (1966) and this term was adopted by several authors (e.g. Mauchline 1972). The term "suprabenthos", introduced probably by Friedrich (1969), was later defined as all the swimming, bottom-dependent animals (mainly crustaceans) which perform, with varying amplitude, intensity and regularity, seasonal or daily vertical migrations above the sea floor (Brunel et al. 1978). These workers preferred the term suprabenthos to hyperbenthos simply because they felt that the latter term would be confusing and would imply "more than benthic" rather than "above the benthos" (Brunel et al. 1978); the term suprabenthos has been adopted by many authors (e.g. Kaartvedt 1989, Sorbe 1989). "Benthopelagic plankton" and "benthic boundary layer macrofauna" have been used to describe the hyperbenthos in deep-sea studies (e.g. Marshall & Merrett 1977, Wishner 1980a,c) but these terms are rarely used in studies of shallower areas (but see Wildish et al. 1992). "Resident", "swarming" or "demersal zooplankton" have been used mainly for tropical hyperbenthos (e.g. Emery 1968, Hamner & Carleton 1979, Alldredge & King 1985). The mobile component of the hyperbenthos, especially mysids, has often been referred to as "micronekton" (e.g. Andersen & Sardou 1992) or "nektobenthos" (Greze 1951, Salemaa et al. 1990, Simm & Kotta 1992) and fish larvae are sometimes grouped as "ichthyoplankton". Wang & Dauvin (1994) and Wang et al. (1994) make a distinction between the "permanent hyperbenthos" (mysids, cumaceans, decapods, amphipods, isopods and pycnogonids) and "near-bottom zooplankton" (subdivided into mesozooplankton: copepods, crustacean larvae, chaetognaths, polychaete larvae; and macrozooplankton: ctenophores and post-larval fish). Micronekton, ichthyoplankton and mesozooplankton are all terms commonly in use in the study of pelagic plankton communities. Other terms used for the same faunal assemblage include "semiplanktonic animals" (Sentz-Braconnot 1967) and "motile epibenthos" (Kritzler & Eidemiller 1972). For consistency, the term hyperbenthos should be used for all animals which spend part or all of their lives in association with the sea bed, the term "merohyperbenthos" applied to those that spend only part of their early life history in the hyperbenthos and recruit to the nekton, epibenthos or endobenthos, and "holohyperbenthos" for animals that spend variable periods of their adult life in the hyperbenthos (Hamerlynck & Mees 1991). Further classification, based on size, dividing the fauna in "macro" – (larger than 0.5 mm or 1 mm) and "meiohyperbenthos" (larger than 32 μ, 45 μ or 63 μ and smaller than 500 μ or 1000 μ) is also recommended.

Thus, the hyperbenthos comprises a broad assemblage of diverse forms related only by their distribution in space and not by phylogeny or exclusively functional attributes (Day et al. 1989). Many move position erratically or regularly, at specific times of the day or year, or at certain life-history stages. For example, some endobenthic animals emerge from the sediment for varying lengths of time and epibenthic animals also swim regularly [their behaviour ranges from haptic (referring to organisms that are normally continuously moving, but which attach themselves to the substratum when scared) to hemisessile (referring to the opposite behaviour)]. Nevertheless, the fact that the hyperbenthos spend part or all of their lives in association with the bottom is a unifying feature. In analogy with the fact that many organisms are so flexible in their diet that trophic relations and levels change seasonally, ontogenetically and geographically, the benthic sub-communities are subject to fluctuations and to the occurrence of borderline members. Still, the hyperbenthos may be considered as a true community (locationally defined, i.e. referring to all organisms within the stratum or habitat) as "a group of organisms occurring together, many of which will interact within a framework of horizontal and vertical linkages" (Giller & Gee 1987). Depending on the location of the animals in relation to the water/sediment interface, the benthos may be divided into three compartments: endobenthic, epibenthic and the hyperbenthic fauna. Further divisions of these main benthic compartments are defined taxonomically.

Methodology

Studies of the distribution and abundance of medium-sized marine fauna have been performed mainly by sampling gear constructed to catch either planktonic or benthic animals (reviews in UNESCO 1968, Eleftheriou & Holme 1984). The often highly mobile animals that live immediately above the bottom are caught only occasionally by such sampling gear and specific sampling devices have to be used to sample the hyperbenthos effectively. The choice of equipment depends largely on local conditions (e.g. size of the ship, power and capabilities of the lifting gear, degree of exposure, depth of the water column, bottom conditions and the type of sample that is required for the specific research topics that are investigated) (Eleftheriou & Holme 1984), and many of the various sledges and traps produced to sample the hyperbenthos have been designed to meet local requirements. Hence, there is at present no need to standardize the gear for sampling the hyperbenthos and the following represents a summary of the gear currently used.

Sampling soft-bottom communities

Intertidal collections

Marine and estuarine intertidal areas can be sampled quite satisfactorily by a variety of hand-held dip nets or push nets (e.g. Jansen 1985). Small sledges, operated at a standard speed and for a fixed length of time, can also produce replicable data (Mauchline 1980, Takahashi & Kawagushi 1995). Colman & Segrove (1955) designed a light, man-hauled, two-level sledge. Mauchline's hand-pulled D-net (Mauchline 1980), or modifications thereof (e.g. Miller 1973), catch mysids efficiently. Standing nets have been used to sample tidal marsh creeks (Cattrijsse et al. 1994).

Remote collections

Heavier and more robust equipment is required to sample neritic habitats. Typically, sledges, consisting of plankton nets mounted in frames towed over the surface of the sediment, are designed to sample at least the lower one metre of the water column such that no contamination of the sample with sediment occurs and can only be used when the bottom is relatively even. An extensive summary of the early epi- and hyperbenthic sledges is given by Bhaud (1979). The most primitive design, used successfully by several researchers, consisted of small-meshed nets fixed to Agassiz (Russell 1928) or otter trawls (Brunel 1979). There are many examples of small, simple sledges (Isaac & Kidds 1953, Lacroix & Bergeron 1962, Sentz-Braconnot 1967, Hamerlynck & Mees 1991). Several lines of development, mainly the addition of opening and closing mechanisms and multiple nets, evolved from these early designs. In relatively shallow areas, no closing mechanism is required as the error introduced by sampling during recovery is assumed to be small (Oug 1977). Sledges with an opening and closing mechanism are preferred for sampling at greater depths since they ensure collection of the targeted fauna (Bossanyi 1951, Greze 1951, Wickstead 1953, Beyer 1958, Frolander & Pratt 1962, Clutter 1965, Macer 1967, Bieri & Tokioka 1968, Omori 1969, Poirier et al. 1969, Bhaud 1979, Sorbe 1983). Usually, opening is triggered mechanically on first contact with the bottom or by a messenger (Beyer's sledge). Accoustically-operated mechanisms have also been described (Aldred et al. 1976). A modified Rothlisberg & Pearcy (1977) sledge, used by Buhl-Jensen (1986), was later equipped with a pneumatic opening and closing device (Fossa et al. 1988). Beyer's epibenthic sledge (illustrated in Holme 1964) was modified (Oug 1977) to sample at different levels in the water column. The light-weight Macer sledge (Macer 1967), rarely used (but see Williams & Collins 1984), was enlarged and modified as the Macer-GIROQ sledge (Brunel et al. 1978) and later again by Dauvin & Lorgeré (1989). After these alterations, it has been quite popular and successful. Presently, multi-level nets are most commonly used (Fager et al. 1966; Dragonet II of Bieri & Tokioka 1968; the modified Beyer sledge of Oug 1977; Macer-GIROQ sledge of Brunel et al. 1978; Sorbe 1983; Hamerlynck & Mees 1991). Diver-pushed nets have been described (Fager et al. 1966, Kritzler & Eidemiller 1972, Potts 1976) and passive fishing with fixed nets can be used in strong currents (Falconetti 1975, Vaissière & Falconetti 1975, Falconetti & Seguin 1977, Sorbe 1981b). Modified sledges with stimulation devices like a tickler chain (Ockelmann 1964) and water-jet or electric currents (Turnbull & Watson 1992) sample the hyperbenthos, along with epibenthic animals and animals buried in the sediment surface.

Sampling over hard substrata

Hard substrata are logistically difficult to sample. For example, most of the conventional sampling gear used to capture hyperbenthos in the open ocean is ineffective on coral reefs as deploying boat-towed devices is extremely difficult in that environment. A host of unique alternative sampling devices has been developed, including anchored swivel nets (Johannes et al. 1970, Vaissière & Seguin 1984), diver-pushed nets (Emery 1968, Hobson & Chess 1978, Hamner & Carleton 1979), nets pushed by underwater vehicles (Schroeder 1974, Potts 1976), suction samplers and airlifts (Emery 1968, Rützler et al. 1980), hand pumps (Metaxas & Scheibling 1994), light traps (Emery 1968, Sale et al. 1976, 1978, Kawagushi et al. 1986), photographic sampling techniques (Hamner & Carleton 1979), emergence traps (Youngbluth 1982), re-entry traps (Alldredge & King 1980, Stretch 1985) and baited traps (e.g. Christiansen et al. 1990). Recently, Setran (1992) described a promising new intertidal trap, and a remotely-operated, bottom-closing drop net to capture mysids over uneven bottoms was described by Lasenby & Sherman (1991). An efficient diver-operated device, utilizing the escape response of motile animals that live up to one metre above the bottom, was used by Carleton & Hamner (1987).

Other methods of sampling

Direct observation by SCUBA diving can be employed for behavioural studies and for assessing the efficiency of sampling gear. Television cameras mounted on sledges may also prove useful to study the hyperbenthos (Holme 1984). An underwater camera, used in association with sledge sampling, provided the opportunity for quantitative comparisons between estimates of population density by photography and actual net catches (Aldred et al. 1976, Rice et al. 1982). Fast-moving animals are seldom seen in photographs (Holme 1984) and the main use of photography seems to be in the assessment of the behaviour of the fishing gear. Indirect methods, such as stomach content analyses of fish, may show the presence of otherwise unreported species and stomach content analysis has been used frequently to describe the bathymetric distribution of deep-living hyperbenthic mysids (Mauchline 1982, 1986, Astthorsson 1984, 1985). High-volume pumps (Sibert 1981, Jahn & Lavenberg 1986) and cooling intakes of nuclear power stations (Moore et al. 1979) can yield information at fixed locations. High-speed plankton samplers and WP2 plankton nets with a large mesh have been used to sample mysids in estuaries (Sorbe 1981b, Williams & Collins 1984), and wheeled Bongo nets are efficient at catching fish larvae (Brewer & Kleppel 1986). Cages lowered to the bottom (Van Cleve et al. 1966), or smaller throw, drop or pull-up traps can also be used (Holme 1984). High-frequency sonars can be used to locate near-bottom scattering layers in the deep sea (Wishner 1980b) and in shallower areas (J. Mees unpubl.).

Efficiency and selectivity of samplers

As mentioned previously, most of the hyperbenthic samplers were designed for specific objectives and for sampling in specific areas, and have met with varying degrees of success and acceptance. A device that can sample hyperbenthic animals quantitatively has yet to be constructed; however, "satisfactory" samples can be taken with plankton nets mounted on sledges. In general, the use of other samplers is based on convenience and on the premise that "it appears to do a better job than others" (UNESCO 1968).

Little information is available on the capture efficiency of hyperbenthic sledges, and a general flaw of most is that they do not sample the lowermost centimetres of the water column. Using a combination of sledge sampling and aquarium observations, Fossa (1985, 1986) showed that mysids may have the highest abundance at or just a few centimetres above the bottom. Huberdeau & Brunel (1982) showed that the Macer-GIROQ hyperbenthic sledge sampled a specific fauna but added that no information was obtained from the lower 28 cm of water column, which may be very rich. Hesthagen & Gjermundsen (1978) assessed the replicability of Beyer's sledge and concluded that replicable samples were possible, although some difficulties arose when deciding which organism belonged where. Using the same data, Schnack (1978) concluded that the replicability of the results obtained by the Beyer's sledge was satisfactory for many groups of animals and density estimates had a similar precision to those of net tow samples in plankton studies. Huberdeau & Brunel (1982) compared the performance, efficiency and selectivity of the Macer-GIROQ sledge with endo- and epibenthic samplers, and reported that the former equipment sampled a very distinct fauna. The replicability of a modified Rothlisberg and Pearcy sledge was tested by Brattegard & Fossa (1991) who reported an acceptable level of replicability for number of individuals and of spread of individuals over species. Thus, if time and money are limited and only one haul is taken at a given station, it is highly probable that the sample will be representative.

Youngbluth (1982) compared three traps for sampling the hyperbenthos (demersal zooplankton); the Alldredge and King trap caught 238 (± 13) $\mathrm{ind.m^{-2}h^{-1}}$, the Hobson and Chess trap 138 (± 23) and the Porter and Porter trap 70 (± 8). Density and species composition depended on the distance between the bottom and the base of the trap, and on the porosity of the trap walls (Youngbluth 1982). Madhupratap et al. (1991) found that direct sampling of demersal zooplankton with a corer yielded densities about 25 times higher than those estimated with emergence traps and that up to 80% of all organisms present in the sediment emerged. Mysids have been observed to avoid capture by swimming in front of trawls (Lasenby & Sherman 1991). Carleton & Hamner (1987) designed a diver-operated trap for mysids which utilized the escape response of the animals. Near-absolute density estimates seem possible with this trap as over 90% of all mysids were taken with only two sweeps. Testing several other sampling methods in a coral reef lagoon, Carleton & Hamner (1987) found their density estimates were several orders of magnitude higher than those obtained with towed devices. For example, in a first trial, the trap took 786, a sledge took 11.7 and a towed plankton net 0.7 $\mathrm{ind.m^{-3}}$; in a second trial, 109 $\mathrm{ind.m^{-3}}$ were caught with the trap versus 22, 6.2 and 1.3 with a sledge, a towed net and a diver-pushed net respectively.

Until more data on field performances are available it is not possible to give a rating for the efficiency of hyperbenthic samplers. It is possible, however, to make some general recommendations. It is advisable to install an opening-closing mechanism, especially when operating in deeper waters. The sledge should be equipped preferably with both an odometer and a current meter, so that densities can be reported per volume of water filtered and per surface area of sea bottom trawled. Mesh sizes of 0.5 mm are the rule, however, in areas where risk of clogging is high a mesh size of 1 mm is acceptable. Towing speed should always be as low as possible.

Treatment and sorting of samples

Unlike other benthic samples, a hyperbenthic sample does not require the extraction of the animals from a large volume of sediment. No initial reduction of sample volume needs to be carried out in the field. Satisfactory preservation is achieved with 4 to 10% buffered formalin (formaldehyde in sea water, with a concentration depending on the water volume of the sampled material). Sorting is a very time-consuming task that may restrict severely the extent of the sampling programme. In areas with high levels of suspended detritus, bulk staining of samples with vital stains (usually rose bengal) can be used to facilitate sorting. Different groups of animals can be stained to different extents by adding an aqueous solution of phenol to the rose bengal (Hesthagen 1970).

For samples containing large quantities of detritus, a counterstaining technique described by Williams & Williams (1974) (the primary stain, rose bengal, is counterstained with chlorazol black E, yielding a high colour contrast) allows improved sorting. Staining with rhodamin B causes the animals to fluoresce when examined under longwave ultra-violet light (Hamilton 1969). Eosin or Lugol's iodine can also be used (Eleftheriou & Holme 1984).

Hyperbenthic communities

Marine hyperbenthic research is a young discipline that commenced at the beginning of this century and the first speculations on the ecological significance of the hyperbenthos did not occur until the late 1950s (Bossanyi 1957, Beyer 1958). In this section, the history of hyperbenthic research is summarized in a more or less chronological order.

Bottom plankton: the roots of hyperbenthic research

By the end of the 19th century, the ineffectiveness of the commonly-used grabs, dredges and trawls to catch small and agile animals had been noted by several researchers who suspected that not even the combined use of all types of ordinary equipment allowed an adequate assessment of the composition of the fauna of soft bottoms (Sars 1870, 1895, 1903, Hjort & Dahl 1900). Sars (1870, 1895, 1903) used various alternative sampling methods, including baited traps, the attachment of "surface nets" or "fine hand nets" to the dredge rope a short distance from the dredge and "a very light dredge, by which only a small portion of the superficial bottom-material is taken up". The latter apparatus (probably the very first hyperbenthic sledge) was not described in detail but was supplied with a bag of fine gauze and mounted on a pair of runners (Sars 1870). Hjort & Dahl (1900) applied a bag of embroidery net to the terminal part of the cod end of an otter trawl. These early collections were made primarily for the purpose of collecting and describing new species. Other collecting gear, mostly light dredges or sled nets without closing devices, were used for qualitative studies by a number of workers (Reighart 1894, Hensen 1895). The animals that escaped were mainly crustaceans (ostracods, copepods, isopods, amphipods, mysids, male cumaceans, and larval and post-larval decapods).

In the first half of this century, scientists recognized and investigated explicitly what they called the "bottom plankton". Early collections, made with fine nets mounted on or inside trawl nets (e.g. Russell 1928), were made off the coasts of Ireland (Holt & Tattersall 1905, Calman 1906, Tattersall 1906), in the English Channel (Russell 1928, 1931, 1933, Tattersall 1938) and off New England (Wilson 1932). Russell (1925, 1926) was probably the first to recognize the importance of the hyperbenthos (although he did not coin a specific term for the zone or the fauna). In the course of extensive researches on the vertical distribution of plankton in the Plymouth area (English Channel), Russell (1925, 1926) found that day-time plankton samples from different depths differed both in quantity and quality (with increasing depth a sudden increase in plankton abundance was observed "which existed nearly to the bottom" and in deeper layers species appeared in the catches that were not represented in the collections from the layers above). It became evident that the fauna very close to the sea bottom had to be sampled properly. This led to the construction of the first semi-quantitative hyperbenthic sampler described in the literature: a fine meshed tow net that could fish inside an Agassiz trawl as it was dragged along the bottom, in a way to only catch animals that swim just above the bottom (Russell 1928). Subsequently, mysids, post-larval fish, chaetognaths and copepods were found to be living very close to the bottom in day-time and Russell (1928) predicted that "it is quite to be expected that in course of time many young stages of animals that have been rarely caught will appear in greater quantity in such collections". Tattersall (1938) used the same net to study the mysid fauna of the same area and concluded that species-specific diurnal, seasonal and ontogenic migrations were common and that "idly swimming just above the bottom" was a normal feature of these animals' lives. Early collections of the bottom plankton in the intertidal were made with tow nets around the same time (Elmhirst 1932, Watkin 1939, 1941: see below).

Simple sledges with or without a closing mechanism were constructed later (Beauchamp 1932, Elster 1933, Walford 1938, Werner 1938). In the early 1950s more elaborate plankton trawls, fitted with opening and closing devices to obtain uncontaminated samples from the bottom layers in deeper waters and intertidal areas, were devised (Bossanyi 1951, Greze 1951, Wickstead 1953, Colman & Segrove 1955). Around this time the "small natant fauna immediately above the sea floor" was seen as an ecological entity and its importance in the diet of fish was recognized, leading to increased interest (Bossanyi 1957). The fauna was found to be diverse and to reach high densities, and Bossanyi (1957) stated that it "undoubtedly plays an important role in the economy of the sea". Although this fauna was usually included in the plankton at this time, Smidt (1951) distinguished the "true benthos" that lived permanently on the bottom, from the "nekto-benthos" which comprised species that occurred both on the bottom and in the water column.

The hyperbenthos as defined by Beyer

Beyer (1958) designed a sledge (described in Holme 1964) to study the bottom plankton populations of the Oslofjord (Norway), and reported a preponderance of a new species of Trachymedusae and otherwise rarely-encountered calanoid copepods. As species that were known generally as plankton were found in much higher concentrations near the bottom, Beyer (1958) concluded that "whatever the reason for the remarkable proximity of the bottom plankters to the sea bed, they should, in accordance with the view held (at that time by Shelford & Boesel 1942, Jones 1950), be considered functional members of the soft bottom animal community whilst they remain in the vicinity of the soft bottom". Beyer (1958) continued that they "thus constitute, together with members of the nekton, the uppermost, *hyperbenthonic* subdivision of the biocoenosis". In addition to using the term hyperbenthos, Beyer (1958) introduced the term hyperpelos to designate those organisms that live just above the mud [by analogy with the terms endopelos and epipelos, referring to animals living in and on the mud, respectively (terms introduced by Remane in 1940)] and distinguished tychobenthonic (<Gk *tycho* accident) from hekobenthonic (<GK *hekon* voluntary) components of the hyperbenthos. The former are basically pelagic species (plankton or nekton) which, due to

negative phototropism, are "accidentally" found in the hyperbenthal (depth-loving animals that are found in the vicinity of the bottom because the bottom happens to be there), while the latter are the true members of the benthonic community or those animals that join it on purpose (animals that are in some way related to the bottom).

Later quantitative field studies

Since the pioneering work of Beyer (1958), several studies of hyperbenthic communities have been published; however, comparison and synthesis of these results is not straightforward for various reasons. A first problem is the arbitrary elimination of species from the species lists (usually on the subjective basis that they do not belong to the hyperbenthos). Secondly, densities are expressed either per unit volume of filtered water or per unit area of trawled surface. Finally, the composition of the species lists depends on the methods used for collecting. In the following sections, emphasis is placed on the gross taxonomic composition, on reported densities and on the general patterns in vertical distribution and seasonality of the hyperbenthos.

Estuaries

As with other faunal comparisons, estuarine hyperbenthic communities have fewer species than their marine counterparts. The hyperbenthos of the St Lawrence Estuary (Dodson et al. 1989, Dauvin & Dodson 1990), and several European estuaries such as the Gironde (France), the Westerschelde (The Netherlands) and the Ems (The Netherlands) (Sorbe 1981b, Mees et al. 1995) have been studied in detail. Sorbe (1981b) reported that the Gironde Estuary had high hyperbenthic densities (e.g. summer mysid densities >300 ind. m^{-3}) and that different salinity zones were characterized by a specific fauna. In addition to estuarine endemics, various freshwater and marine animals were present (Sorbe 1981b). Williams & Collins (1984) sampled the mysid fauna of the Bristol Channel and Severn Estuary with a high-speed plankton sampler and a Macer sledge. Their results showed that *Schistomysis spiritus* peaked in September at a density of 14 m^{-3} (250 m^{-2}) and this constituted 76% of the omnivore biomass. Over one year, *S. spiritus* contributed 43% of the total integrated omnivore standing stock. Mysid abundance was correlated mainly with temperature and salinity (which are subject to seasonal change) and species occurred in well defined salinity zones (Williams & Collins 1984). Greenwood et al. (1985) and Jones et al. (1989) sampled the mysids close to the bottom of the Avon–Heathcote Estuary (New Zealand) with a weighted plankton net and reported densities ranging from 20 to more than 1500 mysids 100 m^{-3}; these authors also found species to be separated along the salinity gradient. The same conclusion of mysid distribution and salinity was reached by Mees et al. (1993a,b, 1995) in studies in the Ems, Westerschelde and Gironde estuaries. In the marine reaches of these European estuaries, generally fewer than 600 ind. 100 m^{-3} were recorded, while in the oligohaline part densities were an order of magnitude higher (e.g. a summer peak of 31 250 ind. 100 m^{-3} for the Westerschelde, Mees et al. 1995). Annual mean densities for two stations in the Westerschelde amounted to 60 ind. 100 m^{-3} in the marine part (ranging from 2 in winter to 190 in spring) and 3000 ind. 100 m^{-3} in the brackish part (ranging from 30 in May to 8450 in April). In the River Tamar Estuary (England), densities of *Mesopodopsis slabberi* increased from less than 5000 ind.

$100\,m^{-3}$ in spring to more than 100 000 in summer, while *Neomysis integer* reached 20 000 ind. $100\,m^{-3}$ in June (Moffat & Jones 1992).

Intertidal areas and beaches

Data on intertidal hyperbenthic communities are very scarce. Some papers report the vertical movements in intertidal waters and early plankton collections with tow nets at the edge of sandy beaches showed that certain species of amphipods swim to the surf zone during the night (Elmhirst 1932, Watkin 1939, 1941). A distinction can be made between local endobenthic species that perform active nocturnal vertical migrations and tidal migrants carried in from sublittoral habitats by the tide. A light, man-hauled two-level bottom sledge, developed by Colman & Seagrove (1955) for intertidal collection, showed that amphipods, mysids and decapods dominated the fauna of a sandy beach in summer. Other taxa included isopods, cumaceans, copepods, pycnogonids, polychaetes and gastropods; few endobenthic species, known to occur in the area, were found and species which were thought previously to inhabit the sand were found to swim for 1/2 to 1/283 of the time that the beach was covered with water (Colman & Seagrove, 1955). The same swimming range was reported by Watkin (1939, 1941). For some species, sex ratios differed in and above the sand and species-specific small-scale vertical zonations were noted. An improved version of this sledge was used to study amphipods in the surf plankton (Fincham 1970). Clear seasonal variations in numbers were again reported, with spring (Elmhirst 1932) or summer (Fincham 1970) maxima. Wooldridge (1983, 1989), San Vincente & Sorbe (1993) and Takahashi & Kawagushi (1995) used sledges to sample the surf zone of sandy shores in South Africa, France and Japan, respectively. In all areas, mysids overwhelmingly predominated the fauna. Densities of the dominant mysid species often exceeded $15\,ind.\,m^{-2}$ on South African beaches. In France, densities of the dominant mysid ranged from 2 (winter) to almost $100\,ind.\,m^{-2}$ (summer); in Japan from $80\,m^{-2}$ (winter) to more than $5000\,m^{-2}$ (summer). Munilla Léon & Corrales (1995) sampled the hyperbenthos of a Mediterranean beach (1 m depth) with a small hand-pulled sledge. Here mysids (27%) and amphipods (23%) dominated the fauna, followed by copepods (16%), post-larval fish (12%) and isopods (7.3%). Total hyperbenthic density was less than $6\,ind.\,m^{-2}$. Migrations of various crustacean groups have been reported over rocky shores (Jansson & Källander 1968) and seagrass beds (Ledoyer 1964) with marked day and night differences. Sibert (1981) provided a detailed study of the spring intertidal hyperbenthos ($>100\,\mu m$) in the Nanaimo Estuary using two pumps at 5 cm and 30 cm above the bottom. Total densities ranged from 400 to $14\,000\,ind.\,m^{-3}$; the dominant taxa were harpacticoid, calanoid and cyclopoid copepods (in several life history stages), various categories of meroplankton, and nematodes; isopods (50–9600 $100\,m^{-3}$), mysids (0–2300 $100\,m^{-3}$), amphipods (200–2000 $100\,m^{-3}$) and cumaceans (40–2600 $100\,m^{-3}$) were also represented in smaller numbers (Sibert 1981). Consistently large differences in population density were observed between the two levels; in the bottom samples densities always exceeded those in the top samples by a factor between 2 and 20 (Sibert 1981). Metaxas & Scheibling (1994) sampled the meiohyperbenthos ($>60\,\mu$) of tide-pools on a rocky shore in Nova Scotia (Canada) with a handpump. Calanoid and harpacticoid copepods, cladocerans, foraminiferans, rotifers and nematodes dominated the fauna. Total hyperbenthic densities were generally lower than $1000\,ind.\,m^{-3}$ in winter and spring, but increased up to $10^7\,ind.\,m^{-3}$ in summer. Cattrijsse et al. (1994)

studied the hyperbenthos that entered and left a creek in a brackish tidal marsh (Westerschelde estuary) using a stow net modified after McIvor & Odum (1986). Monthly samples over 2 yr showed a density range from 10 (winter) to 30 000 (summer) ind. 100 m^{-3}; mysids, amphipods, isopods, and post-larval fish, shrimp and crabs dominated the fauna (Cattrijsse et al. 1994). The mysids, amphipods and isopods were discussed in detail by Mees et al. (1993a) and Cattrijsse et al. (1993). Peak densities of the mysids *Neomysis integer* (24 000 ind. 100 m^{-3}) and *Mesopodopsis slabberi* (20 200 ind. 100 m^{-3}) were observed in early summer and autumn respectively.

Rocky substrata in shallow water

Except for a few papers reporting the performance of new sampling gear, hardly any information is available on the hyperbenthos of hard substrata other than coral reefs. For example, Potts (1976) described a diver-controlled plankton net and Lasenby & Sherman (1991) tested a bottom-closing drop net at depths ranging from 7 m to 27 m in Lake Ontario and caught 50–300 mysids m^{-2}. The same apparatus was used in a shallow (0.1–2 m) lake in New Zealand, where densities up to 800 mysids m^{-2} were reported close to the shore (Lasenby & Sherman 1991). On the California coast, preliminary intertidal collections with a new trap recorded calanoid and harpacticoid copepods, gammarid and caprellid amphipods, mysids and larval crabs (Setran 1992).

Shallow coastal and shelf areas

Using a two-level sledge to a depth of 100 m, Bieri & Tokioka (1968) sampled quantitatively the hyperbenthos of Tanabe Bay (Japan). Gammaridean amphipods occurred in densities up to 80 000 ind. 100 m^{-3} in the water layer from 0–20 cm above the bottom, while the water layer from 20–40 cm above the bottom never contained more than 500 ind. 100 m^{-3}; the same density trend was observed for subdominant groups like mysids (3300 and 50), copepods (7600 and 150), cumaceans (1900 and 0) and decapod larvae (4300 and 100) (Bieri & Tokioka, 1968).

Hesthagen (1970) used a Beyer sledge to a depth of 300 m over the Great Meteor (8 samples) and Josephine seamounts (7 samples), and reported that copepods dominated the fauna; polychaetes, ostracods, decapods and mysids were also abundant. Total hyperbenthic densities ranged from 81 to 3400 ind. 100 m^{-3}. Hesthagen (1973) made the first extensive study on the diurnal and seasonal patterns in the hyperbenthic community of the deeper channels (30 m) of the Kiel Bight. Generally, cumaceans dominated the fauna at densities ranging from 300 (winter) to 26 000 (summer) ind. 100 m^{-3}; subdominant groups were mysids (including many rare and new species), copepods and chaetognaths, at densities rarely exceeding 1000 ind. 100 m^{-3}; representatives of various rarer taxa (coelenterates, cladocerans, isopods, pycnogonids, post-larval fish, amphipods, euphausiids and decapods) were also collected (Hesthagen 1973). Seasonal variations in the Kiel Bight hyperbenthos were investigated further by Boysen (1975a, b, 1976), who reported an annual average (monthly samples in 8 stations from 8 m to 25 m water depth) hyperbenthic density of 1600 ind. 100 m^{-3}; marked seasonality was observed for several groups with maximal densities in February–May and again in September, and minimal densities in December. Regional differences in faunal composition were correlated with (a) sediment type (amphipods were dominant over sand, while cumaceans and polychaetes were found over mud), (b) depth (isopods and fish larvae tended to occur in the shallower stations, mysid species were found to be segregated bathymetrically) and (c) dissolved oxygen concentration (especially important for mysid distribution) (Boysen 1976). Diurnal variations at the Kiel Bight (30 m) were studied by Hesthagen & Gjermundsen (1979). The summer fauna was dominated by one polychaete species (400–1500 ind. 100 m^{-3}), one cumacean (1000–4000 ind. 100 m^{-3}) and one chaetognath (100–700 ind. 100 m^{-3}). Day–night differences consisted mainly of changes in density patterns of cumaceans, mysids, and caridean and paguroid larvae. The former group was present mainly in night catches while all other groups were restricted largely to day catches (Hesthagen & Gjermundsen 1979). Although the existence of a hyperbenthic community in the area was disputed by Anger & Valentin (1976), whose criticism was based on doubts concerning the adequacy of the sampling methodology, subsequent work has confirmed its presence (e.g. Hesthagen & Gjermundsen 1978, Schnack 1978, Huberdeau & Brunel 1982).

Using a modified Beyer sledge (fitted with three nets, to obtain simultaneous, overlapping samples) in a shallow (22–24 m water depth), land-locked fjord on the west coast of Norway, Oug (1977) concluded that the hyperbenthos was a distinct fauna with its own characteristic species distribution, which differed from that obtained by simply adding zooplankton and vagile benthic forms in a fixed proportion. The most common taxa (with maximal recorded densities) were chaetognaths (8900 100 m^{-3}), coelenterates (1700 100 m^{-3}), cumaceans (1430 100 m^{-3}), and cirriped larvae, decapods, calanoids, cladocerans and fish eggs (all latter groups with densities between 500 and 1000 ind. 100 m^{-3}), although a pronounced seasonal change in species composition and density occurred from January to March (Oug 1977). Hesthagen & Gjermundsen (1978) took deep (115 m) day-time samples in Oslofjord (Norway) and reported calanoids ($\sim$1000 ind. 100 m^{-3}), mysids, cumaceans, polychaetes, coelenterates and chaetognaths (each $\sim$500 ind. 100 m^{-3}), amphipods and carideans (between 50 and 100 ind. 100 m^{-3}) and euphausiids (less than 10 ind. 100 m^{-3}). Fossa (1985) and Kaartvedt (1985) also used a modified Beyer sledge in their detailed studies of the small-scale vertical distribution of hyperbenthic mysids in deep Norwegian fjords (150–220 m water depth). A modified Rothlisberg and Pearcy (1977) sledge was used by Buhl-Jensen (1986) and Fossa & Brattegard (1990) to examine the bathymetric distribution of mysids in Norwegian fjords. Buhl-Jensen & Fossa (1991) studied the hyperbenthic crustaceans along a transect from the Skaggerak to the inner Gullmarfjord (Sweden). Hyperbenthic amphipods of the Norwegian continental shelf were compared with the fauna of five adjacent fjords by Buhl-Jensen (1986). In summary, deep-shelf localities (247–520 m), shallow-shelf localities (147–272 m) and fjords were characterized by distinct amphipod communities, although a change in the amphipod fauna was observed at 200–300 m depth. Bathymetric isolation, depth and median grain size of the sediment were found to be correlated significantly with amphipod diversity which, as a result, was higher in shelf sites than in the fjords; Oedocerotidae was the dominant family, especially over mud substrata (Buhl-Jensen 1986). Sainte-Marie & Brunel (1985) observed similar trends in the amphipods of the Gulf of St Lawrence.

Seasonal changes and diurnal vertical migrations of the hyperbenthos of the St. Lawrence Gulf and Estuary were studied extensively at water depths between 10 m and 400 m (Brunel et al. 1978, Brunel 1979). Huberdeau & Brunel (1982), using a two-level Macer-GIROQ sledge at a deep station (350 m) in the same areas, found that the lower net (sampling the section between 28 cm and 64 cm above the bottom) contained 680–1065 ind. 100 m^{-3} (representing 87 species), while the upper net (sampling the section between 106 cm and 142 cm above the bottom) only caught 1–169 ind. 100 m^{-3} (representing 21 species). The same density trend was observed in a shallow station (20 m); the lower net caught 1600 ind. 100 m^{-3} (54 species), the upper net 45 ind. 100 m^{-3} (5 species). Using a slightly modified model of the same sledge, Chevrier et al. (1991) compared the structure of hyperbenthic gammaridean amphipod communities in the Bay of Fundy, Baie des Chaleurs and the St Lawrence Gulf, and reported average densities of 450, 1300 and 120–300 ind. 100 m^{-3}, respectively. Densities in the lower net were consistently higher than those in the upper net. Wildish et al. (1992) used the same gear to sample to 240 m over the Browns Bank (North West Atlantic); samples were obtained in different seasons, over hard bottoms and, in some places, over rocky sands or gravel (34 stations). Day-time densities in the upper and lower nets were not significantly different (3300 ± 1100 and 3850 ± 1690 ind. 100 m^{-3}, respectively); copepods dominated the fauna, with about 75 ind. 100 m^{-3} of other taxa (mainly amphipods); some amphipod and cumacean species had significantly higher densities in the lower net and marked seasonal differences were observed in selected stations (Wildish et al. 1992).

Construction of a new two-level sledge (Sorbe 1983), enabled the continental shelf of the Gulf of Gascogne to be studied in detail (Cornet et al. 1983, Sorbe 1989). Twelve stations along a bathymetric transect (25–237 m depth) provided information on qualitative depth-related and day–night differences. The upper net (sampling the section between 50 m and 100 cm above the bottom) contained between 1.1% and 13.8% of the fauna present in the lower net (which sampled between 0 cm and 50 cm above the bottom) during day and night, respectively. Stations at 31 m and 91 m depth were characterized by two distinct communities, with the shallow station having fewer species (56 versus 104), lower diversity and more pronounced seasonal density fluctuations than the deeper station. Average annual densities were 8730 ind. 100 m^{-3} at 31 m, and 3620 (day) and 2060 (night) at 91 m. In the shallow station, amphipods (68%) and mysids (29%) dominated the fauna, with a minor presence of cumaceans (1.4%), euphausiids and Natantia (both less than 1%). In the deeper station, mysids (44%) and amphipods (27%) still predominated, but in reverse order, while Natantia (11.9%), euphausiids (9.9%) and cumaceans (5.5%) occurred in higher proportions. During the night, the dominance of mysids decreased (17%), while that of amphipods and cumaceans increased to 42% and 16%, respectively. Elizalde et al. (1991) used a modified Macer-GIROQ sledge to study the hyperbenthos at great depths in the Cap-Ferret Canyon (see below).

The hyperbenthos of the shallow (5–10 m depth) coastal zone in the Dutch delta area (24 stations) was studied over one year with a simple sledge (Hamerlynck & Mees 1991, Mees & Hamerlynck 1992, Cattrijsse et al. 1993, Mees et al. 1993a). The annual average density was 160 ind. 100 m^{-3}, with monthly averages ranging from 10 (February) to 660 (June) ind. 100 m^{-3}. Mysids dominated (with a maximum of 150 ind. 100 m^{-3}) but other important permanent members of the hyperbenthos were amphipods, cumaceans and isopods, while temporary hyperbenthic taxa included larval and post-larval stages of polychaetes, carideans, brachyurans and fish; the hyperbenthic community structure showed clear seasonal patterns.

Using a modified Macer-GIRQQ sledge that sampled at four levels (Dauvin & Logeré 1989), the hyperbenthos of a shallow (10 m) station in the Bay of Seine (eastern

English Channel) was studied in two 24-h sampling campaigns in June (Wang & Dauvin 1994, Wang et al. 1994). Mysids and cumaceans dominated the permanent hyperbenthic fauna; the total average density was 220 ind. 100 m^{-3}, average day density was 120 ind. 100 m^{-3} (56% of the animals caught in the lower net), average night density was 480 ind. 100 m^{-3} (with a more even distribution of the animals over the four nets). Other groups (mainly ctenophores, copepods and crustacean larvae) reached average densities of 21 600 ind. 100 m^{-3} (16 600 during day, 33 700 at night). In a deeper station (75 m) in the western English Channel, densities of 30–1720 ind. 100 m^{-3} were reported, with an average of 240. Over this coarse sand substratum, mysids (22%) and amphipods (74%) predominated, and animals were mainly concentrated in the lower net (Dauvin et al. 1994).

Deep sea

Hyperbenthic associations of animals are known from the deep sea, although the fauna is usually termed "benthopelagic plankton" (Marshall & Merrett 1977) or "demersal plankton" (e.g. Grice 1972) and the zone in which it occurs is referred to as the "benthopelagic" or "benthic boundary layer" (Wishner 1980a,c, Childress et al. 1989, Mauchline & Gordon 1991, Hudon et al. 1993, Dauvin et al. 1995, Zouhiri & Dauvin 1996). In the deep ocean, the sea bed can be viewed as a sediment sink, halting the downward drift of particles. Resuspension and biological and geochemical processes within the benthic boundary layer lead to an enrichment of the waters above the sediment. In parallel with this enrichment, a higher biomass is generally observed at the boundary layer relative to the water column immediately above it (Wishner 1980a). Besides an enrichment in biomass, the abyssal benthopelagic zone also contains a higher number of species relative to the overlying water column (Angel 1990). It is inhabited by (a) pelagic species whose ranges are truncated by the sea bed, (b) benthic species that use the zone as a refuge for dispersal or for locating their food, and (c) a specialized fauna that includes many novel species (Angel 1990).

Typically, deep-sea hyperbenthic samples are taken with specially designed plankton nets, benthic trawls or by mounting nets on submersibles (Grice 1972, Wishner & Meise-Munns 1984). A hyperbenthic net, which opens and closes simultaneously with benthic nets, was added to a sophisticated epibenthic sledge designed to sample the deep-sea megafauna, thus sampling the section from 0.6 m to 1.2 m above the sea floor (Rice et al. 1982).

Most early collections from the deep sea were made to describe new species. New hyperbenthic copepods were described from 1200 m to 1700 m off New Zealand (Bradford 1969) and from 1200 m to 1700 m in the Atlantic (Grice & Hülsemann 1970, Grice 1972). The hyperbenthic community on the slopes of the Porcupine Seabight (South West Ireland) has been sampled with a rectangular mid-water trawl; the decapods and mysids were described by Hargreaves (1984, 1985), and the ostracod fauna by Ellis (1985). The first community analysis of the deep-sea hyperbenthos, based on samples taken in the San Diego Trough, the eastern tropical Pacific and the North East Atlantic, was presented by Wishner (1980c). The water layers from 10 m to 100 m above the bottom were sampled at depths of 1100–3200 m with an opening-closing net (with 183 μ mesh size). Copepods formed 80% of the animals collected, and other abundant groups were isopods, ostracods and chaetognaths. Representatives of larger taxa were rare, but this may have been due to net avoidance. In contrast to shallower areas, day samples were similar to night samples. Densities ranged from 2 to 230 ind. 100 m^{-3}. Another difference from shallower areas was the near-absence of larvae of benthic animals, although larval and juvenile stages of many benthic species were reported between 1 m and 5 m above deep-sea hydrothermal vents (Berg & Van Dover 1987). These latter waters are enriched in terms of biomass and abundance with respect to non-vent areas but are depleted in biomass relative to the surface zooplankton.

Recently, the structure and species composition of the hyperbenthic communities of the Arcachon Plateau and the Cap Ferret Canyon (Bay of Biscay) have been described (Elizalde et al. 1991, 1993, Dauvin et al. 1995). Samples, taken from depths of 346–3070 m with a modified Macer-GIROQ sledge (Dauvin & Lorgeré 1989), revealed that asellotan isopods and gammaridean amphipods dominated the fauna, with mysids becoming less important with increasing depth. Three depth intervals, each characterized by a specific hyperbenthic fauna, could be identified. The hyperbenthos of the upper part of the Plateau (muddy-sand substratum between 350 m and 500 m) was characterized by high densities and consisted mainly of asellotan isopods. At intermediate depths (mud substratum between 600 m and 1100 m), amphipods dominated, sometimes accompanied by cumaceans. In the Canyon proper, isopods again predominated, with significant numbers of pycnogonids and tanaidaceans. Densities in the lower net varied with depth [2700 ind. 100 m^{-3} (430 m), 4500 (710 m), 600 (1030 m) and 700 (3060 m)] but were always higher than in the other three nets.

The Catalan Sea slope (western Mediterranean) was sampled between 400 m and 1860 m depth, using a small plankton net attached to a beam trawl (Cartes & Sorbe 1993) and with a Macer-GIROQ sledge (Cartes et al. 1994). This study yielded nine new records of peracarid crustaceans for the Mediterranean. On the upper slope amphipods predominated, whereas cumaceans became progressively more abundant with increasing depth and dominated the lower slope.

Tropical and subtropical areas

Most studies in subtropical and tropical environments deal with sandy lagoons in reef areas. Usually, traps with a wide range of mesh sizes (varying from 63 μ to 333 μ) are deployed, making comparisons of reported densities and species lists difficult (Youngbluth 1982). Comparisons are complicated further by the fact that most studies are restricted in time. As a result of these constraints, only some general features and recent key studies are discussed here (more references can be found therein).

Coral reefs appear to harbour a unique and abundant hyperbenthic fauna not found in the surrounding waters (Sale et al. 1976, 1978, Goswami 1979). Elements of this reef assemblage include resident, swarming or demersal zooplankters (Emery 1968, Hamner & Carleton 1979). The most common taxa are copepods, amphipods, cumaceans, mysids, ostracods, tanaids, caridean and anomuran larvae, polychaetes, chaetognaths, larvaceans, fish larvae and molluscan veligers. Alldredge & King (1985) studied a subtidal sand flat in the Gulf of California and reported copepods, amphipods and isopods predominated the fauna, followed by ostracods, cumaceans, tanaids and polychaetes; carideans, mysids, cephalochordates and decapod larvae were caught only occasionally. All these animals remain closely associated with the substratum during the day (Jacoby & Greenwood 1988) and there is some discussion as to the extent of their upward migration into the water column. Smaller animals have been reported to remain within 0.3 m of the bottom, whereas larger individuals migrated throughout the water column (Alldredge & King 1985). Jacoby & Greenwood (1988) found that all animals, independent of size, moved to at least 0.5 m from the bottom. Studies with emergence traps have indicated that the distribution, abundance and behaviour of these animals varied with location on the reef, season, substratum type, lunar period and daylight, and that these effects varied for different taxa (Alldredge & King 1977, 1980, 1985, Porter et al. 1977, Porter & Porter 1977, Feeley et al. 1979, Hobson & Chess 1979, McWilliam et al. 1981, Ohlhorst 1982, Jacoby & Greenwood 1988). Lewis & Boers (1991), in a study in Barbados, reported marked temporal variability and patchiness based on weekly sampling over one year. Re-entry trapping in a shallow bay in North Carolina showed that demersal zooplankton is taxonomically distinct from the holozooplankton, and that high densities typically occur (Cahoon & Tronzo 1992). Densities reported from emergence trapping range from less than 50 to nearly 500 ind. $m^{-2} h^{-1}$ (references and study areas in Youngbluth et al. 1982) or 160–8000 ind. m^{-2} per night (Jacoby & Greenwood 1988 and references therein).

Most studies have concentrated on demersal zooplankton, referring to organisms that burrow or hide within the reef substrata during the day, rise up into the water column at dusk and return before dawn (Carleton & Hamner 1989). Usually, mysids constitute a very small portion of the samples that are collected by emergence or re-entry trapping. Carleton & Hamner (1989) monitored the seasonal and diel variations in community structure of mysids in the Davies Reef Lagoon (Great Barrier Reef) over one year, and found higher densities during the day than the night. The epibenthic mysid community differed from that of the overlying section of the water column, there was marked seasonality and diel groupings such that densities ranged from 110 to 790 ind. m^{-3} and schooling species occurred at local densities of up to 500 000 m^{-3} (Carleton & Hamner 1989).

Selected topics of hyperbenthic research

Taxonomic interest and diversity

Common features of the hyperbenthos include: (a) most species are endemic, (b) most are present in much higher densities than in either the overlaying water layers or in the adjacent sediment, and (c) most are not there accidentally. Beyer (1958) discussed the species found in abundance in the hyperbenthos but which were rare or absent elsewhere. More recently, there has been recognition of a distinction between the truly hyperbenthic species and a variety of "visiting" or "immigrant" animals that can be classified as endobenthic, epibenthic or planktonic. Huberdeau & Brunel (1982) compared the selectivity of endo-, epi- and hyperbenthos samplers, and showed that the Macer-GIROQ hyperbenthic sledge sampled a specific fauna. A higher diversity in the hyperbenthos, compared with the macrobenthos of the same area, was demonstrated by Cornet et al. (1983). There has been much taxonomic interest in the hyperbenthos. A new species of Trachymedusa was discovered in the Oslofjord (Beyer 1958), Carleton & Hamner (1989) recorded six new mysid species for the Great Barrier Reef, Mees & Fockedey (1993) found a hitherto undiscovered isopod species in the Gironde Estuary and 15% of the 69 gammaridean species collected by Dauvin et al. (1994) were new for the Roscoff fauna. Dauvin et al. (1994) also compared their hyperbenthic catches with macrobenthic samples from the same area, concluding that the former comprised different kinds of species from the latter. Matthews (1961) reported a new calanoid copepod, Fosshagen (1968) and Brattegard (1973) described several new copepod and mysid species collected off the Bahamas and Colombia with a modified Ockelmann detritus-sledge (Ockelmann 1964). Omori (1969) found many new species and high abundances of species that were scarcely collected by ordinary plankton tow nets. The recognition of the hyperbenthal as a specific habitat has increased in recent years, such that many species (of a variety of taxonomic groups) are referred to explicitly as hyperbenthic. Besides mysids, probably the most typical hyperbenthic taxon (Mauchline 1980), several new species, genera and a family of calanoid copepods (Grice & Hülsemann 1970, Grice 1972, Ohtsuka & Mitsuzumi 1990, Ohtsuka et al. 1991, 1992, 1993), a variety of new benthoplanktonic chaetognaths (Casanova 1992), and an entirely novel hyperbenthic ostracod fauna (Angel & Baker 1982, Ellis 1985) have been described.

Many taxa which were thought previously to be exclusively endobenthic, epibenthic or pelagic, are now found to have hyperbenthic representatives. Bentho–pelagic medusae are more numerous and diverse than believed previously with densities of up to 80 ind. m^{-2} on or near the bottom (Larson et al. 1992). Hydromedusae concentrate in the hyperbenthal during the day (Arkett 1984) and the same applies to sea cucumbers (Pawson & Foell 1986). Swimming holothurians were also recorded in high densities from abyssal depths (e.g. Childress et al. 1989). Concentrations of chaetognaths near the bottom were noted by Russell (1928) but a much greater diversity of habitat utilization by different chaetognaths groups is now recognized (Bieri 1991). Decapod larvae are more common on the bottom during the day than during the night (Bossanyi 1957, Hesthagen & Gjermundsen 1979) and some larval polychaetes swim close to the bottom (Qian & Chia 1989). Since the body size of marine invertebrate larvae can impose restrictions on the mode of locomotion, differences in ways of propulsion between life-history stages occur and this affects habitat choice (Chia et al. 1984). Antarctic krill change their habitat from the pelagic zone to the hyperbenthal as a strategy to survive the winter under the coastal fast ice (Kawaguchi et al. 1986). Hyperbenthic fish microhabitat guilds (mainly small-sized fish like gobies) have been described (e.g. Costello 1992, Wilkins & Myers 1992).

Among temporary members of the hyperbenthos, an important taxonomic group is late-stage larval fish. Larger fish larvae are especially abundant in the near-bottom layers. The distribution of larval fish is controlled by both active behaviour and passive transport mechanisms resulting from a combination of biotic and abiotic factors (Norcross & Shaw 1984). Biotic factors include seasonal abundances of adults and larvae, environmental preferences, availability of suitable food, potential predators, and larval behaviour. Abiotic factors include the oceanographical, hydrological and climatological parameters of the area (e.g. temperature, salinity, stratification, turbidity, riverine discharges, weather and water-flow patterns, rates, directions, and anomalies). The relative importance of passive and behaviourally mediated transport is still under discussion. The depth distribution of fish larvae is also discussed by Brewer & Kleppel (1986) and Jahn & Lavenberg (1986).

Small-scale zonation

Population assessment and sampling problems relating to species with uneven vertical and horizontal distributions, and patchiness are discussed by Omori & Hamner (1982). Using nets mounted at different levels on sledges, several authors have investigated the vertical distributional patterns of species residing close to the bottom (Oug 1977, Hesthagen & Gjermundsen 1978, Brunel 1979, Sainte-Marie & Brunel 1983, 1985, Fossa 1985, Kaartvedt 1985, Elizalde et al. 1991, Dauvin et al. 1994, Wang & Dauvin 1994). Swimming activity, and preferred height above the bottom, appears to differ between sexes and between developmental stages of mysids in shallow (Clutter 1967, 1969, Wittmann 1977) and deeper areas (Fossa 1985, Kaartvedt 1985). A valuable tool for measuring swimming activity and classifying species are the coefficients used by, for example, Elizalde et al. (1991) and Dauvin et al. (1994) (especially when a four-level net is used). These latter investigations have shown that both plankton and vagile benthic species differ in their vertical zonation in the near-bottom area. Generally, the highest number of species is found in the lowermost layers sampled (Dauvin et al. 1994). In the deep sea, Dauvin et al. (1995) recognized a vertically increasing density gradient; some species occurred preferentially in the upper layers, while others were equally represented in both depth strata that were sampled.

Diel activity patterns close to the sediment have been documented for several groups. Generally, deep-living hyperbenthic cumaceans and amphipods are associated with the sediment during the day, and swimming activity, with a variety of migration patterns, increases within the lower metres of the water column during darkness (Brunel 1979, Sainte-Marie & Brunel 1983, 1985, Kaartvedt 1986). Although occasional planktonic catches have been reported, the amplitude of the vertical migrations is usually small (Kaartvedt 1989). Direct observations of hyperbenthic mysids show that different species display varying degrees of affinity to the substratum (O'Brien 1988, O'Brien & Ritz 1988). Clutter (1969), studying the swarming and schooling of pelagic invertebrates in Hawaiian waters, found mysids in well defined layers near the sediment surface, usually with specific sediment types and in well defined bathymetric zones. Mauchline (1980) provided evidence that some hyperbenthic mysid species prefer certain types of substrata. In the intertidal zone, small-scale vertical zonations can also be observed at the edge of sandy beaches (Colman & Segrove 1955, Sibert 1981).

Diurnal rhythms and vertical migrations

Many hyperbenthic species show diel and tidal changes in their distribution. Mainly, these are nocturnal (especially in marine and lacustrine environments) or tidally-phased (especially in estuaries) vertical migrations (Hough & Naylor 1992). Nocturnal vertical movements into the water column have been reported for amphipods, isopods, cumaceans, copepods and decapods (Macquart-Moulin 1976, 1984, 1985, 1991), crab larvae (Sulkin 1984) and polychaetes (Evans 1971). Kaartvedt (1985), using sledges at 150 m in Fanafjorden (Norway), found that many of the mysid species found near the bottom during the day undertook nocturnal vertical migrations; even so, a significant proportion of the total population of each species remained in the hyperbenthic layer during darkness. The hypotheses put forward to explain vertical migrations refer to availability of food in superficial layers, advantage of lower metabolism at deeper layers, avoidance of visual predation, horizontal dispersion and breeding migrations. Vertical movements in intertidal waters are well documented (e.g. Russell 1925, Elmhirst 1932, Watkin 1939, 1941, Coleman & Seagrove 1955). Over rocky shores, various taxa are also known to perform vertical migrations into the surf at night (Jansson & Källander 1968, Setran 1992).

Meiohyperbenthos

Studies of meiofaunal recolonization after sediment disturbance indicate that partial recovery occurs within a few tidal cycles (Sherman & Coull 1980). Recruitment for this rapid recovery may occur through hyperbenthic populations. Recent investigations revealed a partially hyperbenthic occurrence of meiofauna which was regularly caught in sediment traps high above the ground (Palmer 1988, Armonies 1988). By analogy to the meiobenthos *sensu stricto*, the term meiohyperbenthos could be introduced, as opposed to macrohyperbenthos (animals larger than 0.5 mm or 1 mm). Periodical hyperbenthic behaviour has been reported for harpacticoids (mainly diatom eaters), encompassing both passive suspension and active emergence for rapid dispersion and recolonization (Armonies 1988, 1989a, 1990, Bell & Sherman 1980, Palmer 1988). Considerable numbers of individuals of turbellarians regularly enter the overlying water column (Armonies 1989b, Giere 1993) and, after distribution through water currents, can colonize new areas in a short while; this hyperbenthic behaviour is preferably nocturnal (Armonies 1989a, 1989b, 1990). High densities of meiobenthic taxa were also reported from water layers over seagrass beds by Bell et al. (1988) and from tidepools on rocky shores (Metaxas & Scheibling 1994).

Role in marine food webs

For most hyperbenthic taxa, basic information on relationships between length, weight and chemical composition is generally not available in sufficient detail for the study of energy fluxes through food webs. Secondary production estimates are scattered and, with few exceptions, are not detailed for any one species. For broad ecological studies, in contrast to experimental studies, information may not need to be precise, as it is pointless carrying out analyses and calculations to a greater accuracy than the sampling methodologies themselves allow. For a review on the productivity of epi- and hyperbenthic species refer to Redant (1989). Some recent studies giving detailed mysid production estimates include Rudstam et al. (1986) for Baltic populations of *Mysis mixta* ($0.6\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), Sorbe (1991) and San Vicente & Sorbe (1990, 1993) for populations of *Schistomysis ornata* ($23\,\mathrm{mg\,AFDW\,m^{-3}\,yr^{-1}}$), *S. kervillei* ($130\,\mathrm{mg\,AFDW\,m^{-3}\,yr^{-1}}$), and *S. parkeri* ($52.6\,\mathrm{mg\,AFDW\,m^{-2}\,yr^{-1}}$) and Mees et al. (1994) for an estuarine population of *Neomysis integer* ($300\,\mathrm{mg\,AFDW\,m^{-2}\,yr^{-1}}$).

From the available literature, it is not clear where the hyperbenthos can be expected to be most important. Whether high hyperbenthic densities are accompanied by decreasing densities of other benthic compartments is also not clear to date. The highest hyperbenthic densities have been reported from the brackish reaches of estuaries, eutrophic shallow coastal areas and medium to deep areas of continental slopes. In very turbid areas, where the hyperbenthos tends to peak, clogging of feeding mechanisms and the risk of burial generally causes sessile guilds to diminish (Pearson & Rosenberg 1987). Alternatively, below a certain threshold of food availability, mobility may become necessary to acquire sufficient food. Mobility may be a further advantage to anticipate stochastic events in highly unpredictable environments like estuaries, for example, to flee adverse oxygen conditions or high concentrations of pollutants (Mees et al. 1993a).

The hyperbenthos plays an important role in the coupling of benthic and pelagic food webs. In sub-Antarctic waters, Perissinotto & McQuaid (1990) found that a population of a shrimp species formed a 5–10 m thick hyperbenthic layer, the larvae utilize the phytoplankton biomass that sinks to the sea floor and constitute, through daily vertical migrations, a link to higher trophic levels.

Food and feeding

Most mysids are omnivores, feeding on detritus, algae and zooplankton (e.g. Mauchline 1980). Since feeding is probably selective on different zooplankton species and size groups (e.g. Cooper & Goldman 1980, Murthaugh 1981), mysids have the potential for structuring zooplankton communities (Fulton 1982a, 1982b). The community structure of phytoplankton (Webb et al. 1987) and diatoms (Wooldridge 1989, Webb & Wooldridge 1990) is also influenced possibly by selective grazing by mysids. Mysid predation has even been reported as a possible important control on meiofaunal densities (Johnston & Lasenby 1982). Most mysids utilize organic detritus to a considerable extent and can be responsible for remineralization of a substantial proportion of the refractile detritus. Hyperbenthic mysids have been shown to be important for nutrient regeneration in the surf zone (Cockroft et al. 1988). Mysids also play an important role as macrophages, carnivores and detritivores in coral reef trophodynamics (Gottfried & Roman 1983, Mullin & Roman 1986, Carleton & Hamner 1989). In the same biotope, demersal zooplankton has been reported to graze on heterotophic particulate matter and nanophytoplankton (Roman et al. 1990). Gowing & Wishner (1992) found a preponderance of gram-positive bacteria in the guts of deep-living copepods, mysids and amphipods.

Predators

Study of the hyperbenthic fauna was encouraged by many authors in its role as a constituent of the diet of fish (e.g. Blegvad 1917) and some of the earliest studies were specifically conducted for that purpose (Greze 1951). A review of the occurrence of mysids in the diet of fish is presented by Mauchline (1980). Although their importance as fish food is widely recognized, the prey communities are rarely termed hyperbenthic. Some recent exceptions are Zander & Hartwig (1982) and Mason & Clugston (1993) who explicitly mention hyperbenthic feeding habits. Hyperbenthic micro-habitat feeding guilds were recognized in the gobiid assemblage in Lough Hyne, Ireland (e.g. Wilkins & Myers 1992) and mysid-feeding guilds were distinguished in several demersal fish assemblages (Blaber & Bulman 1987, Gibson & Ezzi 1987, Moreira et al. 1992). Meiobenthic taxa, notably harpacticoid copepods, contribute significantly to the diet of many species of post-larval and juvenile fish (McCall & Fleeger 1995). Mysids progressively replace copepods as a food source for demersal fish during growth (Sorbe 1981a). Such ontogenic shifts have been observed in several species including, for example, cod (Mattson 1990). The hyperbenthos often predominates the diet of 0-group individuals of commercially important fish and also sustains high densities of non-commercial demersal fish (e.g. gobies), which are an important prey for the larger size classes of the same species. Recently, deep-sea fish have been reported also to forage in the benthic boundary layer (e.g. Mauchline & Gordon 1991, Stefanescu & Cartes 1992).

Availability for fish predation is higher when individuals occur in the hyperbenthal than when they are buried in the sediment (Sorbe 1981a). Although a very small fraction of the populations of essentially endobenthic species can be present in the hyperbenthal, this quantity is not necessarily negligible, since this hyperbenthic fraction is obviously bound to be more readily available for predators. An example is the amphipod *Corophium volutator*. Although less than 0.1% of the population of this species is present in the hyperbenthal, it constitutes a significant part of the diet of demersal and even pelagic fish species (Hughes 1988, Essink et al. 1989). Meiofaunal prey ingested by fish more closely resemble the meiohyperbenthic than the endomeiobenthic faunas. Differential emergence of certain species or life-history stages from sediments increases their susceptibility to predation, and can explain patterns of apparent selectivity (McCall & Fleeger 1995).

Birds (Schneider 1981, Johnson 1984, Cairns 1987, Steele & Montevecchi 1994) and marine mammals (Murison et al. 1984) are also possible predators of the hyperbenthos. For example, sandy-beach mysids make an important contribution as the major food source for some birds (McLachlan et al. 1980, Moran & Fishelson 1971) and the analysis of faecal matter of grey whales has revealed a preponderance of hyperbenthic mysid exoskeleton fragments. Direct consumption by man is rare, although some mysids are fished commercially for this purpose in Asia (Tattersall & Tattersall 1951, Omori 1978). In recent years, numerous invertebrates have been reported to feed on the hyperbenthos. Coelenterates may play an important role as predators in the hyperbenthal (Bossanyi 1957, Möller 1979). For example, the annual average standing stock of the metazoan plankton in the Kiel Bight included 1% hyperbenthic crustaceans (mysids and cumaceans) and 51% coelenterates (Möller 1979). These results may be biased, however, as the sampling method used (Van Veen grab) would underestimate the more active crustacean elements. Juveniles of the sepiolid squid *Sepietta oweniana* forage in the hyperbenthal of Nordic waters, preferentially catching free-swimming mysids (Bergstrom 1985). The diet of *Sepia officinalis* changes during ontogeny, the smallest individuals feed on mysids (Le Mao 1985). Part of the diet of deep-sea octopods also consists, to a large extent, of hyperbenthic material (Villanueva & Guerra 1991). Predatory crustaceans, often in commercially-exploited stocks, include caridean shrimp (Chong & Sasekumar 1981, Siegfried 1982) and rock lobsters (Barkai & Branch 1988).

Concluding remarks

The distinction between benthic and planktonic organisms, although still fundamental, is not a simple dichotomy, particularly when attention is focused on the interface region between the water and the substratum. Special types of equipment are needed to sample this novel region, and species that are now regarded as rare may prove to be very abundant when proper collecting apparatus is used. More information about the biology of individual species of this zone is required to determine its ecological role. The term hyperbenthos is proposed to include all the animals living in the water layer

Table 1 List of terms discussed in the text.

Term	Applied to	Authority or comments
Benthos	All communities of the sea bed	In general use
Plankton	Floating organisms living in the pelagic, to a large extent subjected to water movements	In general use
Macrozooplankton	Larger plankton (>2000 μ)	Arbitrary cutoff points
Mesozooplankton	Medium sized plankton (55–63–200 to 2000 μ)	Arbitrary cutoff points
Nekton	All pelagic animals that are active swimmers	In general use
Micronekton	Smaller active swimmers	In general use
Ichthyoplankton	Pelagic fish larvae	In general use
Benthic Boundary Layer (BBL)	Water/sediment interface, i.e. the water layer just above the surface of the seabed	McCave 1976
Benthopelagic plankton	Fauna associated with BBL	Often used for deep-sea hyperbenthos
BBL macrofauna	Larger animals associated with BBL	Often used for deep-sea hyperbenthos
Predominantly resident in/on the sediment		
Infauna	Animals living buried in the sediment	Syn. endofauna
Endobenthos	Animals living buried in the sediment	In general use
Epibenthos	Animals living on the surface of the sediment	In general use
Endopelos	Animals living in mud	Remane 1940
Epipelos	Animals living over mud	Remane 1940
Macrobenthos	Large fauna (>500–1000 μ)	Arbitrary cutoff points
Meiobenthos	Medium fauna (32–45–63 to 500–1000 μ)	Arbitrary cutoff points
Microbenthos	Small fauna (<32–45–63 μ)	Arbitrary cutoff points
Predominantly pelagic, cm to m above the sediment		
Hyperbenthos	Benthic organisms living close to, but not on or in the sea bottom	Beyer 1958
Hyperpelos	Hyperbenthos of muddy substrata	Beyer 1958
Suprabenthos	Syn. Hyperbenthos	Redundant
Nektobenthos	Syn. Hyperbenthos	Redundant
Hypoplankton	Syn. Hyperbenthos	Redundant
Demersal zooplankton	Syn. Hyperbenthos	Redundant Often used for tropical hyperbenthos
Bottom plankton	Syn. Hyperbenthos	Redundant
Near-bottom zooplankton	Syn. Hyperbenthos	Redundant
Semiplankton	Syn. Hyperbenthos	Redundant
Tychobenthos	Accidental members of the hyperbenthos	Beyer 1958
Hekobenthos	Truely hyperbenthic animals	Beyer 1958
Recommended new terms		
Holohyperbenthos	Permanent members of the hyperbenthos	Hamerlynck & Mees 1991
Merohyperbenthos	Members as larvae	Hamerlynck & Mees 1991
Immigrants	Temporary visitors	
Macrohyperbenthos	Large fauna (>500–1000 μ)	Arbitrary cutoff points
Meiohyperbenthos	Medium fauna (32–45–63 to 500–1000 μ)	Arbitrary cutoff points
Microhyperbenthos	Small fauna (<32–45–63 μ)	Arbitrary cutoff points

close to the sea bed. Large fish and epibenthic crustaceans, though they feed in the hyperbenthal and are thus an integral part of the community, can be considered as accidental catches because they are not sampled efficiently by sledges and they will seriously bias biomass estimates. The position of polychaetes and molluscs is more difficult to decide upon, since, although they have the ability to swim, their presence is sometimes correlated with the amount of sediment in the sledge.

At the present state of knowledge of, for example, mysid and copepod behaviour, it is recommended to report density and biomass data for these groups both per volume and per surface area. Indeed, mysids are known to concentrate near the bottom and to maintain their position even in strong currents (Hough & Naylor 1992).

Although the intensity of hyperbenthic research has increased in recent years, more descriptive baseline studies are needed, particularly for areas such as the North Sea and tropical areas. Special attention should be paid to areas where commercial fishing activity is high and to the nursery areas for the commercially-important species. Although studies of the fluxes from the hyperbenthos to higher trophic levels are available from several areas, there is still a general need for studies on the fluxes from lower trophic levels to the hyperbenthos, including production and consumption estimates for the dominant species.

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References

Aldred, R. G., Thurston, M. H., Rice, A. L. & Morley, D. R. 1976. An acoustically monitored opening and closing epibenthic sledge. *Deep-Sea Research* **23**, 167–74.

Alldredge, A. L. & King, J. M. 1977. Distribution, abundance, and substrate preference of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. *Marine Biology* **41**, 317–33.

Alldredge, A. L. & King, J. M. 1980. Effects of moonlight on the vertical migration patterns of demersal zooplankton. *Journal of Experimental Marine Biology and Ecology* **44**, 133–56.

Alldredge, A. L. & King, J. M. 1985. The distance demersal zooplankton migrate above the benthos: implications for predation. *Marine Biology* **84**, 253–60.

Andersen, V. & Sardou, J. 1992. The diel migrations and vertical distributions of zooplankton and micronekton in the Northwestern Mediterranean Sea. 1. Euphausiids, mysids, decapods and fishes. *Journal of Plankton Research* **14**, 1129–54.

Angel, M. V. 1990. Life in the benthic boundary layer: connections to the mid-water and sea floor. *Philosophical Transactions of the Royal Society of London, Series A* **331**, 15–28.

Angel, M. V. & Baker, A. de C. 1982. Vertical distribution of the standing crop of plankton and micronekton at three stations in the Northeast Atlantic. *Biology and Oceanography* **13**, 319–51.

Anger, K. & Valentin, C. 1976. *In situ* studies on the diurnal activity pattern of *Diastylis rathkei* (Cumacea, Crustacea) and its importance for the "hyperbenthos". *Helgoländer Meeresuntersuchungen* **28**, 138–44.

Arkett, S. A. 1984. Diel vertical migration and feeding behavior of a demersal hydromedusan (*Polyorchis penicillatus*). *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 1837–43.

Armonies, W. 1988. Active emergence of meiofauna from intertidal sediment. *Marine Ecology Progress Series* **43**, 151–9.

Armonies, W. 1989a. Meiofauna emergence from intertidal sediments measured in the field: significant contribution to nocturnal planktonic biomass in shallow waters. *Helgoländer Meeresuntersuchungen* **43**, 29–43.

Armonies, W. 1989b. Semiplanktonic Plathelminthes in the Wadden Sea. *Marine Biology* **101**, 521–8.

Armonies, W. 1990. Short-term changes of meiofaunal abundance in intertidal sediments. *Helgoländer Meeresuntersuchungen* **44**, 375–86.

Astthorsson, O. S. 1984. The distribution and biology of mysids in Icelandic subarctic waters as demonstrated by analysis of cod stomach contents. *Sarsia* **69**, 107–16.

Astthorsson, O. S. 1985. Mysids occurring in the stomachs of cod caught in the Atlantic water south and west of Iceland. *Sarsia* **70**, 173–8.

Barkai, A. & Branch, G. M. 1988. Energy requirements for a dense population of rock lobsters *Jasus lalandii*: novel importance of unorthodox food sources. *Marine Ecology Progress Series* **50**, 83–96.

Beauchamp, R. S. A. 1932. A new dredge. *Internationale Revue der Gesamten Hydrobiologie* **27**, 467–9.

Bell, S. S. & Sherman, K. M. 1980. A field investigation of meiofaunal dispersal: tidal resuspension and implications. *Marine Ecology Progress Series* **3**, 245–9.

Bell, S. S., Hicks, G. R. F. & Walters, K. 1988. Active swimming in meiobenthic copepods of seagrass beds: geographic comparisons of abundance and reproductive characteristics. *Marine Biology* **98**, 351–8.

Berg, C. J. & Van Dover, C. L. 1987. Benthopelagic macrozooplankton at and near deep-sea hydrothermal vents in the eastern Pacific Ocean and the Gulf of California. *Deep-Sea Research* **34**, 379–401.

Bergstrom, B. I. 1985. Aspects of natural foraging by *Sepietta oweniana* (Mollusca, Cephalopoda). *Ophelia* **24**, 65–74.

Beyer, F. 1958. A new, bottom-living Trachymedusa from the Oslofjord. Descripton of the species, and a general discussion of the life conditions and fauna of the fjord deeps. *Nytt Magasin for Zoologi* **6**, 121–43.

Bhaud, M. 1979. Description et utilisation d'un engin de récolte a proximité du sédiment. *Bulletin de la Societé d'Ecologie* **10**, 15–27.

Bieri, R. 1991. Systematics of the Chaetognatha. In *The biology of chaetognaths*, Q. Bone, et al. (eds). Oxford: Oxford University Press, 122–46.

Bieri, R. & Tokioka, T. 1968. Dragonet II: an opening-closing quantitative trawl for the study of microvertical distribution of zooplankton and the meio-epibenthos. *Publications of Seto Marine Biological Laboratory* **15**, 373–90.

Blaber, S. J. M. & Bulman, C. M. 1987. Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**, 345–56.

Blegvad, H. 1917. On the food of fish in the Danish waters within the Skaw. *Reports of the Danish Biological Station* **26**, 17–72.

Bossanyi, J. 1951. An apparatus for the collection of plankton in the immediate vicinity of the bottom. *Journal of the Marine Biological Association of the United Kingdom* **30**, 265–70.

Bossanyi, J. 1957. A preliminary survey of the small natant fauna in the vicinity of the sea floor off Blyth, Northumberland. *Journal of Animal Ecology* **26**, 353–68.

Boysen, H. O. 1975a. Seasonal variations in abundance of hyperbenthic animals in the Kiel Bight. *Merentutkimuslaitoksen Julkaisul/Havsforskningsinstitutets Skrift* **239**, 206–12.

Boysen, H. O. 1975b. Das hyperbenthos in der Kieler Bucht – Zusammensetzung, jahresgang und verbreitung. *Kieler Meeresforschungen* **24**, 151–71.

Boysen, H. O. 1976. Regionale und saisonale unterschiede in der besiedlungsdichte von mysidaceen und dekapodenlarven im hyperbenthos der Kieler Bucht. *Kieler Meeresforschungen* **25**, 54–63.

Bradford, J. 1969. New genera and species of benthic calanoid copepods from the New Zealand slope. *New Zealand Journal of Marine and Freshwater Research* **3**, 473–505.

Brandt, O. M., Fujimura, R. W. & Finlayson, B. J. 1993. Use of *Neomysis mercedis* (Crustacea: Mysidacea) for estuarine toxicity tests. *Transactions of the American Fisheries Society* **122**, 279–88.

Brattegard, T. 1973. Mysidacea from shallow water in Colombia. *Sarsia* **54**, 1–66.

Brattegard, T. & Fossa, J. H. 1991. Replicability of an epibenthic sampler. *Journal of the Marine Biological Association of the United Kingdom* **71**, 153–66.

Brewer, G. D. & Kleppel, G. S. 1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. *Marine Ecology Progress Series* **27**, 217–26.

Brunel, P. 1979. Seasonal changes of daily vertical migrations in a suprabenthic cold-layer shelf community over mud in the Gulf of St. Lawrence. In *Cyclic phenomena in marine plants and animals*, E. Naylor & R. G. Hartnoll (eds). Oxford: Pergamon Press, 383–90.

Brunel, P., Besner, M., Messier, D., Poirier, L., Granger, D. & Weinstein, M. 1978. Le traîneau suprabenthique Macer-GIROQ: appareil amélioré pour l'échantillonage quantitatif étagé de la petite faune nageuse au voisinage du fond. *Internationale Revue der Gesamten Hydrobiologie* **63**, 815–29.

Buhl-Jensen, L. 1986. The benthic amphipod fauna of the west-Norwegian continental shelf compared with the fauna of five adjacent fjords. *Sarsia* **71**, 193–208.

Buhl-Jensen, L. & Fossa, J. H. 1991. Hyperbenthic crustacean fauna of the Gullmarfjord area (western Sweden): species richness, seasonal variation and long-term changes. *Marine Biology* **109**, 245–58.

Cahoon, L. B. & Tronzo, C. R. 1992. Quantitative estimates of demersal zooplankton abundance in Onslow Bay, North Carolina, USA. *Marine Ecology Progress Series* **87**, 197–200.

Cairns, D. K. 1987. Diet and foraging ecology of black guillemots in northeastern Hudson Bay. *Canadian Journal of Zoology* **65**, 1257–63.

Calman, W. T. 1906. The marine fauna of the west coast of Ireland. Part IV. Cumacea. *Scientific Investigations of the Fisheries Board of Ireland* 1904, 3–52.

Carleton, J. H. & Hamner, W. M. 1987. A diver-operated device for the capture of mobile epibenthic organisms. *Limnology and Oceanography* **32**, 503–10.

Carleton, J. H. & Hamner, W. M. 1989. Resident mysids: community structure, abundance and small-scale distributions in a coral reef lagoon. *Marine Biology* **102**, 461–72.

Cartes, J. E. & Sorbe, J.-C. 1993. Les communautés suprabenthiques bathyales de la Mer Catalane (Mediterranée Occidentale): données préliminaires sur la repartition bathymetrique et l'abondance des crustacés péricarides. *Crustaceana* **64**, 155–71.

Cartes, J. E., Sorbe, J.-C. & Sardà, F. 1994. Spatial distribution of deep-sea decapods and euphausiids near the bottom in the northwestern Mediterranean. *Journal of Experimental Marine Biology and Ecology* **179**, 131–44.

Casanova, J. P. 1992. Chaetognaths from Alvin dives in the Santa Catalina Basin (California), with description of two new *Heterokrohnia* species. *Journal of Natural History* **26**, 663–74.

Cattrijsse, A., Makwaia, E. S., Dankwa, H. R., Hamerlynck, O. & Hemminga, M. A. 1994. Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Marine Ecology Progress Series* **109**, 195–208.

Cattrijsse, A., Mees, J. & Hamerlynck, O. 1993. The hyperbenthic Amphipoda and Isopoda of the Voordelta and the Westerschelde estuary. *Cahiers de Biologie Marine* **34**, 187–200.

Chevrier, A., Brunel, P. & Wildish, D. J. 1991. Structure of a suprabenthic shelf sub-community of gammaridean Amphipoda in the Bay of Fundy compared with similar sub-communities in the Gulf of St Lawrence. *Hydrobiologia* **223**, 81–104.

Chia, F.-S., Buckland-Nicks, J. & Young, C. M. 1984. Locomotion of marine invertebrate larvae: a review. *Canadian Journal of Zoology* **62**, 1205–222.

Childress, J. J., Gluck, D. L., Carney, R. S. & Gowing, M. M. 1989. Benthopelagic biomass distribution and oxygen consumption in a deep-sea benthic boundary layer dominated by gelatinous organisms. *Limnology and Oceanography* **34**, 913–30.

Chong, V. C. & Sasekumar, A. 1981. Food and feeding habits of the white prawn *Penaeus merguiensis*. *Marine Ecology Progress Series* **5**, 185–91.

Christiansen, B., Pfannkuche, O. & Thiel, H. 1990. Vertical distribution and population structure of the necrophagous amphipod *Eurythenes gryllus* in the West European Basin. *Marine Ecology Progress Series* **66**, 35–45.

Clutter, R. I. 1965. Self-closing device for sampling plankton near the sea bottom. *Limnology and Oceanography* **10**, 293–5.

Clutter, R. I. 1967. Zonation of nearshore mysids. *Ecology* **48**, 200–8.

Clutter, R. I. 1969. The microdistribution and social behavior of some pelagic mysid shrimps. *Journal of Experimental Marine Biology and Ecology* **3**, 125–55.

Cockcroft, A., Webb, P. & Wooldridge, T. 1988. Nitrogen regeneration by two surf-zone mysids, *Mesopodopsis slabberi* and *Gastrosaccus psammodytes*. *Marine Biology* **99**, 75–82.

Colman, J. S. & Segrove, F. 1955. The tidal plankton over Stoupe Beck Sands, Robin Hood's Bay (Yorkshire, North Riding). *Journal of Animal Ecology* **24**, 445–62.

Cooper, S. D. & Goldman, C. R. 1980. Opossum shrimp (*Mysis relicta*) predation on zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 909–19.

Cornet, M., Bouchet, J.-M., Lissalde, J.-P. & Sorbe, J.-C. 1983. Données qualitatives sur le benthos et le suprabenthos d'un transect du plateau continental Sud-Gasconge. *Cahiers de Biologie Marine* **24**, 69–84.

Costello, M. J. 1992. Abundance and spatial overlap of gobies (Gobiidae) in Lough Hyne, Ireland. *Environmental Biology of Fishes* **33**, 239–48.

Dauvin, J.-C. & Dodson, J. J. 1990. Relationship between feeding incidence and vertical and longitudinal distribution of rainbow smelt larvae (*Osmerus mordax*) in a turbid well-mixed estuary. *Marine Ecology Progress Series* **60**, 1–12.

Dauvin, J.-C. & Lorgeré, J.-C. 1989. Modifications du traîneau Macer-GIROQ pour l'amélioration de l'échantillonage quantitatif étagé de la faune suprabenthique. *Journal de la Recherche Océanographique* **14**, 65–7.

Dauvin, J.-C., Iglesias, A. & Lorgeré, J.-C. 1994. Circalittoral suprabenthic coarse sand community from the western English Channel. *Journal of the Marine Biological Association of the United Kingdom* **74**, 543–62.

Dauvin, J.-C., Sorbe, J.-C. & Lorgeré, J.-C. 1995. Benthic boundary layer macrofauna from the upper continental slope and the Cap-Ferret canyon (Bay of Biscay). *Oceanologica Acta* **18**, 113–22.

Day, J. W., Hall, C. A. S., Kemp, W. M. & Yanez-Arancibia, A. (eds) 1989. *Estuarine ecology: the estuarine bottom and benthic subsystem.* New York: John Wiley, 338–76

Dodson, J. J., Dauvin, J.-C, Ingram, R. G. & D'Anglejan, B. 1989. Abundance of larval rainbow smelt (*Osmerus mordax*) in relation to the maximum turbidity zone and associated macroplankton fauna of the Middle St. Lawrence Estuary. *Estuaries* **12**, 66–81.

Eleftheriou, A. & Holme, N. A. 1984. Macrofauna techniques. In *Methods for the study of marine benthos*, N. A. Holme & A. D. McIntyre (eds). Oxford: Blackwell Scientific, 140–216.

Elizalde, M., Dauvin, J.-C. & Sorbe, J.-C. 1991. Les mysidacés suprabenthiques de le marge sud du canyon du Cap-Ferret (Golfe de Gascogne): repartition bathymetrique et activité natatoire. *Annales de l'Institut Océanographique Paris* **67**, 5–20.

Elizalde, M., Sorbe, J.-C. & Dauvin, J.-C. 1993. Las comunidades suprabentonicas batiales del golfo Vizcaya (margen sur del canon de Cap-Ferret): composicion faunistica y estructura. *Publicaciones Especiales Instituto Espanol de Oceanografia* **11**, 247–58.

Ellis, C. J. 1985. The effects of proximity to the continental slope sea-bed on pelagic halocyprid ostracods at 49 °N, 13 °S. *Journal of the Marine Biological Association of the United Kingdom* **65**, 923–49.

Elmhirst, R. 1932. Quantitative studies between tide-marks. *Glasgow Naturalist* **10**, 56–62.

Elster, H. J. 1933. Eine schlitten-dredge. *Internationale Revue der Gesamten Hydrobiologie* **29**, 290–92.

Emery, A. R. 1968. Preliminary observations on coral reef plankton. *Limnology and Oceanography* **13**, 293–303.

Essink, K., Kleef, H. L. & Visser, W. 1989. On the pelagic occurrence and dispersal of the benthic amphipod *Corophium volutator*. *Journal of the Marine Biological Association of the United Kingdom* **69**, 11–15.

Evans, S. M. 1971. Behaviour of polychaetes. *Quarterly Reviews of Biology* **46**, 379–405.

Fager, E. W., Flechsig, A. O., Ford, R. F., Clutter, R. I. & Ghelardi, R. J. 1966. Equipment for use in ecological studies using scuba. *Limnology and Oceanography* **11**, 503–9.

Falconetti, C. 1975. Etude à proximité du fond du comportement d'un prototype de filet à plancton à orientation variable. *Rapports et Procès-Verbaux des Réunions Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée* **23**, 149–51.

Falconetti, C. & Seguin, G. 1977. Sur une méthode d'utilisation d'un labaratoire sous-marin pour la récolte du zooplancton au voisinage du fond. *Bulletin de la Societé d'Ecologie* **8**, 183–90.

Feeley, M. T., Filer, D. L. & Schwartz, L. 1979. Zooplankton emerging from a Philippine coral reef: a preliminary study. *Journal of Asian Ecology* **1**, 51–6.

Fincham, A. A. 1970. Amphipods in the surf plankton. *Journal of the Marine Biological Association of the United Kingdom* **50**, 177–98.

Fossa, J. H. 1985. Near-bottom vertical zonation during daytime of deep-living hyperbenthic mysids (Crustacea: Mysidacea). *Sarsia* **70**, 297–307.

Fossa, J. H. 1986. Aquarium observations on vertical zonation and bottom relationships of some deep-living hyperbenthic mysids (Crustacea: Mysidacea). *Ophelia* **25**, 107–17.

Fossa, J. H. & Brattegard, T. 1990. Bathymetric distribution of Mysidacea in fjords of western Norway. *Marine Ecology Progress Series* **67**, 7–18.

Fossa, J. H., Larsson, J. & Buhl-Jensen, L. 1988. A pneumatic, bottom-activated, opening and closing device for epibenthic sledges. *Sarsia* **73**, 299–302.

Fosshagen, A. 1968. Marine biological investigations in the Bahamas. 4. Pseudocyclopidae (Copepoda, Calanoida) from the Bahamas. *Sarsia* **32**, 39–62.

Friedrich, H. 1969. *Marine biology: an introduction to its problems and results.* London: Sidgewick & Jackson.

Frolander, H. F. & Pratt, I. 1962. A bottom skimmer. *Limnology and Oceanography* **7**, 104–6.

Fulton, R. S. 1982a. Preliminary results of an experimental study of the effects of mysid predation on estuarine zooplankton community structure. *Hydrobiologia* **93**, 79–84.

Fulton, R. S. 1982b. Predatory feeding of two marine mysids. *Marine Biology* **72**, 183–91.

Gibson, R. N. & Ezzi, I. A. 1987. Feeding relationships of a demersal fish assemblage on the west coast of Scotland. *Journal of Fish Biology* **31**, 55–69.

Giere, O. 1993. *Meiobenthology: the microscopic fauna in aquatic sediments.* Berlin: Springer.

Giller, P. S. & Gee, J. H. R. 1987. The analysis of community organization: the influence of equilibrium, scale and terminology. In *Organization of communities, past and present*, J. H. R. Gee & P. S. Giller (eds). Oxford: Blackwell Scientific, 519–42.

Goswami, S. C. 1979. Diel variations of zooplankton at Kavaratti Atoll (Lakshadweep). *Indian Journal of Marine Science* **8**, 247–51.

Gottfried, M. & Roman, M. R. 1983. Ingestion and incorporation of coral-mucus detritus by reef zooplankton. *Marine Biology* **72**, 211–18.

Gowing, M. M. & Wishner, K. F. 1992. Feeding ecology of benthopelagic zooplankton on an eastern tropical Pacific Seamount. *Marine Biology* **112**, 451–67.

Greenwood, J. G., Jones, M. B. & Greenwood, J. 1985. Reproductive biology, seasonality and distribution of *Tenagomysis macropsis* W. Tattersall, 1923 (Crustacea, Mysidacea) in a New Zealand estuary. *Bulletin of Marine Science* **37**, 538–55.

Greze, V. N. 1951. Pridonni plankton, evo rol v pitanii ryb i metodika uchota [Bottom plankton, its role in the nutrition of fish and methods of its evaluation]. *Zoologicheskii Zhurnal* **30**, 44–50.

Grice, G. D. 1972. The existence of a bottom-living calanoid copepod fauna in deep water with description of five new species. *Crustaceana* **23**, 219–42.

Grice, G. D. & Hülsemann, K. 1970. New species of bottom-living calanoid copepods collected in deepwater by the DSRV Alvin. *Bulletin of the Museum of Comparative Zoology* **139**, 185–227.

Hamerlynck, O. & Mees, J. 1991. Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables. *Oceanologica Acta* (special volume) **11**, 205–12.

Hamilton, A. C. 1969. A method for separating invertebrates from sediments using longwave ultraviolet light and fluorescent dyes. *Journal of the Fisheries Research Board of Canada* **26**, 1667–72.

Hamner, W. M. & Carleton, J. H. 1979. Copepod swarms: attributes and role in coral reef ecosystems. *Limnology and Oceanography* **24**, 1–14.

Hargreaves, P. M. 1984. The distribution of Decapoda (Crustacea) in the open ocean and near-bottom over an adjacent slope in the northern North-east Atlantic during autumn 1979. *Journal of the Marine Biological Association of the United Kingdom* **64**, 829–57.

Hargreaves, P. M. 1985. The distribution of Mysidacea in the open ocean and near-bottom over slope regions in the northern North-east Atlantic during 1979. *Journal of Plankton Research* **7**, 241–61.

Hensen, V. 1895. Methodik der untersuchungen. *Ergebnisse der Plankton Expedition Humboldt* **1B**, 1–200.

Hesthagen, I. H. 1970. On the near-bottom plankton and benthic invertebrate fauna of the Josephine Seamount and the Great Meteor Seamount. "*Meteor*" *Forschungen-Ergebnisse* **D8**, 61–70.

Hesthagen, I. H. 1973. Diurnal and seasonal variations in the near-bottom fauna – the hyperbenthos – in one of the deeper channels of the Kieler Bucht (Western Baltic). *Kieler Meeresforschungen* **29**, 116–40.

Hesthagen, I. H. & Gjermundsen, B. 1978. The replicability of sampling the hyperbenthic region by means of Beyer's 50 cm epibenthic closing net. *Kieler Meeresforschungen* **26**, 1–10.

Hesthagen, I. H. & Gjermundsen, B. 1979. Late summer diurnal migration in the hyperbenthos of Vejsnäs Rinne, Western Baltic. *Kieler Meeresforschungen* **27**, 19–26.

Hjort, J. & Dahl, K. 1900. Fishing experiments in Norwegian fjords. *Report on Norwegian Fishery and Marine Investigations* **1**, 1–125.

Hobson, E. S. & Chess, J. R. 1978. Trophic relationships among fishes and plankton in the lagoon at Eniwetok Atoll, Marshall Islands. *Fisheries Bulletin* **76**, 133–53.

Hobson, E. S. & Chess, J. R. 1979. Zooplankton that emerge from the lagoon floor at night at Kure and Midway Atolls, Hawaii. *Fisheries Bulletin* **77**, 275–80.

Holme, N. A. 1964. Methods of sampling the benthos. *Advances in Marine Biology* **2**, 171–260.

Holme, N. A. 1984. Photography and television. In *Methods for the study of marine benthos*, N. A. Holme & A. D. McIntyre (eds). Oxford: Blackwell Scientific, 66–98.

Holt, E. W. L. & Tattersall, W. M. 1905. Schizopodous Crustacea from the north-east Atlantic slope. *Scientific Investigations of the Fisheries Board of Ireland* 1902–03, 99–152.

Hough, A. R. & Naylor, E. 1992. Distribution and position maintenance behaviour of the estuarine mysid *Neomysis integer*. *Journal of the Marine Biological Association of the United Kingdom* **72**, 869–76.

Huberdeau, L. & Brunel P. 1982. Efficacité et sélectivité faunistique comparée de quatre appareils de prélèvement endo-, épi- et suprabenthiques sur deux types de fonds. *Marine Biology* **69**, 331–43.

Hudon, C., Crawford, R. E. & Ingram, R. G. 1993. Influence of physical forcing on the spatial distribution of marine fauna near Resolution Island (eastern Hudson Strait). *Marine Ecology Progress Series* **92**, 1–14.

Hughes, R. G. 1988. Dispersal by benthic invertebrates: the *in situ* swimming behaviour of the amphipod *Corophium volutator*. *Journal of the Marine Biological Association of the United Kingdom* **65**, 565–79.

Isaac, J. D. & Kidds, L. W. 1953. High-speed diving dredge. *Scripps Institute of Oceanography, Oceanographic Equipment Reports* **4**, 1–7.

Jacoby, C. A. & Greenwood, J. G. 1988. Spatial, temporal, and behavioral patterns in emergence of zooplankton in the lagoon of Heron Reef, Great Barrier Reef, Australia. *Marine Biology* **97**, 309–28.

Jahn, A. E. & Lavenberg, R. J. 1986. Fine-scale distribution of nearshore, suprabenthic fish larvae. *Marine Ecology Progress Series* **31**, 223–31.

Jansen, W. 1985. Fang und verhalten von *Neomysis integer* Leach (Crustacea, Mysidacea) in der Dars-Zingster Boddenkette (südliche Ostsee). *Fischerei-Forschung Wissenshaftliche Schriftenreihe* **23**, 33–6.

Jansson, B.-O. & Källander, C. 1968. On the diurnal activity of some littoral peraicarid crustaceans in the Baltic Sea. *Journal of Experimental Marine Biology and Ecology* **2**, 24–36.

Johannes, R. E., Coles, S. L. & Kuenzel, N. T. 1970. The role of zooplankton in the nutrition of some scleractinian corals. *Limnology and Oceanography* **15**, 579–86.

Johnson, S. R. 1984. Prey selection by oldsquaws in a Beaufort Sea lagoon, Alaska. In *Marine birds: their feeding ecology and commercial fisheries relationships*, D. N. Nettleship et al. (eds). Dartmouth, Nova Scotia: Canadian Wildlife Service, 12–19.

Johnston, N. T. & Lasenby, D. C. 1982. Diet and feeding of *Neomysis mercedis* Holmes (Crustacea, Mysidacea) from the Frazer River Estuary, British Columbia. *Canadian Journal of Zoology* **60**, 813–24.

Jones, M. B., Greenwood, L. G. & Greenwood, J. 1989. Distribution, body size, and brood characteristics of four species of mysids (Crustacea: Peracarida) in the Avon-Heathcote estuary. *New Zealand Journal of Marine and Freshwater Research* **23**, 195–9.

Jones, N. S. 1950. Marine bottom communities. *Biological Reviews* **25**, 283–313.

Kaartvedt, S. 1985. Diel changes in small-scale vertical distribution of hyperbenthic mysids. *Sarsia* **70**, 287–95.

Kaartvedt, S. 1986. Diel activity patterns in deep-living cumaceans and amphipods. *Marine Ecology Progress Series* **30**, 243–9.

Kaartvedt, S. 1989. Nocturnal swimming of gammaridean amphipod and cumacean Crustacea in Masfjorden, Norway. *Sarsia* **74**, 187–93.

Kawagushi, K., Matsuda, O., Ishikawa, S. & Naito, Y. 1986. A light trap to collect krill and other micronektonic and planktonic animals under the Antarctic coastal fast ice. *Polar Biology* **6**, 37–42.

Kritzler, H. & Eidemiller, A. 1972. A diver-monitored dredge for sampling motile epibenthos. *Journal of the Marine Biological Association of the United Kingdom* **52**, 553–6.

Lacroix, G. & Bergeron, I. 1962. Liste préliminaire des invertébrés du banc de Bradelle. *Rapport annuel de la Station de Biologie marine Grande Rivière* 1962, 59–67.

Larson, R. J., Matsumoto, G. I., Madin, L. P. & Lewis, L. M. 1992. Deep-sea benthic and benthopelagic medusae: recent observations from submersibles and a remotely operated vehicle. *Bulletin of Marine Science* **51**, 277–86.

Lasenby, D. C. & Sherman, R. K. 1991. Design and evaluation of a bottom-closing net used to capture mysids and other suprabenthic fauna. *Canadian Journal of Zoology* **69**, 783–6.

Laughlin, R. & Linden, O. 1983. Oil pollution and Baltic mysids: acute and chronic effects of the water soluble fractions of light fuel oil on the mysid shrimp *Neomysis integer*. *Marine Ecology Progress Series* **12**, 29–41.

Ledoyer, M. 1964. Les migrations nyctémérales de lafaune vagile au sein des herbiers de *Zostera marina* de la zone intertidale en manche et comparison avec les migrations en Méditérrannée. *Recueil des Travaux de la Station Marine d'Endoume* **34**, 241–7.

Le Mao, P. 1985. Place de la seiche *Sepia officinalis* (mollusque, Cephalopoda) dans les chaines alimentaires du golfe Normano-Breton. *Cahiers de Biologie Marine* **26**, 331–40.

Lewis, J. B. & Boers, J. J. 1991. Patchiness and composition of coral reef demersal zooplankton. *Journal of*

Plankton Research **13**, 1273–89.

Macer, C. T. 1967. A new bottom-plankton sampler. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **31**, 158–63.

Macquart-Moulin, C. 1976. Rhythmes d'activité persistants chez les péricarides du plancton nocturne de Méditerranée (Amphipodes, Isopodes). *Marine Behaviour and Physiology* **7**, 64–83.

Macquart-Moulin, C. 1984. La phase pélagique nocturne et les comportements migratoires des amphipodes benthiques (Mediterranée Nord-Occidentale). *Téthys* **11**, 171–96.

Macquart-Moulin, C. 1985. Le contrôle des phases pélagiques nocturnes chez les crustacés péricarides benthiques. *Téthys* **11**, 275–87.

Macquart-Moulin, C. 1991. La phase nocturne des cumacés. *Journal of Plankton Research* **13**, 313–37.

Madhupratap, M., Achuthankutty, C. T. & Sreekumaran-Nair, S. R. 1991. Estimates of high absolute densities and emergence rates of demersal zooplankton from the Agatti Atol, Laccadives. *Limnology and Oceanography* **36**, 585–8.

Marshall, N. B. & Merrett, N. R. 1977. The existence of a benthopelagic fauna in the deep sea. *Deep-Sea Research* (suppl.) **24**, 483–97.

Mason, W. T. & Clugston, J. P. 1993. Foods of the Gulf sturgeon in the Suwannee River, Florida. *Transactions of the American Fisheries Society* **122**, 378–85.

Matthews, J. B. L. 1961. A new species of copepod (Calanoida) from western Norway. *Sarsia* **4**, 33–8.

Mattsson, S. 1990. Food and feeding habits of fish species over a soft sublittoral bottom in the Northeast Atlantic. 1. Cod (*Gadus morhua* L.) (Gadidae). *Sarsia* **75**, 247–60.

Mauchline, J. 1972. Assessing similarity between samples of plankton. *Journal of the Marine Biological Association of India* **14**, 26–41.

Mauchline, J. 1980. The biology of mysids and euphausiids. *Advances in Marine Biology* **18**, 1–680.

Mauchline, J. 1982. The predation of mysids by fish of the Rockall Trough, northern Atlantic Ocean. *Hydrobiologia* **93**, 85–95.

Mauchline, J. 1986. The biology of the deep-sea species of Mysidacea (Crustacea) of the Rockall Trough. *Journal of the Marine Biological Association of the United Kingdom* **66**, 803–24.

Mauchline, J. & Gordon, J. D. M. 1991. Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology Progress Series* **74**, 109–15.

McCall, J. N. & Fleeger, J. W. 1995. Predation by juvenile fish on hyperbenthic meiofauna: a review with data on post-larval *Lelostomus xanthurus*. *Vie et Milieu* **45**, 61–73.

McCave, I. N. (ed.) 1976. *The benthic boundary layer*. New York: Plenum.

McLachlan, A., Wooldridge, T., Schramm, M. & Kuhn, M. 1980. Seasonal abundance, biomass and feeding of shorebirds on sandy beaches in the eastern Cape, South Africa. *Ostrich* **51**, 44–52.

McIvor, C. C. & Odum, W. E. 1986. The flume net: a quantitative method for sampling macrocrustaceans on tidal marsh surfaces. *Estuaries* **9**, 219–24.

McWilliam, P. S., Sale, P. F. & Anderson, D. T. 1981. Seasonal changes in resident zooplankton sampled by emergence traps in One Tree Lagoon, Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* **52**, 185–203.

Mees, J., Abdulkerim, Z. & Hamerlynck, O. 1994. Life history, growth and production of *Neomysis integer* in the Westerschelde Estuary (S. W. Netherlands). *Marine Ecology Progress Series* **109**, 43–57.

Mees, J., Cattrijsse, A. & Hamerlynck, O. 1993a. Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, southwest Netherlands. *Cahiers de Biologie Marine* **34**, 165–86.

Mees, J., Dewicke, A. & Hamerlynck, O. 1993b. Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. *Netherlands Journal of Aquatic Ecology* **27**, 359–76.

Mees, J. & Fockedey, N. 1993. First record of *Synidotea laevidorsalis* (Miers, 1881) (Crustacea: Isopoda) in Europe (Gironde Estuary, France). *Hydrobiologia* **264**, 61–3.

Mees, J., Fockedey, N. & Hamerlynck, O. 1995. Comparative study of the hyperbenthos of three European estuaries. *Hydrobiologia* **311**, 153–74.

Mees, J. & Hamerlynck, O. 1992. Spatial community structure of the winter hyperbenthos of the Schelde Estuary, The Netherlands, and the adjacent coastal waters. *Netherlands Journal of Sea Research* **29**, 357–70.

Metaxas, A. & Scheibling, R. E. 1994. Spatial and temporal variability of tidepool hyperbenthos on a rocky shore in Nova Scotia, Canada. *Marine Ecology Progress Series* **108**, 175–84.

Miller, J. M. 1973. A quantitative push-net system for transect studies of larval fish and macrozooplankton.

Limnology and Oceanography **18**, 152–4.

Moffat, A. M. & Jones, M. B. 1992. Bionomics of *Mesopodopsis slabberi* and *Neomysis integer* (Crustacea: Mysidacea) in the Tamar Estuary (S. W. England). In *Taxonomy, biology and ecology of (baltic) mysids (Mysidacea: Crustacea)*, J. Köhn et al. (eds). Rostock: Rostock University Press, 110–20.

Möller, H. 1979. Significance of coelenterates in relation to other plankton organisms. *Kieler Meeresforschungen* **27**, 1–18.

Moore, J. W., Moore, I. A. & Claridge, P. N. 1979. Seasonal changes in density, composition and reproductive biology of crustacean populations in the Severn Estuary. *Crustaceana* **36**, 113–22.

Moran, S. & Fishelson, L. 1971. Predation of sand-dwelling mysid crustacean *Gastrosaccus sanctus* by plover birds (Charadriidae). *Marine Biology* **9**, 63–4.

Moreira, F., Assis, C. A., Almeida, P. R., Costa, J. L. & Costa, M. J. 1992. Trophic relationships in the community of the upper Tagus Estuary (Portugal): a preliminary approach. *Estuarine, Coastal and Shelf Science* **34**, 617–23.

Mullin, M. M. & Roman, M. R. 1986. *In situ* feeding of a schooling mysid, *Anisomysis sp.*, on Davies Reef-MECOR 4. *Bulletin of Marine Science* **39**, 623–9.

Munilla Léon, T. & Corrales, M. J. 1995. Suprabentos de la playa de Rosas (Gerona, Mediterraneo occidental). *Orsis* **10**, 83–90.

Murison, L. D., Murie, D. J., Morin, K. R. & de Silva Curiel, J. 1984. Foraging of the grey whale along the west coast of Vancouver Island, British Columbia. In *The grey whale* Eschrichtus robustus, M. L. Jones et al. (eds), London: Academic Press, 451–63.

Murthaugh, P. A. 1981. Size-selective predation on *Daphnia* by *Neomysis mercedis*. *Ecology* **62**, 894–900.

Norcross, B. L. & Shaw, R. F. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. *Transactions of the American Fisheries Society* **113**, 153–65.

O'Brien, D. P. 1988. Direct observations of clustering (schooling and swarming) behaviour in mysids (Crustacea: Mysidacea). *Marine Ecology Progress Series* **42**, 235–46.

O'Brien, D. P. & Ritz, D. A. 1988. Escape responses of gregarious mysids (Crustacea: Mysidacea): towards a general classification of escape responses in aggregated crustaceans. *Journal of Experimental Marine Biology and Ecology* **116**, 257–72.

Ockelmann, K. W. 1964. An improved detritus-sledge for collecting meiobenthos. *Ophelia* **1**, 217–22.

Ohlhorst, S. L. 1982. Diel migration patterns of demersal reef zooplankton. *Journal of Experimental Marine Biology and Ecology* **60**, 1–15.

Ohtsuka, S. & Mitsuzumi, C. 1990. A new asymmetrical near-bottom calanoid copepod, *Paramisophria platysoma*, with observations of its integumental organs, behavior and *in-situ* feeding habit. *Bulletin of the Planktonological Society of Japan* **36**, 87–101.

Ohtsuka, S., Fosshagen, A. & Go, A. 1991. The hyperbenthic calanoid copepod *Paramisophria* from Okinawa, South Japan. *Zoological Science* **8**, 793–804.

Ohtsuka, S., Huys, R., Boxshall, G. A. & Ito, T. 1992. *Misophriopsis okinawensis*, new species (Crustacea: Copepoda) from hyperbenthic waters off Okinawa, South Japan, with definitions of related genera *Misophria* Boeck, 1864 and *Stygomisophria*, new genus. *Zoological Science* **9**, 859–74.

Ohtsuka, S., Roe, H. S. J. & Boxshall, G. A. 1993. A new family of calanoid copepods, the Hyperbionycidae, collected from the deep-sea hyperbenthic community in the northeastern Atlantic. *Sarsia* **78**, 69–82.

Omori, M. 1969. A bottom-net to collect zooplankton living close to the sea-floor. *Journal of the Oceanographical Society of Japan* **25**, 291–4.

Omori, M. 1978. Zooplankton fisheries of the world: a review. *Marine Biology* **48**, 199–205.

Omori, M. & Hamner, M. W. 1982. Patchy distribution of zooplankton: behavior, population assessment and sampling problems. *Marine Biology* **72**, 193–200.

Oug, E. 1977. Faunal distribution close to the sediment of a shallow marine environment. *Sarsia* **63**, 115–21.

Palmer, M. A. 1988. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Marine Ecology Progress Series* **48**, 81–91.

Pawson, D. L. & Foell, E. J. 1986. *Peniagone leander* new species, an abyssal benthopelagic sea cucumber (Echinodermata: Holothuroidea) from the eastern central Pacific Ocean. *Bulletin of Marine Science* **38**, 293–9.

Pearson, T. H. & Rosenberg, R. 1987. Feast and famine: structuring factors in marine benthic communities. In *Organization of communities, past and present*, J. H. R. Gee & P. S. Giller (eds). Oxford: Blackwell Scientific, 373–95.

Perissinotto, R. & McQuaid, C. 1990. Role of the sub-Antarctic shrimp *Nauticaris marionis* in coupling benthic and pelagic food-webs. *Marine Ecology Progress Series* **64**, 81–7.

Poirier, L., Granger, D., Weinstein, M. & Brunel, P. 1969. Pêches hyperbenthiques et planctoniques quantitatives à l'entrée de la baie des Chaleurs: protocole et méthodes en 1968. *Rapport annuel de la Station de Biologie marine Grande Rivière* 1969, 47–57.

Porter, J. W. & Porter, K. G. 1977. Quantitative sampling of demersal plankton migrating from different coral reef substrates. *Limnology and Oceanography* **22**, 553–6.

Porter, J. W., Porter, K. G. & Catalan, Z. B. 1977. Cited in Jacoby & Greenwood (1988).

Potts, G. W. 1976. A diver-contolled plankton net. *Journal of the Marine Biological Association of the United Kingdom* **56**, 959–62.

Qian, P.-Y. & Chia, F.-S. 1989. Larval development of *Autolytus alexandri* Malmgren 1867 (Polychaeta, Syllidae). *Invertebrate Reproduction and Development* **15**, 49–56.

Redant, F. 1989. Productivity of epibenthic species: a review. *International Council for the Exploration of the Sea* CM 1989/L2, 1–34.

Reighard, J. E. 1894. Some plankton studies in the Great Lakes. *Bulletin of the United States Fisheries Committee* **13**, 127–42.

Remane, A. 1940. Einführung in die zoologische Okologie der Nord- und Ostsee. *Tierwelt Nord- und Ostsee* **I**, 1–238.

Rice, A. L., Aldred, R. G., Darlington, E. & Wild, R. A. 1982. The quantitative estimation of the deep-sea megabenthos; a new approach to an old problem. *Oceanologica Acta* **5**, 63–72.

Roman, M. R., Furnas, M. F. & Mullin, M. M. 1990. Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef, Australia. *Marine Biology* **105**, 73–82.

Rothlisberg, P. C. & Pearcy, W. G. 1977. An epibenthic sampler used to study the ontogeny of vertical migration of *Pandalus jordani* (Decapoda, Caridea). *Fisheries Bulletin of the United States* **74**, 994–7.

Rudstam, L. G., Hansson, S. & Larsson, U. 1986. Abundance, species composition and production of mysid shrimps in a coastal area of the northern Baltic proper. *Ophelia* (suppl.) **4**, 225–38.

Russell, F. S. 1925. The vertical distribution of marine macroplankton. I. An observation on diurnal changes. *Journal of the Marine Biological Association of the United Kingdom* **13**, 769–809.

Russell, F. S. 1926. The vertical distribution of marine macroplankton. IV. The apparant importance of light intensity as a controlling factor in the behaviour of certain species in the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom* **14**, 415–40.

Russell, F. S. 1928. A net for catching plankton near the bottom. *Journal of the Marine Biological Association of the United Kingdom* **15**, 105–8.

Russell, F. S. 1931. The vertical distribution of marine macroplankton. XI. Further observations on diurnal change. *Journal of the Marine Biological Association of the United Kingdom* **17**, 767–84.

Russell, F. S. 1933. The seasonal distribution of macroplankton as shown by catches in the 2-metre stramin ring trawl in offshore waters off Plymouth. *Journal of the Marine Biological Association of the United Kingdom* **19**, 73–82.

Rützler, K., Ferraris, J. D. & Larson, R. J. 1980. A new plankton sampler for coral reefs. *P.S.Z.N.I: Marine Ecology* **1**, 65–71.

Sainte-Marie, B. & Brunel, P. 1983. Differences in life history and success between suprabenthic shelf populations of *Arrhis phyllonyx* (Amphipoda, Gammaridea) in two ecosystems of the Gulf of St. Lawrence. *Journal of Crustacean Biology* **3**, 45–69.

Sainte-Marie, B. & Brunel, P. 1985. Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of Saint Lawrence. *Marine Ecology Progress Series* **23**, 57–69.

Sale, P. F., McWilliam, P. S. & Anderson, D. T. 1976. Composition of the near-reef zooplankton at Heron Reef, Great Barrier Reef. *Marine Biology* **34**, 59–66.

Sale, P. F., McWilliam, P. S. & Anderson, D. T. 1978. Faunal relationships among the near-shore zooplankton at three locations on Heron Reef, Great Barrier Reef, and seasonal changes in this fauna. *Marine Biology* **49**, 133–45.

Salemaa, H., Vuorinen, I. & Vaelipakka, P. 1990. The distribution and abundance of *Mysis* populations in the Baltic Sea. *Annales Zoologici Fennici* **27**, 253–7.

San Vicente, C. & Sorbe, J.-C. 1990. Biologia del misidaceo suprabentonico *Schistomysis kervillei* (Sars, 1885) en la plataforma continental aquitana (suroeste de Francia). *Bentos* **6**, 245–67.

San Vicente, C. & Sorbe, J.-C. 1993. Biologie du mysidacé suprabenthique *Schistomysis parkeri* Norman, 1892 dans la zone sud de Golfe de Gacogne (Plage d'Hendaye). *Crustaceana* **65**, 222–52.

Sars, G. O. 1870. Paraphrased in Beyer (1958).

Sars, G. O. 1895. *An account of the Crustacea of Norway. I. Amphipoda.* Copenhagen.

Sars, G. O. 1903. *An account of the Crustacea of Norway. IV. Copepoda Calanoida.* Bergen.

Schnack, D. 1978. Comments on sampling tests made with Beyer's epibenthic closing net. *Kieler Meeresforschungen* **26**, 11–14.

Schneider, D. C. 1981. Size-selective predation on mysids by birds (plovers). *Marine Ecology Progress Series* **5**, 223–4.

Schroeder, W. W. 1974. Collecting and handling zooplankton and epibenthic organisms underwater. *Marine Technological Society of Japan* **8**, 40–3.

Sentz-Braconnot, F. 1967. Sur un filet permettant la récolte des animaux semi-planctoniques des herbiers de posidonies. *Vie et Milieu* **18**, 453–5.

Setran, A. C. 1992. A new plankton trap for use in the collection of rocky intertidal zooplankton. *Limnology and Oceanography* **37**, 669–74.

Shelford, V. E. & Boesel, M. W. 1942. Bottom animal communities of the island area of Western Lake Erie in the summer of 1937. *Ohio Journal of Science* **42**, 179–90.

Sherman, K. M. & Coull, B. C. 1980. The response of meiofauna to sediment disturbance. *Journal of Experimental Marine Biology and Ecology* **46**, 59–71.

Sibert, J. R. 1981. Intertidal hyperbenthic populations in the Nanaimo Estuary. *Marine Biology* **64**, 259–65.

Siegfried, C. A. 1982. Trophic relations of *Crangon fransiscorum* Stimpson and *Palaemon macrodactylus* Rathbun: predation on the opossum shrimp *Neomysis mercedis* Holmes. *Hydrobiologia* **89**, 129–39.

Simard, Y., Brunel, P. & Lacelle, J. 1990. Distribution and growth of pre-recruit cohorts of the northern shrimp (*Pandalus borealis*) in the western Gulf of St. Lawrence as related to hydrographic conditions. *Canadian Journal of Fisheries and Aquatic Science* **47**, 1526–33.

Simm, M. & Kotta, I. 1992. The life cycle and production of *Mysis mixta* in the Gulf of Riga. In *Taxonomy, biology and ecology of* (*baltic*) *mysids* (*Mysidacea: Crustacea*), J. Köhn et al. (eds), Rostock: Rostock University Press, 45–54.

Smidt, E. L. B. 1951. Animal production in the Danish Waddensea. *Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersögelser, Serie Fiskeri* **11**, 1–151.

Sorbe, J.-C. 1981a. Rôle du benthos dans la régime alimentaire des poissons démer-saux du secteur Sud Gascogne. *Kieler Meeresforschungen* sonderheft **5**, 479–89.

Sorbe, J.-C. 1981b. La macrofaune vagile de l'estuaire de la Gironde: distribution et migration des éspèces, modes de reproduction, régimes alimentaires. *Oceanis* **6**, 579–92.

Sorbe, J.-C. 1983. Description d'un traîneau destiné à l'échantillonnage quantitatif étagé de la faune suprabenthique néritique. *Annales de l'Institut Océanographique* **59**, 117–26.

Sorbe, J.-C. 1989. Structural evolution of two suprabenthic soft-bottom communities of the South Gascogne continental shelf. *Scientia Marina* **53**, 335–42.

Sorbe, J.-C. 1991. Biologia del mysidaceo suprabentonico *Schistomysis ornata* (Sars, 1864) en la plataforma continental aquitana (suroeste de Francia). *Actas del V Simposio Ibérico de Estudias del Bentos Marino* **1**, 273–98.

Steele, D. H. & Montevecchi, W. A. 1994. Leach's storm-petrels prey on lower mesopelagic (Mysidacea and Decapoda) crustaceans: possible implications for crustacean and avian distributions. *Crustaceana* **66**, 212–18.

Stefanescu, C. & Cartes, J. E. 1992. Benthopelagic habits of adult specimens of *Lampanyctus crocodilus* (Risso, 1810) (Osteichthyes, Myctophidae) in the western Mediterranean deep slope. *Scientia Marina* **56**, 69–74.

Stretch, J. S. 1985. Quantitative sampling of demersal zooplankton: reentry and airlift dredge sample comparisons. *Journal of Experimental Marine Biology and Ecology* **91**, 125–36.

Sulkin, S. D. 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Marine Ecology Progress Series* **15**, 181–205.

Takahashi, K. & Kawagushi, K. 1995. Inter- and intraspecific zonation in three species of sand-burrowing mysids, *Archaeomysis kokubol*, *A. grebnitzkii* and *Iiella ohshimai*, in Otsuchi Bay, northeastern Japan. *Marine Ecology Progress Series* **116**, 75–84.

Tattersall, W. M. 1906. The marine fauna of the coast of Ireland. Part V. Isopoda. *Scientific Investigations of the Fisheries Board of Ireland* 1904, 53–142.

Tattersall, W. M. 1938. The seasonal occurrence of mysids off Plymouth. *Journal of the Marine Biological Association of the United Kingdom* **23**, 43–56.

Tattersall, W. M. & Tattersall, O. S. 1951. *The British Mysidacea.* London: Ray Society.

Turnbull, C. T. & Watson, R. A. 1992. Sledges for daytime sampling of juvenile penaeid shrimp. *Fisheries*

Research **14**, 31–40.

UNESCO 1968. Zooplankton Sampling. *Monographs on Oceanographic Methodology* **2**, 1–174.

Vaissière, R. & Falconetti, C. 1975. Prototype d'un filet pour la capture du plancton à proximité du fond. *Rapports et Procès-Verbaux de la Réunions Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée* **23**, 153–4.

Vaissière, R. & Seguin, G. 1984. Initial observations of the zooplankton microdistribution on the fringing coral reef at Aqaba (Jordan). *Marine Biology* **83**, 1–11.

Van Cleve, R., Ting, R. Y. & Kent, J. C. 1966. A new device for sampling marine demersal animals for ecological study. *Limnology and Oceanography* **11**, 438–43.

Villanueva, R. & Guerra, A. 1991. Food and prey detection in two deep-sea cephalopods: *Opisthoteuthis agassizi* and *O. vossi* (Octopoda: Cirrata). *Bulletin of Marine Science* **49**, 288–99.

Walford, L. A. 1938. Effect of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Bulletin of the United States Bureau of Fisheries* **49**, 1–73.

Wang, Z. & Dauvin, J.-C. 1994. The suprabenthic crustacean fauna of the infralittoral fine sand community in the Bay of Seine (Eastern English Channel): composition, swimming activity and diurnal variation. *Cahiers de Biologie Marine* **35**, 135–55.

Wang, Z., Dauvin, J.-C. & Thiébaut, E. 1994. Preliminary data on the near-bottom meso- and macrozooplanktonic fauna from the eastern Bay of Seine: faunistic composition, vertical distribution and density variation. *Cahiers de Biologie Marine* **35**, 157–76.

Watkin, E. E. 1939. The pelagic phase in the life-history of the amphipod genus *Bathyporeia*. *Journal of the Marine Biological Association of the United Kingdom* **23**, 467–81.

Watkin, E. E. 1941. Observations on the night tidal migrant crustacea of Kames Bay. *Journal of the Marine Biological Association of the United Kingdom* **25**, 81–96.

Webb, P. & Wooldridge, T. H. 1990. Diel horizontal migration of *Mesopodopsis slabberi* (Crustacea: Mysidacea) in Algoa Bay, southern Africa. *Marine Ecology Progress Series* **62**, 73–7.

Webb, P., Perissinotto, R. & Wooldridge, T. H. 1987. Feeding of *Mesopodopsis slabberi* (Crustacea, Mysidacea) on naturally occurring phytoplankton. *Marine Ecology Progress Series* **38**, 115–23.

Werner, B. 1938. Uber ein neues, automatisch schliessendes bodennetz. *Internationale Revue der Gesamten Hydrobiologie* **38**, 368–71.

Wickstead, J. 1953. A new apparatus for the collection of bottom plankton. *Journal of the Marine Biological Association of the United Kingdom* **32**, 347–55.

Wildish, D. J., Wilson, W. J. & Frost, B. 1992. Benthic boundary layer macrofauna of Browns Bank, Northwest Atlantic, as potential prey of juvenile benthic fish. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 91–8.

Wilkins, H. K. A. & Myers, A. A. 1992. Microhabitat utilization by an assemblage of temperate Gobiidae (Pisces: Teleostei). *Marine Ecology Progress Series* **90**, 103–12.

Williams, D. D. & Williams, N. E. 1974. A counterstaining technique for use in sorting benthic samples. *Limnology and Oceanography* **19**, 152–4.

Williams, R. & Collins, N. R. 1984. Distribution and variability in abundance of *Schistomysis spiritus* (Crustacea: Mysidacea) in the Bristol Channel in relation to environmental variables, with comments on other mysids. *Marine Biology* **80**, 197–206.

Wilson, C. B. 1932. The copepods of the Woods Hole region, Massachusetts. *Bulletin of the United States Natural History Museum* **158**, 1–635.

Wishner, K. F. 1980a. The biomass of the deep-sea benthopelagic plankton. *Deep-Sea Research* **27**, 203–16.

Wishner, K. F. 1980b. Near-bottom sound scatterers in the Ecuador Trench. *Deep-Sea Research* **27**, 217–23.

Wishner, K. F. 1980c. Aspects of the community ecology of deep-sea, benthopelagic plankton, with special attention to gymnopleid copepods. *Marine Biology* **60**, 179–87.

Wishner, K. F. & Meise-Munns, C. J. 1984. *In situ* grazing rates of deep-sea benthic boundary-layer zooplankton. *Marine Biology* **84**, 65–74.

Wittmann, K. J. 1977. Modification of association and swarming in North Adriatic Mysidacea in relation to habitat and interacting species. In *Biology of benthic organisms*, B. K. Keegan et al. (eds). Oxford: Pergamon Press, 605–12.

Wooldridge, T. H. 1983. Ecology of beach and surf-zone mysid shrimps in the Eastern Cape, South Africa. In *Sandy beaches as ecosystems*, A. McLachlan & T. Erasmus (eds). The Hague: Junk, 449–60.

Wooldridge, T. H. 1989. The spatial and temporal distribution of mysid shrimps and phytoplankton accumulations in a high energy surfzone. *Vie et Milieu* **39**, 127–33.

Youngbluth, M. J. 1982. Sampling demersal zooplankton: a comparison of field collections using three different emergence traps. *Journal of Experimental Marine Biology and Ecology* **61**, 111–24.

Zander, C. D. & Hartwig, E 1982. On the biology and food of small-sized fish from North and Baltic Sea areas. 4. Investigations on an eulittoral mud flat at Sylt Island. *Helgoländer Meeresuntersuchungen* **35**, 47–63.

Zouhiri, S. & Dauvin, J.-C. 1996. Diel changes of the benthic boundary layer macrofauna over coarse sand sediment in the Western English Channel. *Oceanologica Acta* **19**, 141–53.