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From the Hensen net toward four-dimensional biological oceanography

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Abstract

The development of quantitative zooplankton collecting systems began with Hensen (1887 Berichte der Kommssion wissenschaftlichen Untersuchung der deutschen Meere in Kiel 5, 1–107; 1895 Ergebnisse der Plankton-Expedition der Humbolt-Stiftung. Kiel and Leipzig: Lipsius and Tischer). Non-opening closing nets, opening closing nets (mostly messenger based), high-speed samplers, and planktobenthos net systems all had their start in his era — the late 1800s and early 1900s. This was also an era in which many of the fundamental questions about the structure and dynamics of the plankton in the worlds oceans were first posed. Fewer new systems were introduced between 1912 and 1950 apparently due in part to the two World Wars. The continuous plankton recorder stands out as a truly innovative device developed during this period (Hardy 1926b Nature, London 118, 630). Resurgence in development of mechanicallybased instruments occurred during the 1950s and 1960s. A new lineage of high-speed samplers, the Gulf series, began in the 1950s and a number of variants were developed in the 1960s and 1970s. Net systems specifically designed to collect neuston first appeared in the late 1950s. During the 1960s, many focused field and experimental tank experiments were carried out to investigate the hydrodynamics of nets, and much of our knowledge concerning net design and construction criteria was developed. The advent of reliable electrical conducting cables and electrically-based control systems during this same period gave rise first to a variety of cod-end samplers and then to the precursors of the acoustically and electronically-controlled multi-net systems and environmental sensors, which appeared in the 1970s. The decade of the 1970s saw a succession of multi-net systems based both on the Bé multiple plankton sampler and on the Tucker trawl. The advent of the micro-computer stimulated and enabled the development of sophisticated control and data logging electronics for these systems in the 1980s. In the 1990s, acoustic and optical technologies gave rise to sensor systems that either complement multiple net systems or are deployed without nets. Multi-sensor systems with high data telemetry rates through electro-optical cable are now being deployed in towed bodies and on remotely operated vehicles. In the offing are new molecular technologies to identify species in situ, and realtime data analysis, image processing, and 3D/4D display. In the near future, it is likely that the use of multi-sensor systems deployed on autonomous vehicles will yield world wide coverage of the distribution and abundance of zooplankton. © 2002 Elsevier Science Ltd. All rights reserved.

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Contents

1. Introduction	8
2. The late 1800s to the mid-1900s 2.1. A context for plankton sampler development 2.2. Net developments in the first half of the 20th century 2.2.1. Water column samplers 2.2.1.1. Non-opening/closing nets 2.2.1.2. Simple opening/closing nets 2.2.1.3. High-speed samplers 2.2.2. Neuston 2.2.3. Planktobenthos plankton nets	10 10 14 15 15 19 31 41 41
3. Technological advances in the 1960–1990s 3.1. Closing cod-end systems 3.2. Multiple net systems 3.3. Moored plankton collection systems 3.4. Optical systems 3.4.1. Image-forming systems mounted on non-opening/closing nets 3.4.2. Stand-alone image-forming systems 3.4.3. Particle detection systems 3.4.4. Optical instruments for non-quantitative studies 3.5. High-frequency acoustics	47 47 53 57 60 60 63 71 75 79
 4. The current state of plankton sampling systems 4.1. Integration of multi-sensor systems 4.1.1. Winch controlled towed systems 4.1.2. Undulating towed bodies 4.1.3. Tethered self-propelled ROVs and DSRVs 4.2. The evolutionary history of zooplankton sampling systems 4.3. Intercomparisons of sampling efficiency and selectivity of zooplankton sampling systems 	81 81 82 82 82 85 87
 5. Future developments	87 87 88 91
6. Acknowledgments	93
Appendix A	93

1. Introduction

The recent history of plankton sampling began with Thompson in 1828 who is usually given credit for inventing a net he used to sample crab and barnacle larvae (Fraser, 1968). From this simple collecting device has arisen an astounding array of instrument types and collecting strategies for sampling zooplankton. The history of nets and their use in collecting zooplankton from the world's oceans, continental shelves, coastal

embayments and freshwater bodies are almost as varied as the interests of zooplankton biologists. This account of the tools that have been employed to collect zooplankton builds on the work of an number of investigators. Kofoid (1911a) provided in-depth descriptions of the workings of opening/closing devices of the 19th Century. Fraser et al. contributed to the 1968 zooplankton methodology manual (UNESCO, 1968). Jossi (1970) produced a comprehensive bibliography of zooplankton sampling devices from late 1800s to the late-1960s. We also used other individual researchers' descriptions of equipment development, which provided a historical context for their own efforts. This is by no means a complete accounting, but we hope that we have captured the main trends in the instrumentation and technology developments that have led to the sampling tools currently available. A basic premise in this account is that the advance of sampling tool development followed the introduction of new enabling technologies. This view was supported recently in a review of the current status of zooplankton research in which it was stated that inadequate methodologies and instrumentation limited the pace of advances in this area of research (Marine Zooplankton Colloquium 2, 2001). A chronological listing of the instrument systems we have reviewed (Appendix A) complements the categorization of the systems present in the text and in Figs. 1–5. The tremendous strides in the development of zooplankton sampling equipment that have taken place in the last few decades give us optimism that the 21st Century will see even more remarkable developments in sampling technology and as a result, a new level of understanding of the patterns and dynamics of ocean zooplankton populations.



Fig. 1. A time line for the development of non-opening/closing nets since Hensen introduced his methodology and plantobenthos net systems.



Fig. 2. A time line for the development of opening/closing net systems. The left line is for nets which typically fished while hauling to the surface and the right line is for nets which fished while falling to depth.

2. The late 1800s to the mid-1900s

2.1. A context for plankton sampler development

Zoogeographers, ecologists, and fisheries biologists are interested in describing zooplankton populations and communities over large oceanic areas in order to determine their structure and function, their geographical distribution, and their relation to environmental parameters (McGowan, 1971, 1974). However, interest has also been focused on the distribution of organisms on a range of scales from less than a meter to hundreds and thousands of meters (Cassie, 1956; Wiebe, 1970; Haury, McGowan, & Wiebe, 1978; Dickey, 1988; Davis, Gallagher, Berman, Haury, & Strickler, 1992a). Investigators studying the oceanic distributions of populations and communities must obtain information from samples taken at stations usually separated by great distances (tens to hundreds of kilometers). Implicit in these studies are assumptions that plankton samples taken with nets quantitatively represent population and community parameters in the parcel of water sampled and that the parcel sampled contains representative numbers and kinds of organisms in the area around the station. The extent to which these assumptions can be accepted depends on the magnitude of various errors associated with the sampling method. Therefore, a knowledge of the accuracy and precision of sampling is required for quantitative studies of ecological processes. This involves estimates of the number of species or sub-species, as well as estimates of their abundances and changes in these. Both intra- and interspecific interactions influence distributions including, the effects of predators on prey, herbivores on primary producers, and competitors on each other. This knowledge is also necessary



Fig. 3. A time line for the development of high-speed net systems. Note the four lineages beginning on the left with the CPR which still is in use today, the relatively small samplers beginning with Apstein's system, the 'Gulf' series beginning with the Fry's metal net, and a miscellaneous set of high-speed samplers on the right.

to test and use theoretical ecological models such as those discussed by Riley (1963); Fasham (1993); Aksnes, Miller, Ohman, and Wood (1997); Lynch, Gentleman, McGillicuddy, and Davis (1998); Miller, Lynch, Carlotti, Gentleman, and Lewis (1998); Carlotti, Giske, and Werner (2000); and many others, since comparisons of observed and expected changes are dependent on reliable field observations and error estimates.

Prior to the fundamental work of Hensen (1895), little thought was given to these assumptions or to methods of quantitative sampling. Samples of plankton were obtained and analyzed solely by qualitative techniques. Research into sampling error in the field and in the laboratory, and attempts to develop quantitative methods in plankton research began about the time of the German Plankton Expedition in the 1880s. Victor Hensen introduced a then bold new methodology for quantitative plankton sampling. According to Jenkins (1901) and Dakin (1908), Hensen was attempting to answer two questions in a quantitative way:

- 1. What does the sea contain at a given time in the shape of living organisms in the plankton, i.e. what are the numbers and kinds of things in the sea at any given time?
- 2. How does this material vary from season to season and from year to year?

Basically, these are the same questions that we are still asking. Apparently many planktologists were grasping for a new methodology because Hensen's ideas were almost universally accepted. Hensen's basic premise was that plankton were evenly distributed in the oceanic waters and because of this one could



Fig. 4. Time lines for the development of multiple net systems, closing cod-end systems, and neuston net systems all of which had their start in the middle of the 20th century.



Fig. 5. A time line for the development of optical and electronic based zooplankton sensing systems. Note the division between electronic and optical counting systems on the right and optical imaging systems on the left. One group of the latter (VPR and ISVC) can be traced back to the LHPR.

take small samples that would be representative of large oceanic areas providing the volume of water filtered by the net could be determined exactly and providing the organisms caught by the net would not escape through the net mesh. The methodology developed and the experiments performed to achieve their goals covered the construction of the nets and net materials, measurement of net filtration efficiencies, employment of the nets at sea, and analysis of samples in the laboratory. Many of the sources of error associated with sampling plankton by nets and with counting methods to analyze the samples were identified and means to circumvent or reduce their effects were studied. Hensen recognized that there were large scale spatial variations in the concentrations of planktonic forms. His estimates of sampling error, based on vertical tows, indicated that replicate tows differed by only 10–15 % in the volume of plankton caught. For this reason, he assumed that the organisms were distributed uniformly over areas 60–100 nautical miles square. Thus, Hensen concluded that large oceanic areas could be accurately characterized with relatively few quantitative samples.

Hensen had his antagonists. Ernst Haeckel believed that organisms were irregularly distributed both in time and space, and that Hensen and his approach were not only wrong, but misleading. Thus, Haeckel (1890) sharply criticized Hensen and presented a large body of evidence to support the contention that plankton were distributed non-uniformly vertically and horizontally in time and space. Haeckel (1890, p. 572):

Accounts have been published of the results of the plankton expedition of Kiel, by Victor Hensen,...and others. The essential details of these accounts have been repeatedly published in the German newspapers, to the general effect that the proposed goal was reached and the most important question of the plankton was happily solved. I very greatly regret that I cannot agree with this favorable verdict. The most important generalizations which the plankton expedition of Kiel obtained on the composition and distribution of the plankton in the ocean stand in sharp contradiction to all previous experience; one or the other is wrong. It seems to me that Hensen has incautiously founded a number of far-reaching erroneous conclusions on very insufficient premises. Finally, I am convinced that the whole method employed by Hensen for determining the plankton is utterly worthless, and that the general results obtained thereby are not only false, but also throw a very incorrect light on the most important problems of pelagic biology.

Haeckel's criticisms of Hensen's basic premise were, however, not well taken for at least two reasons:

- 1. some of his other criticisms were later proven wrong, biasing the credibility of those which were valid; and
- 2. much of what Hensen set forth was recognized as being needed and views which should have been questioned, were not.

The criticism was initially overlooked or dismissed (Hardy, 1936b). This is particularly evident in a review of Hensen's methods by Jenkins (1901). Eventually, aspects of Hensen's methodology were questioned by others. The view that organisms that were caught stayed caught with the particular type and size of gauze Hensen used, came under criticism from Kofoid in 1897 and Lohmann in 1903. They showed that with certain organisms, the losses were substantial. Sometime later, investigators began wondering whether a single net tow taken at a station gave an accurate representation of the number and kinds of organisms in the surrounding waters. Once this question was asked, most investigators responded similarly. They took replicate net tows at a single location and looked at the error. Results obtained from repeated net tow experiments carried out by Herdman and co-workers off the Isle of Man, were among the first to question the validity of the assumption of uniformity in distribution (Dakin, 1908; Herdman & Scott, 1908; Johnstone, 1908; Herdman, 1921; Johnstone, Scott, & Chadwick, 1924). Herdman (1921): "The degree of uniformity in the distribution of plankton through the water of a sea-area which is under what seem uniform

physical conditions is still a vexed question". However, the doubts were raised only with respect to the water adjacent to land; in oceanic areas "...the irregularities of the plankton which are so apparent near the land do not exist..." (Johnstone, 1908, p. 150). Later Gardner (1931) used two series of net tows taken off the east coast of England to study the reliability of single net tows in survey programs. He concluded that the variation in the size of catch in repeated net tows was most likely due to the lack of uniformity in the distribution of the organisms. Wiebe and Holland (1968) summarized the results of these studies in a table giving the error associated with a single net tow. In these studies, the error of a single observation at a station location varied from one-half or double to more than one-fifth or five times. That is, for a sample value from one station to be significantly different from another station at the 95% probability level, it would have to be less than the lower limit or greater than the upper limit.

Hardy (1926a, 1936c) presented the first convincing, quantitative evidence that oceanic planktonic forms are strongly aggregated. He warned that this might make survey station samples unrepresentative of the quantities of different organisms in the surrounding waters (Hardy, 1936c, 1953, 1955) : "It is essential to know whether the nets used at any station in a survey give fairly representative samples of the quantities of different organisms in the surrounding waters, or whether the unevenness in the distribution of these organisms may not make the samples unrepresentative".

Yet in re-analyzing three sets of published data, Winsor and Walford (1936) concluded that the differences between replicate tows could be accounted for by variations in the volume of water filtered by the nets and that, therefore, the distribution of the plankton could be assumed to be random. The same conclusion is either implied or stated in the nearshore studies of Winsor and Clarke (1940) and Barnes (1949b) and in the lake studies of Ricker (1937, 1938).

The idea that zooplankton were basically randomly or evenly distributed throughout most oceanic areas persisted until about 1950, when Barnes and Marshall (followed by a number of others) finally laid the idea to rest. Work with plankton pumps (which are not subject to some of the errors associated with nets) by Barnes (1949a); Barnes and Marshall (1951), and Anraku (1956), with a plankton trap by Langford (1938), and further studies with nets by Silliman (1949), Motoda and Anraku (1955), Motoda, Anraku, and Minoda (1957), Tonolli (1949), Taft (1960) and Hopkins (1963) showed that a large amount of the variability in sets of replicate samples was due to non-random, usually 'patchy', distribution of the organisms. Additional errors, caused by mechanical problems resulting in variation of water filtered by the net were still considered important.

Since the 1950s, the concept of plankton patchiness has become a dominant underlying theme in many kinds of research, but there is still little real understanding about the structure of aggregations of oceanic animals or the changes that might take place in spatial structure over time and space. More importantly, the functional importance of plankton patchiness, while the subject of a number of papers, remains elusive. The nature of the zooplankton species ambit, defined by Haury et al. (1978) as the biological and physical forces that govern the behavior of individuals as they mature from egg to adult, remain to be defined and quantified. This has been the focus of research with the advent of sampling systems that can quantify the distribution and abundance of plankton on scales that they experience (Davis et al., 1992a; Schultze et al., 1992). The biology of individuals is critical to understanding the dynamics of populations as a whole and will be a focus of 4D oceanography efforts.

2.2. Net developments in the first half of the 20th century

Net system development has paralleled the quest for understanding of the distribution of plankton. Until very recently, biological sampling of the deep ocean has depended upon winches and steel cables to deploy a variety of instruments. For the most part three kinds of samplers developed in parallel: water-bottle samplers that take discrete samples of small volume of water (a few liters); pumping systems that sample intermediate volumes of water (tens of liters to tens of cubic meters); and nets of many different shapes

and sizes that are towed vertically, horizontally, or obliquely and sample much larger volumes of water (tens to thousands of cubic meters) (Fraser, 1966). In the latter part of the 20th century, high-frequency acoustics and optical systems also became important. This section will focus principally on the net systems.

2.2.1. Water column samplers

2.2.1.1. Non-opening/closing nets Although nets have been used since the time of Thompson (~1828), as noted above, it was Hensen's seminal paper that marked the start of 'quantitative' plankton sampling. The net designed by Hensen (1887) (Fig. 1; Plate 1A,B) consisted of a 38 cm diameter ring (0.1 m^2) connected by a 'head piece' of solid fabric to a larger 100 cm diameter ring from which was hung a conical net of silk bolting cloth (#20 mesh ~0.05 mm aperture) (Jenkins, 1901), (Plate 1A). A collecting bucket was attached to the cod-end of the net. This relatively simple net design was deployed vertically. The net was lowered to the selected depth, cod-end first, so as not to filter any water for collecting purposes, and then hauled back to the surface to provide an integrated sample of the water column. Volume of water filtered was computed assuming the net trajectory was vertical and using a calculated filtration capacity for a given mesh. This large net, now known as the Hensen egg net, was scaled down so that the head piece ring was 14 cm and the net ring was 40 cm (Apstein, 1896). According to Dakin (1908), the Apstein net became the most widely used net system in German investigations of his time.

Numerous variants of the simple non-opening/closing plankton net have been developed, as the hydrodynamics of nets became better understood. Nets which were principally towed vertically seem to have dominated this class of samplers. Examples are the 25 cm diameter Juday net (Juday, 1916) (Plate 1C,D); the 50 cm diameter International Standard Net (Ostenfeld & Jespersen, 1924) (Plate 1E); the British Nseries of nets including the 70 cm diameter N70 and the 100 cm diameter N100 (Kemp, Hardy, & Mackintosh, 1929) (Plate 1F); the 45 cm diameter Norpac net (Motoda et al., 1957; Motoda, 1994) (Plate 1G); the 113 cm diameter Indian Ocean Standard Net with a $1-m^2$ mouth opening (Currie, 1963); the 57 cm diameter WP2 net (Fraser, 1966; UNESCO, 1968) (Plate 2A), and the 100 cm diameter ICITA net (Jossi, 1966) (Plate 2B). Additional designs met the need to collect larger volumes of water i.e., the obliquely towed 1-m diameter CalCOFI net (Ahlstrom, 1948) (Plate 2C), and the need to tow a net without obstructing the mouth opening, i.e., the MARMAP Bongo net (Posgay & Marak, 1980) (Plate 2D,E) which was a successor to the opening/closing Bongo net developed by McGowan and Brown (1966). These design requirements led to nets that were towed obliquely from the surface down to a maximum depth of tow and then back to the surface. Most often these nets were used in programs that surveyed large ocean areas. In the western Pacific, the Japanese have used nets to survey plankton and fish eggs and larvae since the early 20th century (Nakai, 1962) (Plate 3A,B). Nakai described five different net types (Marutoku, Marunaka, Maruchi, Marudai, Kitahara) which were either used in vertical, or horizontal tow mode, with or without a flowmeter, and sometimes with a modified Nansen-style closing mechanism or a Discovery-type mechanism. The Marutoku net was similar to the International Standard Net (Ostenfeld & Jespersen, 1924) and the Kitahara was patterned after the Hensen net. Nakai (1962) provided detailed silk netting specifications in admirable detail (his Table 3). He also described a flowmeter that still is manufactured (by TSK) and widely used.

A widely used open net of unusual design for collection of macrozooplankton and micronekton, is the Isaacs–Kidd Midwater Trawl (IKMT) (Isaacs, 1953) (Plate 3D). This net has a pentagonal mouth opening and a dihedral depressor vane as part of the mouth opening. Four sizes of IKMTs, 3 foot (91 cm), 6 foot (183 cm), 10 foot (304 cm), and 15 foot (457 cm) are often cited (e.g. Foxton, 1963; Aron, 1962; Aron, Raxter, Noel, & Andrews, 1964; Pearcy & Hubbard, 1964). IKMTs were usually towed obliquely and at speeds up to 8.5 kts. Another net of unusual design was the Octagon Net described by Sameoto and Jaroszynski (1976) (Plate 3C). This net had a 75 cm diameter iron channel octagon mouth opening which was attached to the towing wire with stainless steel snap swivels and held from sliding down by a stop on the wire. The net mouth was so close to the towing wire that Sameoto and Jaroszynski thought avoidance



Plate 1. Some non-opening/closing nets developed in the late 19th and early to mid-20th centuries. The Juday, N-70, and Norpac nets were also used with an opening closing mechanisms. (A) The Hensen net (Jenkins, 1901). (B) The Hensen net (Wimpenny, 1937). (C) The Juday net (Juday, 1916). (D) The International Standard net (Ostenfeld & Jespersen, 1924). (E) The N-70 net (Kemp et al., 1929). (F) The Norpac net (right two nets – Motoda et al., 1957). (G) The Indian Ocean net (Currie, 1963).



Plate 2. Non-opening/closing nets developed in the latter half of the 20th century. (A) The WP2 net (Fraser, 1966). (B) The ICITA net (Jossi, 1966). (C) The CalCOFI net circa 1993 (L. Postel photo). (D) The MARMAP Bongo net (Posgay & Marak, 1980). (E) The Bongo net with CTD circa 1999 (Wiebe, photo).

(the act of an individual zooplankton moving away from the net mouth to avoid capture) of the pressure wave from the wire was unlikely. This net used 1 mm nylon mesh and was towed at speeds up to 7 kts. The Gimbal Ring Zooplankton Sampler (Kozasa, 1984) was also unusual. It consisted of a double gimbaled frame 100 cm tall×65.5 cm wide which supported a ring net 30 cm in diameter. A bridle was attached to the top of the frame and a weight to the bottom so the net mouth was free of obstructions. Nester (1987) described a horizontal ichthyoplankton tow-net system based on the Blackburn and Keith (1962) system (described below) in which a 50 cm diameter circular net ring was mounted in a 53 cm×53 cm rectangular frame. The net was a cylinder-cone with 0.333 mm nylon mesh. A towing bridle was attached to a spreader



Plate 3. Non-opening/closing nets developed in the latter half of the 20th century (continued). (A, B) The Marutoku, Marunaka, Maruchi, Marudai and Kitahara plankton nets (Nakai, 1962). (C) Octagon net (Sameoto & Jaroszynski, 1976). (D) The IKMT (Isaacs et al., 1953). (E) Reeve net circa 1999 (Wiebe, photo). (F) Reeve net (Reeve, 1981).

bar to keep the net opening clear of the bridle and a depressor was attached to the bottom of frame. This system had two flowmeters one inside the net and one outside, and was usually towed at 3 kts.

Open nets to collect live animals have been devised. Reeve (1981) designed a conventional ring net with a large weighted cod-end (30–110 l) (Plate 3E,F). The net is lowered to particular depth and then hauled slowly back to the surface (5–10 m/min). Reeve (1981) also describes a double net system with no bridle and flotation at the net mouth that is attached to a roller mechanism that rides on a tow wire. The roller system is locked in place by a pressure release device. Once below a set pressure, the roller and nets are released and they float slowly up the wire, gently collecting the zooplankton, without being influenced by the motion of the vessel and associated vertical wire movements.

Non-opening/closing nets with rectangular mouth openings were not widely used until Tucker (1951) built what is now known as the Tucker trawl (Plate 4A,B). It had a 183 cm×183 cm mouth opening. Tucker designed the trawl to collect animals associated with the deep scattering layers, principally euphausiids, siphonophores, and midwater fish. It was equipped with a time-depth recorder. Blackburn and Keith (1962) described a very similarly constructed net with a 152 cm×152 cm rectangular mouth opening attached to metal tube frame which was designed to catch micronekton and to be towed at 5 kts (Plate 4C,D). An Isaacs depressor (Isaacs & Kidd, 1953; Ahlstrom, Isaacs, Thrailkill, & Kidd, 1958) was attached to each bottom corner of the frame to keep the mouth opening vertical at the desired towing speed. More recently, Walker and Davies (1986) described the Lowestoft Frame trawl which came in two versions, one with a 142 cm rectangular mouth opening on a side and the other with a 100 cm mouth opening (Plate 4F). Tucker's simple trawl design gave rise to a substantial number of opening/closing net systems, as described below in sections 2.2.1.2 and 3.2.

Today, non-opening/closing net systems are still widely used for survey sampling. The CalCOFI surveys which until 1978 used the open 1-m ring net (Ahlstrom, 1948) (Plate 4E), now use a variant of the Bongo Net (Plate 2E). The change to a bridleless net was done to improve the efficiency of collecting zooplankton by reducing avoidance (Ohman & Smith, 1995). The Northwest Atlantic continental shelf surveys being conducted by the NMFS Northeast Fisheries Science Center also use the open Bongo net (Posgay & Marak, 1980). The WP2 net is widely used in European plankton work. A Double Juday net is used in fjord work in Norway (Aksnes & Magnesen, 1983).

2.2.1.2. Simple opening/closing nets It was recognized from the late 1800s that plankton were not uniformly distributed vertically (i.e. different species lived in different portions of the water column) and devices to enable nets to be opened and closed needed to be developed (Fig. 2). Thus, early on, nets evolved from those of very simple design (a simple ring net) to nets that could obtain depth-specific samples. Even before the Hensen net and the associated sampling practices were widespread, there was considerable effort to develop devices that enabled the closing, or the opening and closing, of nets at depth (Kofoid, 1911a, 1912). The dominant means of controlling the opening and closing of nets was by mechanical release devices that were attached to the towing wire. Weighted 'messengers' traveling down the towing wire by gravity, struck catches (usually spring loaded) and released a support line, thus transferring tension onto another line that either allowed a net to open, or resulted in choking the net mouth off. The Nansen (1915) closing mechanism and its variants were very popular during most of the early to mid-20th century (Plate 5A). This system was used with the assumption that a net lowered cod-end first in the water would not catch plankton. The net was then hauled upward and was met by a messenger timed to reach the net at an appropriate depth. This released the tow line and allowed a looser line to take up slack and choke off the net below the net mouth. A variant of this method was described by Hart (1935) (Plate 5B). His closing net consisted of a rod of wood or pipe that was outfitted with a combination wire clamp and closing release at the top and a snap hook at the bottom to secure the device to the wire. Attached to the rod was a net with a bridle that was inserted into the release latch. Midway along the pipe was a second snap hook that was attached to the mid-section of the net; at the bottom another snap hook secured the



Plate 4. Non-opening/closing nets developed in the latter half of the 20th century (continued). (A–B) The Tucker trawl and time depth recorder (Tucker, 1951). (C–E) The Tucker trawl and meter net (Blackburn & Keith, 1962). (F) The Tucker Trawl (Walker & Davies, 1986).



Plate 5. Some opening/closing nets developed in the late 19th and early 20th century. (A) The Nansen net (Nansen, 1915). (B) The Hart net (Hart, 1935). (C) The Hoyle net (Hoyle, 1889). (D) The Kofoid net (Kofoid, 1912).

bottom portion of the net. Multiples of these units could be attached to the wire at various depth intervals as the wire was lowered vertically into the water. Plankton collections were made as the nets were hauled up until a messenger hit the release and released the bridle and the next messenger in the chain, thus closing the net.

In spite of its popularity, the Nansen closing net design had significant disadvantages. Kofoid (1911a) produced a comprehensive review of the early development of available opening/closing net systems and discussed the pros and cons of 37 systems described in the literature between 1880 and 1911. One of the first double messenger systems was described by Hoyle (1889) (Plate 5C). Hoyle's summary of its features

said that it worked well at any depth, enabled the operator to control when the net was opened/closed, and allowed a number of nets to be used on the same 'rope'. He discussed the disadvantages of using messengers to actuate the opening/closing mechanism and in a remarkable statement for the time (p. 110) said "these disadvantages can, I think, best be remedied by adapting to this tow-net the electrical apparatus which Professor Chrystal has applied with such success to the reversing of deep sea thermometers...no attachment of obstacles to the line will check the current and its action will be instantaneous". The system was to be tested in the summer of 1889 and Herdman (1891) reported that "Mr W.E. Hoyle's deep-water closing net has now been modified in the direction indicated in last year's report, so that it can be opened and closed not by the agency of sliding weights, but by an electric current". Another report the following year reiterated and expanded on the description of an electrically-controlled opening/closing mechanism for nets (Haddon, Herdman, & Hoyle, 1891), but this mechanism does not appear to have been adopted by the community. The next report of an electrically-operated net system appeared in the 1930s, when Van Cleve (1937) described a solenoid-based electrical double-release mechanism. Perhaps the reason that this prescient development failed to take root until nearly 50 years later is the same as given by McConnell (1982) for other electrically operated oceanographic devices at the turn of the 20th century: "The use of electricity to telemeter and register from probe to ship proved cumbersome and slow to handle, and so was abandoned by the turn of the century".

Kofoid (1911a) described his own new and unique system for sending a net down closed, opening it, and then closing it again (Plate 5D). It involved a pair of hemispherical metal bands to which the mouth of the net was attached. One messenger released the first hemispherical band, which swung forward and down 180°, opening the net. A second messenger released the remaining hemispherical band which then swung down, closing the net. In spite of its mechanical elegance, this net was not widely adopted in marine sampling. Leavitt (1935) said his reason for not using Kofoid's system was that it was "...too small and too expensive...". But another reason must have been that only one of the Kofoid nets could be deployed at a time, because it had to be towed at the end of the wire.

Leavitt (1935, 1938) went on to describe a double-messenger system that allowed several ring nets (either 100 or 200 cm in diameter) to be towed on the wire at different depths and simultaneously opened and closed (Plate 6A). Double messenger systems like that of Leavitt's have endured. For example, Omori (1965) described three ring nets with a mouth opening of 160 cm diameter (the ORI-C, ORI-200, and ORI-33) used by the Ocean Research Institute (ORI) in Tokyo (Plate 6B). These nets were either equipped with a Nansen-style messenger closing device or a Motoda (1959) double messenger release. Hopkins, Baird, and Milliken (1973) used a double-trip mechanism to operate a 180 cm×180 cm Tucker trawl (Plate 6C). Sameoto and Jaroszynski (1976) also used one with 100 cm×100 cm and 400 cm×400 cm openings (Plate 6D). Recent papers describe modifications to this now-very-old method of opening and closing ring nets to improve their reliability (Bourdillon, Castel, & Macquart-Moulin, 1978) (Plate 7A), to enable the net to be deployed through the air/sea interface without being contaminated (Clayton & Pavlou, 1978) (Plate 7B,C), or to reduce other kinds of contamination (Tuel & Knauer, 1982; Kimmerer, 1984) (Plate 7D,E).

While Leavitt designed his gear to use large diameter ring nets to sample the larger midwater zooplankton off southern New England, Clarke and Bumpus (1939, 1950) designed a much smaller two-messenger zooplankton collection system that could be deployed as multiple units on the wire and, like the Kofoid system, had a positive means of opening and closing the mouth of the net (Plate 8A). A frame attached at the top and bottom to the towing wire supported a cylindrical tube 12.7 cm in diameter and 16 cm long, to which a net was attached. In the mouth of the tube was a flat plate (like a stove pipe damper plate), which closed off the cylinder when the net was deployed. When the first messenger released a spring-loaded latch, the plate was rotated 90°, opening the net; a second messenger rotated it another 90° to close the net. A flowmeter at the back of the cylinder recorded flow through the net. Two groups apparently independently built scaled-up versions of the Clarke–Bumpus sampler. Paquette, Scott, and Sund (1961) described a version with a 25.4 cm diameter mouth opening and Yentsch, Grice, and Hart (1962) described



Plate 6. Double messenger systems opening/closing net systems developed in the mid-20th century based on ring net and rectangular net designs. (A) The Leavitt net (Leavitt, 1935). (B) The ORI net (Omori, 1965). (C) A modified Tucker Trawl (Hopkins et al., 1973). (D) A modified Tucker Trawl (Sameoto & Jaroszynski, 1976).



Plate 7. Variants on the double messenger opening/closing net designs from the latter half of the 20th century. (A) An opening/closing mechanism (Bourdillon et al., 1978). (B, C) An opening/closing net (Clayton & Pavlou, 1978). (D) An opening/closing net (Tuel & Knauer, 1982). (E) An opening/closing net (Kimmerer, 1984).



Plate 8. Variants on the double messenger opening/closing net designs from the mid-20th century. A) The Clarke–Bumpus Sampler (Clarke & Bumpus, 1939). (B) A modified Clarke–Bumpus Sampler (Yentsch et al., 1962). (C) The Barnes net (Barnes, 1953). The Motoda Horizontal net (Motoda, 1971).

a version with a 30 cm diameter mouth opening (Plate 8B). This net system proved to be quite popular and it is still possible to purchase a Clarke–Bumpus sampler today. Another messenger based net system which utilized a framework attached to the towing wire was the MTD Horizontal net (Motoda, 1971), (Plate 8D). The circular net (56 cm diameter) was a cylinder (80 cm length)/cone (110 cm length) and was mounted on wire with a triangular framework so that up to 10 could be towed simultaneously.

Barnes (1949b) showed that the Nansen method of closing nets could result in a "...clear tendency for a loss of catch to result on closure", as did Currie and Foxton (1957). To avoid this, Barnes (1953) developed a rather unique closing mechanism consisting of a hemispherical metal cowling mounted in front of a net ring with an opening sized so that a closing lid shaped to fit the cowling could be accommodated when the net was open (Plate 8C). A Nansen messenger closing mechanism was used to release the spring loaded closing lid which pivoted over the net mouth thus closing it without a loss of the catch.

Toward the end of this era dominated by the use of mechanical devices, tripping mechanisms activated

by pressure (Bé, 1962; Yentsch et al., 1962), by combinations of messengers and flow-meter revolutions (McGowan & Brown, 1966), or clocks (Davies & Barham, 1969, described below) were developed (Plate 9). The McGowan and Brown Opening/Closing Bongo net was of unique design because it had two circular hoops, 70 cm diameter, joined by a central axle which was clamped to a cable leaving the net mouths unobstructed (Plate 9D). A Dacron cloth 'door' covered each mouth opening which, when released by a



Plate 9. Variants on the double messenger opening/closing net designs from the mid-20th century (continued). (A, B) The messenger operated MPS (Bé, 1959). (C) The Bè pressure release for MPS (Bé, 1962). (D) The McGowan and Brown Bongo Net (McGowan & Brown, 1966). (E) An opening/closing Tucker trawl (Davies & Barham, 1969).

messenger, folded into the net mouth. The flowmeter was set to release the nets after a predetermined volume of water was filtered. A variant of the Bongo net was described by Brown (1975) (Plate 10A). An open pair of 50 cm diameter circular net hoops were mounted on each end of a 150 cm wide cross-strut which was attached to a towing cable. A pair of nets were attached to the bottom of the hoops and their cod-ends were attached to a spreader bar which was also attached to the wire. The nets were lowered to a maximum depth to haul. Then during the haul back to the surface, a messenger was used to close the nets either by releasing the hoops so that they turned 90° or by releasing the nets which fell back and were pursed closed by throttling lines attached to the cross-strut. A non-opening/closing form of this net, termed the 'CalVET' net has been used by CalCOFI for vertical net tows (Smith, Flerx, & Hewitt, 1985). Sameoto and Jaroszynski (1976) modified the Bongo by constructing a single ring 75 cm in diameter and



Plate 10. A vertical hauled closing Bongo Net and four pop-down net systems. (A) A modified Bongo net (Brown, 1975). (B) A free-fall net (Buchanan-Wollaston, 1911). (C) The Free-fall net (Heron, 1982). (D) Two views of a messenger operated Plummet net (Daley, photos). (E) The Streamer net (Ishida, 1963).

mounting it to the wire using the Octagon Net mounting mechanism described above. A double messenger mechanism opened the cloth door and closed the net. Brown (1975) also described an opening-closing IKMT that utilized a timer release mechanism. The IKMT was outfitted with a 'flap' of material that extended from the net mouth to the back end of the net and a three-stage cod-end. At the start of a haul, the flap was down and animals were collected in stage 1 of the cod-end. A timer released the flap which rode to the top of the net and animals were collected in the stage II cod-end. A second timer release caused the stage II cod-end to be released, pursed, and replaced with the stage III cod-end.

The end of this era also resulted in the first of the multiple net systems (Bé, 1959). Bé's first system was a four messenger system that enabled three 50 cm×50 cm rectangular nets supported by a box framework to be opened and closed sequentially (Plate 9A,B). This system was designed for vertical towing, but in a second version, which used a pressure-activated release mechanism (Plate 9C), oblique or horizontal towing was also possible (Bé, 1962). This second system (the multiple plankton sampler, MPS) also carried three nets that were preset to sample 0–100, 100–250 and 250–500 m depth intervals. A single net system, the Bathypelagic Sampler (BPS), was used to sample 500–1000 m. Depth-flowmeter readings were continuously recorded on a smoked glass cylinder.

There are a few non-traditional approaches to collecting plankton that are worth noting, although none has received wide-spread support. A number have in common that they were designed to catch plankton on the downward fall of the net rather than the reverse, principally in an effort to reduce or eliminate zooplankton avoidance of the net mouth (Clutter & Anraku, 1968). These are the so-called pop-down nets (Fig. 2). Buchanan-Wollaston (1911) described a tall rectangular framework in which a net was positioned with the mouth facing downward about mid-way in the frame with stops to prevent it from moving upward within the frame as the frame itself free fell to depth while collecting a sample (Plate 10B). When strain was put on the recovery line, the net fell to the bottom of the frame where it was latched into a recovery position and in the process the net was throttled closed. A similar free-fall plankton net was designed by Heron (1982), but without the frame (Plate 10C). In this case, a modified WP2 net attached to a weighted ring was allowed to fall until it came to the end of its recovery line which strangled the net near the mouth opening when the slack was taken up. This system was intended for use in making upper ocean measurements on surveys. Tom English (University of Washington) developed a downward fishing net called the plummet net (Plate 10D). Subsequent versions were used by other researchers at the University of Washington (Daly & Macaulay, 1988; Hovekamp, 1989, 1991), and elsewhere (Lancraft, Hopkins, Torres, & Donnelly, 1991). The plummet net used by Hovekamp (1989) has a 100 cm diameter mouth with a lead weighted net ring and a net with 0.571 mm mesh. For downward collecting, the net was lowered by the cod-end to a pre-determined depth and a messenger was used to release the cod-end attachment and draw tight a choke collar near the mouth of the net. Another version of a downward-fishing, vertical, closing plummet net has a 1 m² rectangular mouth opening with a net that is attached to two bars that run along a pair of net bar glides along parallel sides. A double messenger system is used to open the net as it falls to depth and to close it as it reaches the bottom of the haul. The net, ~180 cm in length, has been used with a range of mesh sizes depending on the size of the target organisms i.e., 0.163 mm (Lancraft et al., 1991), 0.560 mm (Daly & Macaulay, 1988, 1991), and 0.163 mm, 0.560 mm, and 1.600 mm Nitex (Daly & Macaulay, 1991). According to Daly (personal communication), the first messenger releases a bridle attached to the opening net bar under tension from a shock cord. The second messenger releases two bridles, one attached to the back of the net frame and the other to the closing net bar. The net frame assumes a vertical position, allowing the second net bar to fall, closing the net, and retrieval begins.

The Streamer plankton sampler of Ishida (1963, 1964) is designed to sample a set volume (600 l) at a specific depth determined by the length of the recovery line (Plate 10E). In the net mouth is a hinged door, which is open as the net falls to depth. The back of the net is open so water is flushed through the net as it falls. When the net reaches maximum depth, the recovery line closes the back of the net. As the net is lifted to the surface, the doors close, sealing the mouth and securing a catch in 600 l. The Adriatic Plankton

Sampler works on a similar principal (Kršinic, 1990) (Plate 11A). A cylindrical sampler is sent to depth with the cylinder net (50 cm in diameter with 0.25 mm mesh) closed and upside down (cod-end facing upward). A messenger releases the bottom margin of the cylinder allowing it to drop ~100 cm to an open position and at the same time closing half-circle doors. A second messenger releases the first support bridle and the sampler turns upright for recovery. This sampler collects about 250 l of water. The parachute net of Wheeler (1941) is the ultimate free fall net system (Plate 11B). It had a 275 cm diameter 'parachute' net opening tapering over a distance of 350 cm to a 100 cm diameter mosquito netting net. It was put over the side of the ship and released to fall to ocean bottom (in one case to ~2400 m) weighted by



Plate 11. Two additional pop-down nets, a net for sampling under ice, and a combination net and pump system. (A) The Adriatic net (Kršinic, 1990). (B) A free-fall parachute net (Wheeler, 1941). (C) The English Umbrella net (Macaulay & Daly, 1987). (D) The Plankton-bar net system (Tonolli, 1951).

concrete weights. The weights were released by salt block dissolution, and the net equipped with a gasoline filled container floated backwards to surface. The design of the cod-end bucket enabled the catch to be retained during the trip back to the surface.

Tom English developed a collapsible opening-closing net for sampling under sea ice which was described in Macaulay and Daly (1987) (Plate 11C). This net, known as the English umbrella net, was designed to fit through a hole in an ice flow closed, and open once underneath. The net mouth was rectangular and supported by four metal rods extending from a hub at the center of the interior of the net to each corner of the mouth. The rods were hinged on the hub and when brought together they closed the net mouth. A bridle extended from the hub to a single messenger release mechanism and a weight was hung below the net with attachments at the rod ends in the corner of each net. The net was lowered vertically to the maximum sampling depth and then hauled back to the surface. A messenger was dropped as the net was being hauled up in order to close the net at the intended minimum sample depth. When the release was tripped, the slack was taken up by a second bridle attached to the four corners of the net, thus closing the net and allowing it to pass through the ice hole. Nets typically used were 200 cm on a side and 300 cm long made from 0.22 mm nylon mesh. Another 'umbrella' net was briefly described by Rakusa-Suszczewski (1972) to sample organisms sitting on the undersurface of the ice or in the water just below it. This system was deployed through a 12 cm diameter ice hole and once below the ice, it was rotated to make the collection.

Tonolli (1951) developed a method for continuously sampling plankton from several depths simultaneously, using a combination of nets and a pumping system (Plate 11D). Along a towing cable, a bundle of plastic pipes was strung with a given pipe entering the mouth of a net attached to the towing cable and passing to the cod-end where it was passed through an opening in the net and doubled back to attach to where a cod-end bucket would normally be attached. Water and plankton were pumped out of the codend and up the wire into a filtering apparatus by means of a vacuum pump. Five nets were normally used with equidistant spacing on the towing wire. Tonolli named the system the "…plankton-bar, since it supplies specimens of plankton from various depths by the opening of taps".

Grice (1962) developed an automatic multiple net plankton sampler that was deployed on the nuclear submarine, SSN SEADRAGON, to collect the first series of horizontal plankton samples from under the Arctic Ice Pack right to the North Pole (Plate 12A). The conning tower (sail) of the submarine was equipped with a 9 cm diameter intake pipe that led to a sampler with a revolving circular ring with 24 positions to which nets could be attached. The nets, made of 0.223 mm Nitex nylon mesh, were 1.9 cm in diameter×30.5 cm long. Nets were placed on alternate openings and a battery powered timer and motor rotated the nets into and out of position to collect a sample at two hour intervals. The submarine surfaced after the 24 h cycle of sampling was completed, the nets were removed and frozen, and a new set of nets installed. Sampling schedules of 0.5, 6 or 12 h were also possible with this sampler.

A uniquely operated closing midwater trawl (Tucker style), with a 300 cm×700 cm rectangular mouth opening and 1800 cm long net, was described by Enzenhofer and Hume (1989) (Plate 12B). The net was made from five sets of mesh with coarse mesh at the front and fine mesh at the back (600 cm of 10.2 cm mesh, 400 cm of 5.1 cm mesh, 300 cm of 1.9 cm mesh, 300 cm of 1.3 cm mesh and 200 cm of 0.3 cm mesh). There were two towing cables: one for the top spreader bar and one for the bottom, with each cable going to a separate winch. The net was lowered with tension on the bottom spreader so that the net went down to depth closed. Tension was then transferred to the top spreader to open the net. At the end of a tow, tension was again taken by lower spreader to close net and haul it back to the surface. This system was designed for relatively shallow water work.

Finally Murphy and Clutter (1972) designed and used a plankton purse seine to capture fish larvae living near the sea surface that were inadequately collected by meter nets (Plate 12C). This seine, made of 0.333 mm nylon mesh, was 3048 cm long and 640 cm tall. In comparisons with the meter net, it did catch



Plate 12. Additional unique plankton samplers. (A) The SSN Sea Dragon Plankton net (Grice, 1962), a serial net sampler. (B) A two winch/warp opening/closing Tucker trawl (Enzenhofer & Hume, 1989). (C) The plankton purse seine (Murphy & Clutter, 1972).

significantly more fish larvae, especially during the day, and the lengths of the larvae caught were substantially bigger.

2.2.1.3. High-speed samplers The development of high-speed samplers came in response to the need for sampling in bad weather, to use for plankton sampling between stations while the ship was underway, or to reduce the effects of net avoidance by the larger zooplankton (Fig. 3). The first primitive high-speed samplers were developed in the early 1900s (Apstein, 1906; Zacharias, 1907; Monti, 1910) (Plate 13A–C). They were relatively small diameter tubes (5–12 cm diameter) between 26 and 50 cm in length, with a conical nose cone with an aperture of 1.5–4 cm and a bridle attached near the front of the device.

It was Hardy (1926a, 1936b) that provided the first widely used device: the Hardy plankton indicator (Plate 13D). Similar to the earlier designs cited above, it was intended to provide herring fisherman with a device that they could tow underway to obtain a sample that they could use to relate the quantity and



Plate 13. Early high speed samplers. (A) Apstein high-speed sampler (Apstein, 1906). (B) The Zacharias high-speed sampler (Zacharias, 1907). (C) The monti high-speed sampler (Monti, 1910). (D) the Hardy Plankton Indicator (Hardy, 1926b). (E) The Standard Plankton Indicator (Hardy, 1936a). (F) The Small Plankton Indicator (Henderson et al., 1936).

quality of plankton to the number of herring in the vicinity (Glover, 1953). The original version was a 17.8 cm in diameter main body and 91.4 cm in length, with a circular filtering disk on which the plankton were collected. It was subsequently modified (and re-named the standard plankton indicator (Plate 13E)) to make it smaller (7.6 cm diameter body and 56 cm length), more streamlined, and equipped with a depressor and stabilizing fins. An even smaller version, the Small Plankton Indicator, was developed for use when the nets were deployed and the ship was making ~2 kts (Henderson, Lucas, & Fraser, 1936; Glover, 1953) (Plate 13F). Glover (1953) described a modification of the Small Plankton Indicator which he called the Small Plankton Sampler because it had a small net (3.2 cm in diameter×8.9 cm long) inside the metal

casing (Plate 14A). This sampler was designed so that several could be deployed on a towing wire at higher towing speeds. Miller (1961) subsequently modified the Small Plankton Sampler increasing its size to a 10.1 cm diameter aperture opening on a body tube of 14 cm internal diameter and 61 cm overall length (Plate 14B). Attached to the back of the tube was a 91 cm long nylon net of three meshes (0.947,



Plate 14. Early high speed samplers (continued). (A) The Small Plankton Sampler (Glover, 1953). (B) The Miller high-speed sampler (Miller, 1961). (C) The metal high-speed sampler (Fry, 1937). (D) Erdmann high-speed sampler (Erdmann, 1937).

0.526 and 0.264 mm). Multiple units were used on the towing wire at speeds of 7–8 kts with a multiplane kit otter depressor (Colton, 1959) at the end of the wire.

In the 1930s, three other high-speed plankton collectors were constructed and described. Pierce's (1937) design, similar to Hardy's, had a diving fin and an internal conical silk net. It was towed successfully at 5 kts, but failed at 8 kts. The first of the samplers with a metal cone mesh plankton net was described by Fry (1937) (Plate 14C). Its overall length was 152 cm and it was towed with a three-part chain bridle at speeds up to 10 kts. Erdmann (1937) described a high-speed sampler similar in appearance to Hardy's Plankton Indicator that had a double messenger system that enabled the mouth to be opened and closed Plate 14D). Sheard (1941) and later Gauld and Bagenal (1951) used a net of curious design having a conical net with the tail flipped inward (Plate 15A). Short bridles were attached to a ring sewn into the back end of the cod-end sleeve and attached to the front of the net. A three-part bridle was attached to the ring in the mouth of the net and the net was towed at speeds up to 7 kts. Sheard (1941) found "The only difficulty occurs in removing organisms from the net...However, I have not found this to be a serious disadvantage".

The late 1940s and 1950s saw the development of several high-speed sampling devices developed for use in waters off the West and Gulf coasts of the United States. Smith and Ahlstrom (1948), citing the work of Hardy, built and used a high-speed collector (towed at 9 kts) with a brass cone and an aperture of 2.54 cm, supporting a net 5.08 cm in diameter and 25.4 cm long (with No. 56xxx grit gauze). The Isaacs Sampler was an improved version with a 2.5 cm mouth opening expanding to a diameter of 7.6 cm, and an overall length of 130 cm (Ahlstrom et al., 1958) (Plate 15B). A Monel metal mesh (23 mesh per cm) plankton filter (~5.2 cm in diameter and 36 cm long) was used to collect the sample. The system was equipped with a flowmeter, depth sensor (from a bathythermograph), and recording unit. Multiple units could be attached to the wire and towed at up to 10 kts.

During this same time, the 'Gulf' series of high-speed samplers was developed. The first was the Gulf I-A, which Arnold (1952) said, "superficially resembled the Scripps high-speed plankton collector designed by John Isaacs..." (Plate 15C). It had an outer cylinder 151 cm long and 11.7 cm in diameter, which tapered at the front to a 2.4 cm diameter aperture. Mounted inside was another cylinder 7.6 cm in diameter and 91 cm long, with Monel mesh No. 10 screen (0.38 mm mesh), which filtered the plankton. It was equipped with a flowmeter and towed at ~9 kts. A much larger high-speed sampler, the Gulf III was described by Gehringer (1952a, 1962) (Plate 15D). It had a 40.7 cm diameter nose piece and the main encasement was a 50.2 cm diameter cylinder 152 cm long made of Monel metal. Inside was a 49.5 cm diameter conical net 137 cm long made with No. 10 screen (0.38 mm mesh ~No. 1 silk). It also was equipped with a flowmeter and was towed at 4–5 kts. To help get it to depth, a Scripps cable depressor (Isaacs, 1953) was used. The Gulf V (Arnold, 1959) was an un-encased and scaled-down version of the Gulf III described by Gehringer (1952a, 1962) (Plate 16A). It had a 41 cm diameter mouth opening with a frame 130 cm long and a conical Monel mesh net with 30 meshes per cm.

The Gulf III and Gulf V samplers have been very popular, and have been modified numerous times. Fish and Snodgrass (1962) added a five-bucket cod-end sampling device to the Gulf III which was electrically activated from a deck unit through a two-conductor cable (Plate 16B). They named it the Scripps–Narragansett high-speed MPS. HAI (shark) was the German version of the Gulf III (Hempel, 1960, 1964), which had an entrance 18 cm in diameter and net mesh of 0.4 mm (Plate 16C). It was towed at ~6 kts. Depth was telemetered to the surface through a single conductor towing cable. A hemispherical nose cone and an opening/ closing lid similar to that described by Barnes (1953) was added to the HAI (Kinzer, 1966) (Plate 16D). The mouth opening (22 cm diameter) was adjusted to accommodate the closing lid. One messenger was used to move the lid aside, opening the mouth of the sampler; a second messenger was used to move the lid back over the mouth opening at the end of the tow. The German system further evolved when 'Nackthai' (naked shark), a modified Gulf V sampler, was developed (Nellen & Hempel, 1969) (Plate 16E). It had a 20 cm diameter nose cone aperture expanding to 38 cm diameter over a length



P.H. Wiebe, M.C. Benfield / Progress in Oceanography 56 (2003) 7-136

Plate 15. High speed samples of the 1950s including the first Gulf samplers. (A) The Sheard high-speed net (Gauld & Beganal, 1951). (B) The Isaacs sampler (Ahlstrom et al., 1958). (C) The Gulf 1-A High-speed sampler (Arnold, 1952). (D) The Gulf III high-speed sampler (Gehringer, 1952a).



Plate 16. Gulf high-speed samplers and descendants. (A) The Gulf V high-speed sampler (Arnold, 1959). (B) The Scripps–Narragansett high-speed MPS (Fish & Snodgrass, 1962). (C) HAI, the German version of the Gulf III (Hempel, 1960). (D) The opening/closing HAI (Kinzer, 1966). (E) The Nackthai Gulf V sampler (Nellen & Hempel, 1969).

of 53 cm. Attached to the back of the cone was a net 120 cm long. The framework in which the net was supported was 45 cm×45 cm×190 cm long (overall sampler length=243 cm). A comparison was made between the Hai and the Nackthai samplers which showed the Nackthai filtered more water and caught significantly more plankton and fish; a result attributed to its non-encased net (Nellen & Hempel, 1969).

During the same period, Beverton and Tungate (1967) also modified the Gulf III sampler, which was subsequently called the Lowestoft Sampler (Plate 17A). This encased system normally used a 42 cm diameter nose cone aperture with a 76.6 cm diameter body, 244 cm in length. The internal conical net was made of nylon netting of 0.27, 0.305 or 0.42 mm mesh, or Monel metal screen of 0.27, 0.42 or 0.56 mm mesh. It was a multiple sampler because it had two auxiliary samplers with nose cones of 5-9 cm diameter and a main body 16.5 cm diameter (with 0.061-0.270 cm mesh), and a phytoplankton or water sampler with an aperture of 0.1 cm and a body diameter of 11.5 cm. A flowmeter was mounted in the nose cone. Lockwood (1974) scaled the Lowestoft Sampler down to a 50 cm diameter mouth opening, with a 213 cm long open body with a nose cone (either 35.6 or 25.5 cm diameter opening); hence it became a modified Gulf V (Plate 17B). A nylon net attached to the back of the cone had 24.6 mesh per cm. The system had two flowmeters, one inside the mouth and another outside on the frame. It was designed for small boat use and was towed at ~ 3 kts. The Ministry of Agriculture, Fisheries, and Food MAFF/Guildline High-



Plate 17. Descendants of Gulf high-speed samplers. (A) The Lowestoft Gulf III high-speed sampler (Beverton & Tungate, 1967).
(B) The Modified Lowestoft sampler (Gulf V — Lockwood, 1974). (C) The Gulf VII Pro high-speed sampler (Nash et al., 1998).

speed samplers (Milligan & Riches, 1983) were also a modified Lowestoft Sampler. The first had a 40 cm diameter conical nose cone aperture with a 76.6 cm diameter and a body 275 cm long. A second system had a 20 cm diameter nose cone aperture with a 53.3 cm diameter body that was 275 cm long. These systems had a Guildline CTD sensor unit with oxygen, pH and digital flowmeter as additional probes with telemetry through a conducting cable. Most recently, Nash et al. (1998) described the Gulf VII/Pro net and MAFF/Guildline High-speed samplers that are routinely towed at 5–7 kts (Plate 17C). The basic system consists of an un-encased frame 275 cm long and 76 cm in diameter with a conical nose cone. There are smaller and larger variants of the frame and nose cone. The standard mouth opening is 40 cm in diameter. A conical net, 230 cm long with 0.28 mm nylon mesh, is attached to the back of the cone. Both systems are equipped with pressure, temperature, and conductivity sensors, and a flow metering package either transmits to ship via conducting cable or logs internally. Other environmental sensors can be accommodated. Data are scanned and recorded twice per second.

A variety of other kinds of high-speed samplers were developed during the 1950s and 1960s. Motoda (1953) developed a high-speed plankton sampler for horizontal towing near the surface that could collect a series of samples during a tow. It had a metal encasement 10 cm in diameter and 100 cm in length, and a tapered nose with two 2-cm openings. Within the encasement was a net, which was attached to a pair of fixed disks. The cod-end opened to an internal cylinder which had multiple net sections, each 1.5 cm diameter by 18 cm long, to store the samples. The system was equipped with a pressure sensor and a flowmeter and the latter was used to drive a mechanism that rotated successive nets into position for collecting a sample. The system was towed up to ~8 kts. Cassie (1956) described the evolutionary development of a high-speed net for use in fisheries research that had a brass cylinder 6 cm in diameter and 6 cm long with bridle attachment lugs and different length nets attached to the back (Plate 18A). Model 1 had a 180 cm bolting cloth net with 16 or 30 meshes per cm; Model 2 was shorter (90 cm), the net was made out of brass gauze with 16 meshes per cm, and two metal rods (struts) connected the brass cylinder to the cod-end bucket; Model 3 was even shorter (60 cm) and had four metal rods (struts). All were towed from the stern of a vessel at ~8 kts on a 40 m tow line. Bary, De Stefano, Forsyth, and Van den Kerkhof (1958) thought their high-speed sampler, known as the 'Bary Catcher' was the first to incorporate an opening/closing mechanism in the mouth of the sampler (that credit probably goes to Erdmann, 1937) (Plate 18B,C). The Catcher had a 22.9 cm diameter mouth opening; behind a closing valve, the cylindrical chamber was 19.5 cm in diameter with an outer fiberglass shell of 213 cm in overall length. Two metal nets were used, one with 15.7 meshes per cm and one with 3.9 meshes per cm. It had a depth-flowmeter (like that of Currie & Foxton, 1957) in the tail and could be towed at up to 10 kts. More than one unit could be attached to the wire and towed either vertically or horizontally.

Jashnov (1961) developed a vertical high-speed sampler with a rectangular mouth opening that could be closed using the Juday method. It was towed upward at 5 kts. Williamson (1962) built an automatic high-speed plankton sampler with a body that was 29.2 cm tall by 14 cm wide by 114 cm long, not including the side fins (Plate 18D). The aperture was 1.9 cm x 1.9 cm with a series of 21 nets attached to the bottom of rectangular 'trap doors'. These were sequentially closed by means of a cam/screw assembly driven by a ships log (propeller). Each net was ~ 6.35 cm long and made of nylon cloth with 23.6 meshes per cm. Effective sampling speeds were 5–11 knots and a sample length was 1–20 km. More than one sampler could be used on the towing wire and it was meant to provide information on the spatial distribution of plankton on scales larger than typical plankton nets and smaller than the CPR (see below). The Clarke Jet net (Clarke, 1964) was an encased high-speed sampler which had an elaborate internal passageway designed to reduce the flow speed of water within the sampler to that normally experienced by a slowly towed net (Plate 18E). It had a 12 cm diameter mouth opening with an overall length of 125 cm, used nylon netting with 0.44 mm mesh, and could be towed at speeds up to 10.5 kts. Another high-speed sampler was described by Wlodek and Szwaj (1964), which looked similar to that of Alhstrom et al. (1958).

The continuous plankton recorder (CPR) is in a class by itself when it comes to high-speed plankton



Plate 18. Other high-speed samplers of the 1950s and 1960s. (A) the Cassie High-speed Sampler (Cassie, 1956). (B, C) The Bary Catcher (Bary et al., 1958). (D) The automatic high-speed sampler (Williamson, 1962). (E) The Clarke Jet net (Clarke, 1964).

samplers (Plate 19A,B). Developed by Hardy (1926b; Glover, 1962) for use in Antarctic waters during the 1920s, it evolved over 30 years to become the main-stay in a plankton survey program in the North Atlantic that has had no equal anywhere in the worlds oceans. This encased sampler weighs 87 kg and is \sim 50 cm wide \times 50 cm tall \times 100 cm long. The 1.27 cm \times 1.27 cm rectangular aperture expands into a larger tunnel



Plate 19. The CPR high-speed sampler and a descendant. (A) Evolutionary sequence of the CPR (Hardy, 1936a). (B) The CPR circa 1993 (Wiebe, photo). (C) The UOR 1975 (Wiebe, photos).

opening. The tunnel passes through the lower portion of the sampler and out the back. Below the tunnel is one spool of silk gauze (23.6 meshes per cm) 15.25 cm wide that threads across the tunnel and captures the plankton. A second spool of silk gauze lies above the tunnel and is threaded to meet the first gauze strip as it leaves the tunnel, sandwiching the plankton between the two strips. The gauze strips are wound

up on a take-up spool that resides in a formalin-filled tank that preserves the plankton, located above the flow-through tunnel. The take-up spool is driven by a propeller on the back of the sampler, behind the tail fins. The CPR is normally towed along commercial shipping lanes by ships-of-opportunity at a standard depth of between 6 and 10 m and at speeds of up to 20 kts. Samples represent a towing distance of ~10 nautical miles (18.52 km).

One of the disadvantages of the CPR is that it only samples the surface layer of the ocean. The Undulating Oceanographic Recorder (UOR) described by Bruce and Aiken (1975) was an effort to extend the vertical sampling capability of high-speed plankton collection systems (Plate 19C). The UOR is an encased streamlined towed body 98 cm wide×75 cm tall×156 cm long, weighing 180 kg. It can be programmed to undulate between 7 and 15–70 m (wave length 3–30 km) at towing speeds of 7–15 kts. A 1.9 cm aperture leads to a tunnel at the end of which, plankton are collected on gauze rolls (15.2 cm wide silk with 0.3 mm mesh) using the same mechanism as used in the Hardy CPR. The UOR carries sensors to measure temperature, salinity and pressure with data logged internally at 30 observations per minute. A propeller drives the rollers winding up the gauze and provides the power for the electronics. The system has about a 12 h towing duration.

2.2.2. Neuston

Nets to collect neuston, the zooplankton that live within a few centimeters of the sea surface, are primarily non-opening/closing designs (Fig. 4). These specialized nets have a relatively recent history. Zaitsev (1959, 1970) appears to have been the first to build a net to sample zooplankton neuston (Plate 20A). His rectangular mouth opening design (in this case, 60 cm wide×20 cm tall) is typical of most of the subsequent neuston systems. Most neuston nets came either with a single net collecting animals right at the water surface (Zaitsev, 1959; Willis, 1963; David, 1965; Bieri & Newbury, 1966; Sameoto & Jaroszynski, 1969; Lippencott & Thomas, 1983; Sconfietti & Cantonati, 1990) (Plates 20A-F and 21A) or vertically stacked sets of two to six nets extending from the surface to ca 100 cm depth (Zaitsev, 1961; Danielssen & Tveite, 1968; Hempel & Weikert, 1972; Ellertsen, 1977; Schram, Svelle, & Opsahl, 1981) (Plate 21B-D). They were generally towed at 1-2 kts from the side of the vessel on a boom to avoid the ship's wake. However, the system described by Sameoto and Jaroszynski (1969) had a rectangular mouth opening aluminum box frame equipped with foam flotation on top, a pair of fins on the side, a fin on the bottom, and a long net (927 cm) (Plate 20E). A two-part towing bridle was attached to one side and the sampler kited out away from the side of the vessel beyond the ships wake when towed at 8–11 kts. The Booby II (Bieri & Newbury, 1966) also was towed by a bridle attached to one side of the frame to keep it away from the ship (Plate 20B). The Manta net (Plate 21A) was equipped with paravanes and an asymmetrical bridle that could be adjusted to guide the net away from the ship (Brown & Cheng, 1981). A somewhat different design for a neuston sampler described by Miller (1973) was a 'push-net' (Plate 21E). In this system, a pair of rectangular nets, each with a 60 cm×60 cm mouth opening, are positioned side-by-side in a framework and mounted in front of a small catamaran boat that pushes the frame through the water at ~ 2.6 kts.

2.2.3. Planktobenthos plankton nets

Like the sea surface, the ocean bottom is a special habitat region for zooplankton that complicates their sampling. Although there is a long history in developing gear to sample zooplankton living here (Fig. 1), much less effort has been expended compared to that invested in developing samplers for the water column. Hutchinson (1967) termed these animals planktobenthos. Reighard (1894) and Hensen (1895) appear to have been the first to have designed nets specifically to sample plankton living very near the bottom (Plate 22A). The net designed by Russell (1928) is typical of the early efforts (Plate 22B). The net made of 'stramin' (~6.25 strands per cm), had a rectangular mouth 122 cm wide×30 cm tall and was 240 cm in length. It was mounted in an Agassiz trawl frame so that it was centered inside the trawl net, which was also fixed to the frame and cleared the bottom by ~17.8 cm. No provisions were made to prevent contami-



Plate 20. Single net neuston collection systems. (A) The Neuston net (Zaitsev, 1959, 1970). (B) The Booby II Neuston net (Bieri et al., 1966). (C) A neuston net (Willis, 1963). (D) A neuston net (David, 1965). (E) A neuston net (Sameoto & Jaroszynski, 1969). (F) A neuston net (Sconfietti & Cantonati, 1990).


Plate 21. Multiple net neuston collection systems. (A) The Manta Net (Brown & Cheng, 1981). (B) Multiple neuston net (Hempel & Weikert, 1972). (C) A multiple neuston net (Ellertsen, 1977). (D) A multiple neuston net (Schram et al., 1981). (E) A Neuston Push net (Miller, 1973).



Plate 22. Early towed planktobenthos collection systems. (A) The Hensen planktobenthos sampler (Hensen, 1895). (B) The Russell sampler (Russell, 1928). (C) The opening/closing planktobenthos sampler (Bossanyi, 1951). (D) The opening/closing planktobenthos sampler (Wickstead, 1953).

nation of the collection during the lowering of the net to the sea floor or the hauling back to the surface. A similar design was described by Beauchamp (1932). The absence of an opening/closing mechanism was remedied by Bossanyi (1951) whose sledge on runners was equipped with a rectangular net ~91 cm wide×61 cm tall and ~ 213 cm long made from netting with 15.7 meshes per cm (Plate 22C). Hinged on each side of the net mouth was a pair of spring loaded doors which were attached to arms which extended perpendicular from the side of the frame. The doors closed off the mouth of the net during lowering and hauling, and were opened when the arms struck the sea floor and swung back. This system, however, only worked well on bottoms that were sandy or muddy.

To circumvent substrate dependence, Wickstead (1953) built an epi-benthic plankton sled with a rectangular mouth opening 61 cm×30 cm (Plate 22D). A sheet aluminum door, hinged horizontally about a third the distance down from the top of the net mouth, had two connecting arms extending backwards to a pair of rectangular vanes. Locking mechanisms were released when the sled landed on the bottom and the flow of water against the vanes and the door kept the door open during a tow. When the tow was stopped, the weight of the vanes and the door caused the door to close and a locking mechanism to activate. Clutter (1965) designed a self-closing epi-benthic plankton sampler principally to collect zooplankton over a smooth bottom from a small boat (Plate 23A). A 32 cm×32 cm rectangular mouth opening net was attached to a metal box framework, which was 37 cm tall×37 cm wide×30 cm long. The net was ~30 cm long had 0.333 mm nylon mesh. A scaled up version with 70.1 cm×70.1 cm mouth opening was also described. The system was lowered to the sea floor where an anchor attached to the net frame by a spool of line became fixed. The net was towed at ~1.5 kts away from the anchor until the line was fully extended whereupon it triggered a choke rope closing the net. The distance covered by the sampler was ~10 m.

The Bottom Plankton Sampler used by Macer (1967) had features similar to the devices of Bossanyi (1951) and Wickstead (1953) (Plate 23B). A metal framework with sled runners supported a plywood box having a ~30 cm×20 cm rectangular mouth opening with a net attached to its back. A spring-loaded door was mounted in the mouth with pivots top and bottom at the mid-point of the door. A piece of metal flat stock (61 cm long) with two spring-loaded steel pins (the 'shoe') was attached to the underside of the box several cm behind the mouth so that it could pivot vertically. One pin provided a stop to keep the door shut while the sampler was lowered to the sea floor or returned to the surface (the shoe was down). The other pin provided a stop to keep the door open while the sampler was being towed on the bottom and the shoe, pressed against the sea floor, was up. A flowmeter was mounted in the rear of the box. A similar system was described by Frolander and Pratt (1962). Their 'Bottom Skimmer' was a double runner sled 46 cm wide×23 cm tall×132 cm long with a roller on the forward lower cross strut (Plate 23C). Sheet lead was attached to the bottom near the front, and a pair of metal float balls snap-hooked to the top to keep sled right-side-up. Inside was mounted a Clarke-Bumpus cylinder and net (63.5 cm length. This system was towed at speeds of 1-2 kt. Omori (1969) described a bottom plankton sampler with a rectangular net 350 cm long, having a 70×70 cm mouth opening. The net frame was attached to a sled made of iron (75 cm wide×90 cm long×25 cm tall) with a plastic runner on the bottom. The system was deployed with the ship nearly stopped and then towed on the bottom at 2-3.5 kts. A messenger was used to close the net mouth before retrieval.

An entirely different strategy has been to employ manned submersibles or deep-towed vehicles to collect deep-sea planktobenthos. Grice and Hülsemann (1970) used a pair of nets (0.233 mm mesh) mounted on the front of DSRV Alvin for making net collections at depths > 1000 m (Plate 23D). The mouth openings were 'D' shaped and hinged so that on descent and ascent of the submersible, the nets could be turned back away from the flow and would not filter. The Alvin manipulator arm was used by the pilot to open and close the net. In spite of precautions, these nets suffered from contamination from plankton further up in the water column. A new system was devised by Grice (1972) for use on Alvin, which eliminated the contamination (Plate 23E). A pair of nets was attached to a pair of rectangular frames, 61 cm wide x 31 cm tall, each of which had a metal door hinged at the top that when closed, effectively sealed the net



Plate 23. Planktobenthos collection systems developed in the mid-20th century. (A) A closing planktobenthos sampler (Clutter, 1965). (B) An opening/closing planktobenthos sampler (Macer, 1967). (C) A planktobenthos sampler (Frolander & Pratt, 1962). (D, E) Opening/closing planktobenthos samplers on DSRV Alvin (Grice & Hulsemann, 1970, left), (Grice, 1972, right).

mouth. The Alvin arm was again used by the pilot to open and close the door. The nets (0.239 mm mesh) were positioned about 20 cm above the bottom and normal 'pushing' speed was 1 kt.

A multiple net system was used by Wishner (1980) on the Deep-Tow towed body (Spiess & Tyce, 1973) (Plate 24A). Three rectangular mouth opening nets, ~30 cm wide×44 cm tall and 130 cm long, were mounted on a metal framework. This framework was attached to the bottom of the Deep-Tow and system used for sampling within a few tens of meters above the deep-sea floor. The unobstructed nets were opened/closed by surface commands transmitted via conducting cable to a release mechanism. This net system was adapted for use on DSRV Alvin for near-bottom studies of plankton in the vicinity of hydrothermal vent sites (Kim & Mullineaux, 1998). The opening and closing of the nets was under pilot control.

On other benthic habitats, such as coral reefs, towing a bottom sampler to collect zooplankton may be difficult or ill-advised. Fixed or stationary net systems that orient to the current's flow and filter out zooplankton drifting by (Johannes, Coles, & Kuenzel, 1970) (Plate 24B), nets pushed by divers (Emery, 1968; Porter, 1974), and traps (Alldredge & King, 1977; Porter & Porter, 1977) have also been used to capture plankton close to the bottom. A different approach was taken by Rützler, Ferraris, and Larson (1980) to collect zooplankton on or near the bottom in coral reef areas with variable or little current flow (Plate 24C). They built the horizontal plankton sampler (HOPLASA), which created its own current. An 18.5 cm diameter×40 cm long plexiglass cylinder housed an electric motor and propeller assembly and a flow meter. Attached to the back end was an 80 cm long net with 0.25 mm nylon mesh. Typical sampling duration was 5 to 8 h with flows between 20 and 30 cm per second. The HOPLASA is very similar to a sampler designed to sample another 'benthic' habitat, the under surface of sea ice. Fukuchi, Tanimura, and Hoshiai (1979) describe a sampler, the NIPR-I, composed of a cylinder (24 cm×57.5 cm) containing a motor driven propeller and a flow meter. Water is pushed into a net (20 cm diameter×39 cm length with 100 m mesh) attached to the rear end of the cylinder. The system was used to sample under sea ice to depth of 10 m. Although not reviewed in this paper, light traps of various designs have been used effectively to sample zooplankton and ichthyoplankton around coral reefs and other structurally complex habitats (Lindquist, Hernandez, Clavijo, & Whittaker, 2001).

3. Technological advances in the 1960–1990s

At the start of this era, Aron (1962, p. 29) in a review paper said "the development of plankton sampling equipment has been dishearteningly slow...The development of instruments for capturing the larger plankton has hardly begun...little attention has been paid to securing simultaneous environmental data". In the late 1950s and 1960s, conducting cables and transistorized electronics began to be adapted for oceano-graphic use and sophisticated net systems became more capable of more than just collecting animals at specific depth intervals. For his part, Aron contributed significantly to the incorporation of new technology into zooplankton collection systems.

3.1. Closing cod-end systems

The first multiple sampler cod-end system was neither electrically driven nor controlled (Motoda, 1953) (Plate 25A), but was a scaled-up version of the serial device in the high-speed sampler described above (Fig. 4). Five cod-end nets (3.5 cm in diameter×5 cm in length, made of silk with 22.2 meshes per cm) were arranged in a circle and attached to a supporting disk. During a vertical tow, each cod-end was successively rotated into position at the back of the net, using a flowmeter as a driving mechanism. Depending upon the gearing, layers sampled ranged from 60 to 240 m. Much later, Motoda (1994) described a self-closing cod-end box with two net bags to collect the catch (Plate 25B). The net was sent down



Plate 24. Variants of planktobenthos systems from the 1970s and 1980s. (A) A multiple opening/closing planktobenthos sampler on Deep Tow (Wishner, 1980). B) fixed plantobenthos sampler (Johannes et al., 1970). (C) A current generating planktonbenthos sampler (Rützler et al., 1980).



Plate 25. Mechanical or acoustically operated cod-end sampler devices for use at the back of plankton nets. (A) The Motoda multiple cod-end sampler (Motoda, 1953). (B) The SGR self-closing cod-end (Motoda, 1994). (C) A single closing cod-end (Yentsch et al., 1962). (D) The catch dividing bucket (Foxton, 1963).

vertically and when towed horizontally, a counter balance weight opened one net bag. When the net was brought to the surface, the weight shifted, closing one net bag and opening another.

A serial sampler with a design similar to that of Motoda (1953), but controlled electrically from the surface, was used on a high-speed sampler (Fish & Snodgrass, 1962) (Plate 16B). A single-sample codend design was developed by Yentsch et al. (1962) (Plate 25C). It was a cylinder 12.7 cm in diameter and 50.8 cm long, and had a spring loaded damper valve at each end. The cod-end was used on a 75 cm diameter net and was sent down with both dampers open to allow water to flow through the net. A squib (i.e. explosive charge) detonated electrically via conducting cable from the surface released the back damper, closing it and starting the sample collection. At the end of a tow, a second squib was fired to close the other damper, thus securing the sample. Extending this idea, Foxton (1963) built a catch-dividing bucket (CDB) consisting of a tube which split into two segments, each with a cod-end net (Plate 25D). Where the single tube split into two, a spring loaded metal flap blocked flow into one or the other of the splits. A pressure release mechanism like that described by Bé et al. (1959) was used to change the position of the flap. Attached to the back of an IKMT, the CDB was sent to depth in one position. At a pre-set depth, the flap was released to the alternate position and the net fished to deeper depths. When the net again passed the pre-set depth, the flap reversed positions, closing the side of the cod-end that fished the deeper stratum and re-opening the first side for the return to the surface. Another variant on this approach was developed by Aron et al. (1964) in their construction of the Mark III Discrete Depth Plankton Sampler (DDPS) for use with an IKMT or a 1-m diameter net (Plate 26A). This cod-end was a tube 147 cm long and 10 or 15 cm in diameter, with four catch chambers separated by a solenoid-activated damper door. As with the Yentsch et al. (1962) cod-end, all doors in the cod-end were open while lowering the net to allow the animals to pass through the net. At the desired depth, doors were closed sequentially starting at the back. The last chamber was left open while the net was hauled to the surface. The Aron et al. (1964) system was one of the first to carry underwater electronics to sample depth and temperature, and to telemeter the data up a single conductor cable for display at the surface.

The MPS (Bé, 1962) was turned into a cod-end sampler for an IKMT by Pearcy and Hubbard (1964) (Plate 26B). They scaled the MPS down to a 35 cm square frame and attached to the back end of an IKMT net. The pressure release mechanism was set so the cod-end sampled depths of ~950–500 m, 500–155 m and 155 m to the surface. This system was modified by adding environmental sensors and an electronically-controlled opening/closing mechanism (Mesecar, 1980).

The Longhurst–Hardy plankton recorder (LHPR) was an innovative modification of the CPR (Longhurst, Reith, Bower, & Siebert, 1966) (Plate 26C). A pair of 50 cm diameter nets were mounted side-by-side in a towing frame. Attached to the cod-end of one net was a plankton recorder box with a tunnel chamber entering the center of the box splitting into two sections running along the sides of the box and opening at the rear. Two rolls of gauze (0.333–0.505 mm mesh), threaded across the tunnel at the point of the split, filtered the plankton from the water/plankton mix which flowed out of the back of the net. The gauze strips were spooled onto a single reel situated between the split tunnels. The take-up spool was advanced in discrete steps (15–60 s) by an electronics package on the tow frame, sandwiching the plankton between the two strips of gauze. Data on pressure, temperature, and flow were logged on an internal recorder; power was supplied by a NICAD battery pack. The LHPR was normally towed at 1.5–2.5 kts and collected about 100 samples. Longhurst designed the LHPR to collect high-resolution data on vertical distributions, while Wiebe (1970) built a modified version for studies of fine to coarse-scale horizontal plankton distributions (Plate 26D).

The LHPR had problems with hang-ups and stalling of animals in the net which caused smearing of the distributions of animals and losses of animals from the recorder box (Haury et al., 1976). The system was redesigned to reduce these sources of bias and used in studies of plankton patchiness in a variety of coastal and oceanic North Atlantic locations (Haury & Wiebe, 1982; Haury et al., 1983) (Plate 26E). The modified LHPR recorder box and electronics was mounted without a net on the conning-tower of the US Navy research submarine DOLPHIN and used in an experiment to study effects of turbulence on the distribution of zooplankton in the surface waters off Monterey Bay, California (Haury et al., 1990). In this study, environmental sensors included a 1.2 MHz ADCP, temperature, conductivity, and pressure sensors, two-axis sensors to measure turbulent velocity fluctuations and a pair of 119 kHz acoustic transducers to examine turbulence and bubble entrainment.

Another substantial modification of the LHPR was made by Williams, Collins, and Conway (1983). They used an unenclosed Lowestoft Sampler (Beverton & Tungate, 1967) 130 cm high×92 cm wide×357 cm long and with an expanding (35.6–76 cm diameter) nose cone (Plate 27A). An LHPR recorder box with 0.28 mm nylon mesh gauze was attached to the cod-end of the main net. A second recorder box was



Plate 26. Electronically driven cod-end samplers. (A) The Mark III discrete depth plankton sampler (Aron et al., 1964). (B) The Bè MPS as a cod-end sampler (Mesecar, 1980). (C) The LHPR recorder box and flowmeter (Longhurst et al., 1966). (D) The Wiebe LHPR circa 1966 (J. Smith, photo). (E) Left: a modified LHPR box; right; a LHPR test frame (Haury et al., 1976).



Plate 27. More recently developed combination high-speed sampling frames and electrically controlled cod-end samplers. (A) The LHPR/Lowestoft sampler circa 1993 (Wiebe, photo). (B) The modified LHPR (Bone, 1986). (C) ARIES (Dunn et al., 1993a).

attached to the end of 0.053 mm polyester mesh net and the unit positioned on top of the main frame. The mouth of this net was attached to a nose cone with either a 2.6 or a 5.1 cm diameter mouth openings expanding to 7.7 cm. The system acoustically telemetered depth, flow and temperature (IOS). It also carried a chlorophyll sensor with a recorder system. The nose cones of both nets had doors that were shut when the system was deployed and opened remotely. It was designed to be towed at up to 6 kts.

The LHPR was further modified by Bone (1986) for use in catching Antarctic krill. This version had a tubular frame 185 cm high×125 cm wide×640 cm long and with an 81 cm nose cone expanding to 100 cm diameter (Plate 27B). It was used with a recorder box (with 1.55 mm nylon mesh gauze) attached to the cod-end of a conical net 300 cm long with the same mesh. The mouth of the recorder box was equipped with an opening/closing unit which shunted water from the net to the open sea when closed and into the recorder when open. An IOS system acoustically telemetered depth, flow and temperature, and controlled the recorder box opening/closing unit. An underwater electronics package recorded temperature, depth, flow, and controlled the gauze advance. It was designed to be towed at up to 4 kts.

A descendant of the LHPR is the Autosampling and Recording Instrumental Environmental Sampler (ARIES—Dunn, Hall, Heath, Mitchell, & Ritchie, 1993a), (Plate 27C). This cod-end plankton sampling device is a stretched version of the Lowestoft-modified Gulf III (similar to William's et al., 1983, LHPR frame) with a 35.6 cm diameter opening nose cone which expands to 76 cm diameter. Within the framework are three sampling systems. A plankton net attached to the back of the nose cone leads to a multiple cod-end system consisting of a 2000 cm long by 16 cm wide belt outfitted with 110 6-cm diameter cod-ends with 0.2 mm mesh. A drive motor periodically increments the belt, moving the nets from a feed spool, into position to collect a sample at the back of the net, and then onto a take-up spool. Water samples are collected with 60 250-ml bottles mounted in a carousel similar to a conventional rosette sampler. A data logger records temperature, conductivity, pressure, flow, and sampling events at intervals of between 1 s and 60 min. User-selected plankton and water sampling rates are adjustable from 1 to 60 min. An acoustical telemetry system transmits depth information for realtime monitoring of the system. Typical towing speeds are 4–5 kts.

3.2. Multiple net systems

The built-in problems of cod-end sampling systems (including hang-up of animals on the netting, smearing of distributional patterns, or the non-entrance of animals into the cod-end sampler) were finally resolved by design of multiple net systems that carried 3–20 nets. These enabled an investigator to sequentially open and close nets in specific portions of the water column (Fig. 4). The systems, many of which are currently being used throughout the world's oceans, carry sensors to measure water properties such as temperature, pressure/depth, conductivity/salinity, chlorophyll fluorescence, oxygen, beam transmittance and downwelling light. They also measure sampling properties (e.g. volume of water filtered, net speed and altitude from the bottom) and net function including an alarm to indicate when a net closes.

The start of the development of such systems began with Tucker (1951) and his simple nonopening/closing trawl system (Plate 4A). Davis and Barham (1969) used timing clocks to open and close the Tucker trawl mouth (Plate 9E). Their nets were modified from that described by Tucker (1951) so that the first 500 cm of the net mesh was 1.1 cm Marlon netting and the last 200 cm was 0.33 mm nylon mesh. A depth-telemetering pinger was used to monitor net depth during a tow and a depth-time recorder was used to make alternate record. The same year, Clarke (1969) described the Rectangular Mouth Opening Trawl (RMT), a 283 cm×400 cm rectangular flexible mouth opening (8 m^{2}) with 1188 cm long 5 mm mesh net. The net mouth was opened and closed acoustically and a pinger was used to determine the depth of the net. Telemetered data were recorded on a depth sounder recorder. This system evolved into the N.I.O. Combination Net (RMT 1+8) which was a combination 100 cm×141 cm rectangular flexible mouth opening net and a 283 cm×400 cm mouth opening, with the small one above the larger on the same towing framework (Baker, Clarke, & Harris, 1973) (Plate 28A). The 1 m² net was 423 cm long and had 0.32 mm nylon mesh. Data telemetry was improved to include temperature and flow. The RMT 8 was also scaled up to 25 and 90 m² mouth openings. The RMT system was modified into a multiple net system by Roe and Shale (1979) (Plate 28B). This combination plankton-and-nekton collecting system was equipped with three 1-m² and three 8 m² nets that opened and closed by acoustic command. Also transmitted acoustically



Plate 28. Acoustically or electrically controlled opening-closing net systems based on the Tucker trawl design. (A) The RMT 1+8 (Baker et al., 1973). (B) The Multiple RMT 1+8 (Roe & Shale, 1979). (C) A multiple opening/closing Tucker trawl (Frost & McCrone, 1974, Wiebe, photo). (D) The 1- m^2 MOCNESS (Wiebe et al., 1976; Wiebe et al., 1985, Wiebe photo).

were depth and flow. Griffiths, Brandt, and Cavill (1980) described modifications to enable handling off smaller vessels without a crane using 'Kelly's eyes' and a chain rather than link wire. More recently, the acoustic command and telemetry system for the RMT 1+8 has given way to a micro-computer controlled unit connected by conducting cable to an underwater electronics unit (Dimmler & Klindt, 1990). The nets are opened and closed by command at the surface, and sensors include pressure, temperature, conductivity, tilt-angle of net mouth and flow from two flowmeters. The data acquisition rate is four times per second with data processing and display occurring in realtime.

The Tucker Trawl spurred other developments. Frost and McCrone (1974) built a modified Tucker Multiple Net Trawl with 100 cm×141 cm rectangular flexible mouth opening nets 6 m in length and constructed with 0.33 mm nylon mesh (Plate 28C). The five nets it had originally were later increased to nine nets. Also constructed was a 200 cm×282 cm mouth opening trawl with five nets of 6.35 mm stretch mesh. The system was powered electrically through conducting wire and controlled from the surface. Depth, net angle and flowmeter revolutions were monitored on deck. A modified Tucker trawl system with a rigid mouth opening was built by Wiebe, Burt, Boyd & Morton (1976) Wiebe et al. (1985) (Plate 28D). Named the Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS), the original version had a 100 cm×141 cm mouth opening with nine 0.333 mm nylon mesh nets each 6 m long. Instead of a cable connecting the top and bottom of the framework, stainless steel rods were used on each side of the mouth opening along which the bars supporting the net dropped. This provided a fixed area mouth opening that facilitated calculations of water volume filtered. The system was powered electrically on conducting wire and originally was controlled from a surface deck unit. The current version of the MOCNESS is computer controlled. Sensors include pressure, temperature, conductivity, fluorometer, transmissometer, oxygen and light. Systems may be built with 1/4, 1, 2, 4, 10 and 20 m² mouth openings, all with rigid mouths and using the same release mechanisms, sensors, and computer logging and controls (Plate 29A-D). Sameoto, Jaroszynski, and Fraser (1977) built a MPS based on MOCNESS and N.I.O. system designs (Plate 30A). It had a 100 cm×100 cm mouth opening with 10 nets (0.243 mm mesh). It had a non-rigid mouth opening with net bars similar in design to MOCNESS that slid down side cables. A depressor was mounted below the bottom net bar. It had an electronics system powered electrically and controlled from surface deck unit through conducting wire. Data logging included depth, roll, pitch and temperature. A non-telemetering self-recording flowmeter was mounted in each net. Burd and Thompson (1993) used a Rosette Controlled Tucker Trawl system with 100 cm×140 cm rectangular flexible mouth opening frame equipped with seven nets made with 0.33 mm mesh (Plate 30B). A rosette release mechanism was used to open and close nets by commands transmitted from the ship via conducting cable. The frame carried pressure, temperature, conductivity and transmissometer sensors. Flow past the frame was measured with an ADCP.

The design of the Bé (1962) MPS was also the basis for more sophisticated sampling systems. The Bedford Institute of Oceanography net and environmental sensing system (BIONESS) was built on this plan (Sameoto, Jaroszynski, & Fraser, 1979, 1980) (Plate 30C). It consisted of a 146 cm×146 cm steel box 74 cm deep, which carried ten nets with 100 cm×100 cm mouth openings. The net bars were stacked horizontally one behind the other and were dropped sequentially. A depressor plate was attached to the bottom of the metal housing. The system was powered electrically on conducting wire and controlled from surface deck unit. Data logging included depth, roll, pitch, flow, temperature and conductivity. There was also a 0.25 m² system (Plate 30D). Weikert and John (1981) modified the MPS so that it carried five 250 cm long nets made from 0.3 mm mesh which were opened and closed electronically via conducting cable (Plate 31A,B). This system, called the Multinet, also transmitted pressure, but lacked a flowmeter. A scaled up version of BIONESS was the large opening closing high speed net and environmental sampling system (LOCHNESS — Dunn, Mitchell, Urquhart & Ritchie, 1993b) (Plate 31D, E). In this case, the rectangular framework was 300 cm on a side and 200 cm deep; it carried five nets each 230 cm×230 cm in mouth opening and 1400 cm long with 2 mm knotless polyester mesh. Attached to the back of the framework



Plate 29. Variants of the MOCNESS. (A) The 20 m² MOCNESS circa 1982 (Wiebe, photo). B) The 10 m² MOCNESS circa 1992 (L. Madin, photo). (C) The 1/4 m² MOCNESS circa 1982 (Wiebe, photo). (D) The double 1 m² MOCNESS circa 1982 (Wiebe, photo).

was a hydroplane stabilizer fin. The system used a modified IOS acoustic telemetry system to monitor depth, battery voltage, flow and net function and to control net opening and closing. An underwater data logger and battery pack was mounted on top of the frame to log depth, conductivity, temperature, and other parameters. Tow speeds with this system were up to 6 kts. Another variant of the MPS was developed by Terazaki (1991). The ORI vertical MPS (Plate 31C) has a 100 cm×100 cm rectangular mouth and can be equipped with four to ten nets each 510 cm long with 0.33 mm nylon mesh. The nets are opened/closed by surface commands transmitted via conducting cable to an underwater unit.



Plate 30. Variants of multiple net systems based on the Tucker trawl and or the Bé MPS (see Plate 9). (A) A modified MOCNESS (Sameoto et al., 1979). (B) A modified Tucker trawl (Burd & Thomson, 1993). (C) The 1-m² BIONESS circa 1993 (Sameoto et al., 1977, Wiebe, photo). D) The Mini-BIONESS equipped with an OPC (M. Benfield, photo).

3.3. Moored plankton collection systems

Only a few instrument systems have been developed to autonomously collect time-series samples of plankton from specific locations. The scarcity of such systems is largely due to the difficulty of providing sufficient energy to power them for long periods. The O'Hara Automatic Plankton Sampler was patterned



Plate 31. Descendants of the Bé MPS. (A) A multi-net rigged for a vertical tow (Weikert & John, 1981. —Niehoff, photo. (B) Postel photo). (C) The ORI vertical MPS (Terazaki, 1991). (D,E) The LOCHNESS (Dunn et al., 1993b).

after the CPR, and LHPR (1984) (Plate 32A). This sampler had two rolls of 0.457 mm Nitex mesh. One roll was stepped across the tunnel to collect plankton being drawn through the sampler by a 2 HP outboard battery powered motor. The gauze was taken up by a second spool in a formalin filled chamber. A second roll of gauze was wound onto the take-up spool to sandwich the plankton. A preset number of flow meter



Plate 32. Moored plankton collection systems. (A) The O'Hara automatic plankton sampler (O'Hara, 1984). (B) The moored automated plankton sampler (Lewis & Heckl, 1991). (C, D) The moored, automated, serial zooplankton pump (Doherty & Butman, 1990; L. Garland, photo).

counts determined the length of time of filtering for each sample and up to 12 samples could be collected over a 30 min period. A modified version of the O'Hara (1984) system was built by Lewis and Heckl (1991) (Plate 32B). Their moored automated plankton sampler consisted of a series of ten small nets (12.5 cm×16 cm in diameter and 13 cm in length) made with 0.253 mm Nitex mesh. Each net had an inner collar area which was sewn into a 20 cm wide vinyl belt, similar in design to that of ARIES — Dunn et al. (1993a). The belt with nets started on one spool, was stepped into the tunnel downstream of the inlet to collect plankton, and was taken up with a second spool in a formalin filled container. Water was drawn through the system by a 2 HP outboard battery powered motor. An electronics package turned the system on and off, and logged flow. Several 'net boxes' could be put in series to increase the number of samples collected.

Another autonomous system, the Moored, Automated, Serial Zooplankton Pump (MASZP), was based on the LHPR (Doherty & Butman, 1990) (Plate 32C,D). This self-contained pump and plankton collection system was mounted in a metal frame, 91 cm in diameter and 200 cm tall, which could be deployed on a mooring or bottom tripod. Water flowed into the pump tunnel entrance (5 cm diameter) from all horizontal directions. Two strips of plankton gauze (0.1 mm mesh) on supply spools cut across the intake tunnel and were wound onto a take-up spool at discrete intervals during sampling. Sample volume was calculated by pump displacement and pump revolutions. Sampling was controlled by a battery powered micro-computer controller and data logger, and could be based on time and/or an external event. Either forty 1000-l samples or eighty 500-l samples could be collected. An electro-magnetic current meter was used with the sampler.

3.4. Optical systems

Optical systems provide a number of advantages over net-based systems (see Foote, 2000 for a review of optical principles and sampling systems). Their greatest advantage is an increase in the vertical and horizontal spatial resolution of the sampling system. Rather than integrating abundances of a particular taxon over the length of a net tow, optical systems have the potential to provide abundance data at short temporal intervals along the tow path. This information can be provided for any taxon or size class of interest. Further, fragile taxa that may be damaged by net collection can be detected by optical instruments without damage.

Optical survey instruments can be divided into two categories, based on whether the systems produce an image of their zooplankton targets (e.g. video, photographic and digital camera systems) or use the interruption of a light source to detect and estimate the size of particles (e.g. the optical plankton counter (OPC)) (Fig. 5). Both types of sensors have the potential to produce fine-scale spatial information about the distributions of particles. Image-forming systems yield information on the identities and dimensions of their target particles while particle detection systems produce information on the abundances of different size classes of particles along their trajectories. Optical systems were initially deployed in conjunction with conventional net samplers and have more recently been developed as stand-alone sensing systems (Fig. 5).

The genesis of optical sensing systems designed to quantify the abundances of plankton and other particles is generally regarded as relatively new developments, yet their evolution can be traced back nearly fifty years. The first attempts to quantify plankton optically appear to have been made during the 1950s in Europe, North America and Japan. Most of these instruments were not quantitative because the dimensions of the imaged volume were poorly defined.

3.4.1. Image-forming systems mounted on non-opening/closing nets

The use of image-forming optical systems began in earnest during the late 1970s when Ortner, Hill, and Edgerton (1981) placed a 35 mm still camera with a high-capacity film magazine in front of the cod-end of a conical 70 cm diameter, 0.202 mm mesh plankton net attached to a rigid frame (Plate 33C). This system, which provided in situ silhouette photography of zooplankton as they passed into the cod-end of



Plate 33. Image forming camera and television systems for surveying zooplankton. (A) The IR and schematic of IR components (D. Schnack, photo). (B) The ISVC (P. Tiselius, photo). (C) P. Ortner's Camera-net System on the R/V Pelican (S. Cummings, photo). (D) A MOCNESS with a VPR circa 1999 (P. Alatalo, photo).

a plankton net, was a field application of the laboratory-based silhouette photography system described by Ortner, Cummings, and Aftring (1979). The camera provided a series of photographic images at points along the trajectory of the net separated by less than 1 m. Systems based on this design have been used to investigate anchovy (*Anchoa mitchilli*) egg distributions (Houde, Ortner, Lubbers, & Cummings, 1989),

walleye pollock (*Theragra chalcogramma*) egg distributions (Reed, Schumacher, & Kendall, 1988), and estuarine zooplankton and ichthyoplankton (Olney & Houde, 1993).

Ortner's camera-net system was an early attempt to address several limitations inherent in conventional net sampling systems: limited spatial resolution, relatively long sample processing time (rinsing, splitting, preservation, and enumeration), and damage of fragile organisms during collection and processing. The photographs provided a record of the spatial heterogeneity along the path of each tow, which would otherwise have been lost during accumulation of the sample in the cod-end. Coupling the optical system to a net allowed concentration of plankton taxa, many of which were present in low densities. The short path length of the imaging cell permitted the use of the system in estuarine waters where turbidities would otherwise limit the effectiveness of optical systems. Later versions of the camera-net system incorporated a pair of plankton nets. Environmental and system-orientation sensors enabled spatial mapping of the physical conditions that were associated with zooplankton distributions. Sample processing time was lower for the photographic data than for the net samples. Olney and Houde (1993) estimated a mean saving of 24.6 h per sample by using the camera system. The camera system also provided a record of the distributions and identities of fragile gelatinous forms that were damaged in the net or dissolved after preservation.

The camera-net system provided several advances over conventional net systems, but also suffered from several limitations. The overall sample volume was small, detecting only \sim 5% of the volume collected in the net (Olney & Houde, 1993). In spite of a large-capacity film magazine (800–1000 frames), the endurance of the system was potentially limited to a few minutes when the objective was to obtain data at the finest spatial resolution (i.e., <1 m). Ortner et al. (1981) sampled at 0.3 Hz while Olney and Houde (1993) sampled at 1 Hz. These rates provided tow durations of 4.5 and 15 min, respectively. Data analysis required film development and examination under a microscope. This delay meant that the users were not provided with even a qualitative estimate of the nature of their sample content and distribution until after a cruise. Comparisons with net tow data suggested that rare taxa, such as fish larvae, were under-sampled by the optics. The issues of low sample volume, limited image capacity and sampling rate, lack of real-time feedback, and under-sampling of rare taxa became important considerations in the development of subsequent image-forming systems. To varying degrees, these issues continue to limit the performance of current optical sampling systems.

Following the first public television broadcast in 1939, the promise of video became clear to oceanographers. In the 1960s, oceanographers, who were attempting to understand the nature of the deep scattering layer, considered the use of video systems and Rachel Carson suggested that an underwater television camera might help to identify the nature of the deep scattering layer (Carson, 1961). However, it was to be almost 20 more years before the development of optical survey systems began to produce practical, quantitative tools for the enumeration of zooplankton and other small particles in the oceans.

A step in this development was the replacement of the 35 mm still camera in Ortner et al.'s cameranet system with a video camera. Development of the ichthyoplankton recorder (IR) has been described by Froese et al. (1990); Welsch et al. (1991); and Wieland, Hermann, Kreikemeies, Lenz, Mees, & Schnack (1992) (Plate 33A). The IR employed a video camera mounted in front of the cod-end of a high-speed Gulf V-type net (Nackthai — Nellen & Hempel, 1969). Separate interlaced video fields were telemetered to the surface via conducting cable and recorded on SVHS videotape at 50 Hz (Welsch et al., 1991). The image volume was 4.5 cm² (15 mm wide×15 mm high×20 mm long — Lenz et al. (1995)). The primary advantages of the IR over the 35 mm camera-net system were increased horizontal spatial resolution, and an increase in tow endurance. Video and environmental data were telemetered to the ship at 50 Hz, while the system was towed at 5 kts. This sampling rate and tow speed yielded an estimated maximum horizontal spatial resolution of 5 cm (Welsch et al., 1991). Lenz et al. (1995) estimated a typical horizontal spatial resolution of 3 cm. Data from the IR system could be continuously recorded on SVHS tape with only brief gaps during tape changes.

A more recent adaptation of the video-net technology was developed by Akiba (1999). His system uses

a plankton net and a pair of pumps to concentrate and size-fractionate zooplankton prior to passage through a flow-cell where they are illuminated by a xenon strobe with a 1 μ s (microsecond) pulse and imaged by a video camera (640×480 lines). His system was also strongly influenced by the video plankton recorder (VPR) (see section 3.4.2) and employs an automated image classification system.

One of the consequences of the transition from still cameras to video cameras and film to tape has been a trade-off between image area (and consequently, volume) and resolution. Olney and Houde (1993) using Ortner et al.'s (1981) camera-net were able to image a large area of water (46.5 cm²) because their recording medium (photographic film) had a high density of photosensitive particles. The replacement of film with videotape necessitated a reduction in the image area because of the reduced pixel-density of the chargecoupled device (CCD) array. Lenz et al. (1995) imaged a much smaller image area (2.25 cm²) because their video camera CCD had a density of 384×256 pixels. This trade-off between resolution and image volume has imposed a limit on the image volumes used by subsequent video camera systems, based on commercially available video standards such as the North American Television Standard (NTSC). The advent of higher-resolution formats (high-definition television, high-speed digital still cameras, and digital video cameras) will permit larger image areas and volumes without loss of resolution.

Camera-net and net-video combinations are attractive because the net concentrates zooplankton prior to imaging. For organisms that are less abundant, this technique increases the likelihood of their detection by the camera. Net-based ground truthing of the optical data is simplified by mounting the camera on the same platform as the net. These advantages come at a cost: passage through the net alerts the organisms to the presence of the sampling system and potentially enhances net avoidance. Further, a logical endpoint in the evolution of optical systems is the development of *stand-alone* systems that are largely independent of attached net systems. Consistent with this pattern, the next generation of optical, image-forming survey systems has been designed to operate without nets.

3.4.2. Stand-alone image-forming systems

The evolution of quantitative stand-alone image-forming systems really began with the pioneering studies utilizing qualitative still and television systems during the 1950s. These systems are described more fully in section 3.4.4.

The VPR (Davis, Gallager, Bermann, Haury & Striculer, 1992a; Davis, Gallagher, & Solow, 1992b) was developed as a towed instrument capable of imaging zooplankton within a defined volume of water. The VPR was inspired by a combination of samplers and approaches including the LHPR, silhouette photography, benchtop video microscopy, and a benchtop imaging system (Strickler, 1977). The original VPR had four video cameras; each camera imaged concentrically-located volumes of water ranging from less than 1 ml to 1000 ml (Davis et al., 1992a) (Plate 34A). The image volumes were illuminated by a high-intensity, short-pulse duration (~1 μ s) xenon strobe synchronized to the sampling rate of the cameras. The strobe was positioned ~1 m from the cameras and orientated to provide dark-field illumination (Davis et al., 1992a). The cameras and strobe were mounted on a prong-shaped frame, so the imaged volume was located near the leading edge of the vehicle in water relatively undisturbed by the frame. A CTD package and telemetry hardware were mounted further back on the frame. The video cameras provided 570 horizontal×485 vertical TV lines and video data were stored on high-definition, broadcast-quality BETA-CAM-SP videotape. The large data volume produced by four video cameras and environmental sensors necessitated the use of an electro-optical cable to provide the necessary bandwidth to transfer the VPR data to the surface.

Both the camera-net and IR systems collected images within a volume of water constrained by the dimensions of the imaging chamber in the cod-end. One of the challenges posed by imaging an unconstrained volume of water illuminated by an obliquely-mounted strobe was to determine the depth of field. Although the width and height of the image were clearly defined by the limits of the camera field, the depth of field was more problematical. Each video field potentially contained in-focus images of organisms



Plate 34. Variants of the VPR. (A) The VPR prototype circa 1996 (M. Benfield, photo). (B) More recent version of the VPR (P. Alatalo, photo). (C) The Vertical Profiling VPR being launched on Georges Bank circa December 1999 (P. Wiebe, photo). (D) The VPR in a surface skimmer circa 2000 (S. Gallager, photo).

that were located within the depth of field as well as out-of-focus images of organisms located in front or behind the imaged volume. Some images were just slightly out-of-focus for animals positioned close to the image volume, but there were also unrecognizable, highly blurred images of animals well outside the video camera's depth of field. The early solution to this problem was to train the data analyst to recognize out-of-focus animals by videotaping tethered individuals of different taxa as they were moved through the depth of field.

Data were initially analyzed by manually viewing each videotape one field at a time using a monitor with an overlaid MATLAB measurement routine (see Benfield, Davis, Wiebe, Gallager, Lough, & Copley, 1996 for a description of this technique). The identity of each target was determined by the observer and recorded in a file using a pull down menu. Then, a point-and-click interface allowed the operator to measure the dimensions of each zooplankton target. This proved to be highly labor intensive because each hour of videotape required examination of 216 000 video fields. Zooplankton densities were estimated by dividing the number of individuals of each taxonomic category observed in a section of videotape by the cumulative volume imaged over the same time period. The mean density at a particular point in time can be located in three-dimensional coordinate space by relating the time an image was taken to the VPR's navigational datafile containing time, longitude, latitude and depth.

The four-camera VPR has been modified to a two-camera system (Plate 34B). Early testing determined that two cameras operating at high magnification (0.6 ml) and low magnification (26 ml) provided the most useful information. The high-magnification camera provides detailed images of individual animals. These images often contained sufficient taxonomic information to permit identification to the genus and species levels. The wide-field camera provided images of larger organisms (such as ctenophores, euphausi-ids, and medusae) and multiple targets (such as several copepods). Positioning the imaged volume at the leading edge of the tow-body, and having wide separation of cameras and strobe permitted imaging of undisturbed animals in their natural orientations. Such data made it possible to measure in situ orientations of copepods such as *Calanus finmarchicus* (Benfield, Davis, & Gallager, 2000a) and pteropods *Limacina retroversa* (Gallager, 1997) from which their behavior could be inferred.

Since its early deployments in 1991, the VPR and its data analysis system have undergone modification and refinement (Davis, Gallager, Marra, & Stewart, 1996). Structural changes to the VPR have included reduction in size and a shift from a prong-shaped speed-rail frame to a small, fiberglass V-fin tow-body (Davis, Gallager, Marra & Stewart, 1996). Handling of the smaller and lighter VPR is considerably easier; its smaller size also permits deployment from much smaller vessels.

By far the greatest advance has been in the area of optical data extraction and analysis. A large proportion of video fields contain images that are devoid of in-focus zooplankton targets. Manual analysis of tapes requires the operator to scan many empty images and to distinguish and ignore images that contain outof-focus targets. Such a process is too slow to keep up with the rate at which data are acquired, and introduces potential errors due to the subjective nature of decisions about the inclusion or exclusion of out-of-focus targets. These problems led to the development of an automated image-processing system capable of locating and extracting focused targets of zooplankton.

The current image processing system consists of a Pentium III computer running the Windows NT operating system, and equipped with a pair of image-processing boards manufactured by Imaging Technologies. The system is capable of digitizing each video field in real time and scanning the fields for targets using user-defined search criteria for brightness, focus, and size. Targets that meet these criteria are called regions of interest (ROI). ROIs are cropped within user-defined limits and written to disk with a filename that corresponds to the imaging time. ROIs can be extracted and displayed on a monitor, providing users with a qualitative assessment of the taxonomic composition of the water column in real time. The primary advantages of this system are substantial saving in analysis time and removal of subjective bias in the rejection of out-of-focus targets. Identification of the extracted ROI's still requires a trained human operator. The latest development in the VPR image-processing system is a zooplankton identification program (Tang et al., 1998). The initial performance of this system is encouraging (Tang et al., 1998). Using artificial intelligence, it has been used at sea to provide near-real-time maps of the distributions of the copepod, *C. finmarchicus* and hydroid colonies on Georges Bank (Davis, Gallager, Tang, Vincent, & Ashjian, personal communication).

A number of VPR-based systems are currently in operation or under development (Plates 33D and 34A–D). A single-camera system, now upgraded to a dual camera VPR, is mounted on the BIOMAPER II vehicle (see section 4.1.1). Internally-recording VPRs have been constructed by placing a small Hi-8 format VCR within a pressure housing. One of these systems has been used to quantify radiolarians and foramini-ferans by Dennett, Caron, Michaels, Gallagher, and Davis (2002) and another has been mounted on a 1-m² MOCNESS net system by Gregory Lough (National Marine Fisheries Service) to map the fine-scale distributions of the larval cod prey items (Plate 33D). A moored system called the autonomous vertically profiling plankton observatory (AVPPO) utilizes an internally recording, two-camera VPR and has been deployed on Georges Bank and in shallow waters near Cape Cod (Thwaites, Gallager, Davis, Bradley, Girard, & Paul, 1998) (Plate 34C). The most recent version utilizes a 1 megapixel Pulnix digital camera operating at 30 Hz to image zooplankton within a volume comparable to the original VPR, but at substantially higher resolution.

The high cost and technological sophistication of the VPR has prompted construction of a less complex, relatively inexpensive video system called the in situ video camera (ISVC) (Tiselius, 1998), which can be deployed by horizontal towing or vertical profiling (Plate 33B). The ISVC is a single-camera system based on the VPR design. It has been simplified by using PVC pipe pressure casings, conducting cable, lower-cost video and strobe units, eliminating a slip-ring assembly on the surface winch, and by making the on-board CTD and/or fluorometer packages optional. The camera, strobe, and associated electronics are mounted in individual pressure housings and secured to an aluminum frame fitted with a stabilization fin (Tiselius, 1998). Video data are transmitted via conducting cable and are stored on an SVHS recording deck after being stamped with time-code. Calibration follows the method of Davis et al. (1992a,b) where a tethered target is moved through the camera's depth of field (Tiselius, 1998). Data analyses are performed using manual examination of video fields.

Image resolution constraints inherent in the use of standard video formats have driven the development of optical systems that utilize higher-resolution formats. A modification of the continuous underway fish egg sampler (CUFES) (see section 3.4.3) utilizes a line-scanning digital camera to quantify the abundances of fish eggs (Checkley, Motos, Uriarte, Santos, Trivedi, & Iwamoto, 1999). This machine is mounted on board a ship and channels the sample stream from a surface intake, through a fish egg concentrator, and through a viewport. The water is imaged with a digital camera and recorded on a micro-computer based image processor. Near-real-time estimates of egg abundances are possible with this system.

Ross and Mackas at the Institute of Ocean Sciences, Canada have developed a VPR-based camera system utilizing an internally recording digital video recorder (Canon ZR10) with a synchronized strobe (T. Ross, personal communication). Their system is used to quantify the distributions of macrozooplankton and is mounted on the upper mast of the towed ocean microstructure instrument (TOMI) (Plate 35A). The camera faces 20° into the flow and images a volume of ~40 ml at a point 36 cm in front of the mast. It is tow-yo'd or towed horizontally at 1 m/s.

The shadowed image particle profiling and evaluation recorder (SIPPER) utilizes high-resolution digital line-scanning cameras to quantify zooplankton passing through a laser light sheet (Samson, Hopkins, Remsen, Langebrake, Sutton, & Putton, 2001) (Plate 35C). The SIPPER has been mounted either on a towed vehicle called the high resolution sampler (HRS) or a 53.34 cm diameter autonomous underwater vehicle (AUV). In either case, water flows unidirectionally through an intake where it passes through a 96 mm wide×96 mm tall×1 mm thick continuous light sheet formed by a 635 nm laser. Light from the sheet then converges on a 46 mm diameter imaging lens attached to an EG&G digital line scan-camera. SIPPER contains a pair of light sheet and camera systems, allowing images to be collected from two planes rotated by 90°. One system employs a line-scan camera with a 4096 pixel array, and the other uses a 2048 pixel array. These cameras provide a continuous digital record of targets that pass through the light sheets. Data are stored on high capacity hard drives and images of targets are reconstructed using custom image processing software. The system can provide a continuous record of the contents of up to 30 m³ per hour. Changes in flow rate can distort the reconstructed images of targets, so SIPPER incorporates an optical flow meter that measures the transit times of particles between the two light sheets and estimates current velocity with an accuracy of 1.5%. SIPPER is still in the developmental stage; however, it appears capable of producing strikingly detailed images of both large and small zooplankton including highly transparent taxa such as lobster phyllosoma larvae and ctenophores.

The need for systems to quantify the abundance of marine snow prompted development of profiling systems based on both still and video cameras. Honjo, Doherty, Agrawal, & Asper (1984) constructed a profiling system called the Large Amorphous Aggregates (LAA) camera. The LAA camera employed a photographic camera (Benthos 372 equipped with a 28 mm lens) and a pair of Benthos 383 strobes to photograph marine aggregates. Light from the strobes passed through a Fresnel lens to produce a collimated beam oriented orthogonally to the plane of the camera (Honjo et al., 1984). The resulting image volume was 106 cm×156 cm×40 cm. The system was lowered at 20 m min⁻¹ while sampling at 20 s intervals.



Plate 35. Variants of image forming optical systems for zooplankton and marine snow studies. (A) A digital video camera recording system (indicated by arrow) mounted on a TOMI vehicle (T. Ross, photo). (B) The ZOOVIS (M. Benfield, photo). (C) SIPPER mounted within the HRS (T. Sutton, photo). (D) The UVP (G. Gorsky, photo).

The system had a film capacity of 1600 images. When the system was deployed off the coast of California, it provided images of live crustacean and gelatinous zooplankton, in addition to marine snow.

Gorsky, Aldorf, Kage, Picheral, Garcia, and Favole (1992) describe a video profiling instrument used to quantify the vertical distribution and size frequency of marine snow (Plate 35D). The original underwater video profiler (UVP) consisted of a Hi-8 video camera (phase alternating standard (PAL) television standard at 50 Hz) imaging a collimated light sheet coupled with a CTD, data logger, and batteries. The camera was aimed downwards into a sheet of light located 90 cm from the camera. The light sheet could be produced by either continuous or strobed sources. The continuous illumination provided a parallel light of 150 W produced by 75 W sources that faced each other and illuminated a field of 19.2×14.3 cm×1.5 cm thick. The camera pointed downward and was oriented a 90° to the light sheet. The strobed lighting system

consisted of four 75 W Birns underwater strobes aimed perpendicularly to the camera illuminating a volume of ~100 L. The UVP recorded data internally and could be programmed to start and stop data acquisition at set temperatures, depths or times. Tape duration set an upper limit (3 h) on deployment endurance. The system was pressure-resistant to over 1000 m and weighed 160 kg in air (Gorsky et al., 1992). Data from the continuous illumination system were processed with an image analysis system that included a SONY video tape recorder, a micro-computer with a frame-grabbing card, and custom software. After digitization onto a 512×512 pixel matrix, each image was thresholded and examined for particles; the diameters and areas of each particle were quantified using the software (Gorsky et al., 1992).

Since the development of the first UVP, the instrument has been upgraded and modified. The most recent version UVP model III (Gorsky, Picheral, & Stemmann, 2000b) is mounted on a $1.1\times0.9\times1.25$ m galvanized frame. Illumination is a structured 10 cm thick light sheet produced by a pair of 54 W Chadwick Helmuth strobes that are synchronized with a pair of Exavision XC644 black and white CCD videocameras. The strobe pulse duration (30 µs) permits the UPV model III to be lowered at 1.5 m s^{-1} without image smearing. The cameras are aimed perpendicularly to the light sheet and image volumes of 1.3 and 6.5 1 are stored on a pair of internally-recording Hi-8 recorders. The UVP model III can also utilize four 100 W spotlamps to illuminate a larger non-structured volume of water. Environmental data are provided by a SeaBird Seacat SBE19 CTD equipped with a fluorometer and nephelometer. Power is provided by four 24 V batteries and control is from a Texas Instruments 370 microprocessor. The primary application of the UVP has been study of marine snow (Gorsky et al., 1992, 2000b), although the instrument has also been used in strobed mode to examine the distributions of macrozooplankton (Baussant, Gasser, Gorsky, & Kantidakis, 1993; Gorsky, Flood, Youngbluth, Picheral, & Favole, 2000a; Gorsky et al., 2000b). The preliminary description of the system reported that particles in the 90–5000 µm range were clearly visible in the light sheet.

The zooplankton visualization and imaging system (ZOOVIS — Benfield, Shaw, & Schwehm, 2000b; Wiebe & Benfield, 2001) is a profiling instrument designed to quantify the distribution and abundance of mesozooplankton to depths of 250 m (Plate 35B). ZOOVIS is based on the UVP, but incorporates a high resolution 2048×2048 pixel, 2 Hz, 14 bit monochrome BioXight digital camera (Pixelvision Inc) synchronized with a strobed light sheet 10 cm high and 2 cm thick with a pulse length of 25 µs. The camera is aimed down at 90° relative to the light sheet providing dark-field illumination. The image volume is variable depending upon the settings used on the zoom lens and can image a maximum illuminated volume of 500 ml. A CTD including fluorometer and transmissometer are coupled with the system. Power for ZOOVIS is transmitted from the surface while command and control and optical/CTD data flow bi-directionally via multiplexed optical fibers within an electro-optical 14 mm diameter cable spooled on a winch equipped with conductive and optical slip-rings. An underwater backplane PC is networked with a surface PC via an ethernet connection and serves to relay command and control from the surface PC to the underwater camera system and CTD.

The towed optical plankton survey instrument (TOPSI) and the large area plankton imaging system (LAPIS) are new systems currently under development that are designed to quantify the distribution and abundance of gelatinous organisms in the 1–100 cm size range (L. Madin, WHOI, personal communication). Both are analogous to optical nets and will employ vertically oriented structured light sheets produced by red light-emitting diode (LED) arrays. TOPSI will have a 2 m² field of view and internal data recording while LAPIS will have a 4 m² field of view and support fiber-optic telemetry to a surface acquisition system. Specifications for TOPSI include: an aluminum frame allowing varied arrangements of the components and stable horizontal flight at tow speeds of 1–2 kts; a 2 m² field of view illuminated by a 15 cm thick light sheet produced by an array of LEDs operating at 620 nm; an internal battery pack with power for over 1 h; imaging with a monochrome high definition video camera combined with high-resolution optics; video images recorded on an internal digital video recorder, with a 1 h recording time; environmental data (depth, temperature, conductivity) and operational parameters (horizontal flow speed, vertical angle, power status) obtained with a standard MOCNESS underwater sensor and computer package, which will also provide

control functions and telemetry to the ship via standard conducting cable (not fiber-optic). TOPSI would be plug-compatible with any MOCNESS net and would require no specialized topside equipment. LAPIS would consist of a larger version of TOPSI and would be capable of data telemetry to the surface via a fiber optic cable. A prototype of TOPSI was assembled and tested at sea during 1999.

Bergström, Gustavsson, and Strömberg (1992) mounted a color video camera on the front of a Sea Owl II remotely operated vehicle (ROV) and used it to quantify the vertical distribution of gelatinous zooplankton off the west coast of Sweden. The color video camera was aimed forward and a rectangular calibration frame of 0.4 m^2 was used to define the field of view within which targets were counted. A flow meter provided an estimate of the distance along each transect, which enabled an estimate of the density of targets per unit volume. Data were collected on the ctenophore *Bolinopsis infundibulum* at five depth strata between 7 and 110 m (Bergström et al., 1992).

The need for instruments capable of resolving the three-dimensional positions and identities of small particles within a large volume of water led to the development of holographic imaging systems. One of the advantages of using holographic imaging is that the holograms do not have the depth of field constraints of conventional photography. Any target between the laser source and the recording medium can be reconstructed in focus. Holographic imaging of plankton was first reported by Knox (1966), who used a ruby laser to produce holograms of live plankton in a laboratory. His system represented a substantial advance because it provided a high-resolution record of mesoplankton in a large volume (>1 l). Knox (1966) recorded his on-axis hologram on photographic emulsion by immersing the plate in a container filled with seawater and live zooplankton. After development, the hologram was reconstructed by illuminating it with a Helium-Neon continuous gas laser and viewed with a microscope. Although an in situ system was not developed using this technology, Knox (1966) proposed the feasibility of such a system as well as a microscope calibrated for motion in three planes to record the three-dimensional positions of each organism. Knox's still holographic system was refined to record movies of live plankton in the laboratory using an Argon-ion laser pulsed at 50 µs intervals (Knox and Brooks, 1969). Their animated on-axis holograms were recorded on 35 mm film without magnification; each image recorded the contents of a $2.2 \times 1.6 \times 7.1$ cm (25 cm³) volume of water. Details of copepods as small as 10 μ m were resolved with this technique. Holograms were examined visually; however, conventional still cameras and movie cameras with still photography capability were proposed to record holograms for subsequent viewing (Knox & Brooks, 1969). Animated holography was further developed by Stewart, Beers, & Knox (1973) and Heflinger, Stewart, & Booth (1978), who employed off-axis holography and shorter laser pulse lengths (4 μ s) to record holograms of moving copepods at higher resolution. Holograms were reconstructed using light-field or dark-field illumination; they reported satisfactory results for volumes of 'many cubic centimeters' at working distances of 10 cm (Heflinger et al., 1978).

The development of holographic systems was dormant during the 1980s and for most of the 1990s until revived and refined by Katz, Donaghay, Zhang, King, and Russell (1999), with the development of the submersible holocamera (Plate 36A–C). This instrument consists of an in-situ, internally-recording in-line holographic camera that records up to 300 holograms on a film emulsion. It uses a battery-powered ruby laser equipped with multiple flashlamps. A CTD is mounted on the vehicle. The instrument can be deployed in a static or profiling mode, with a fiber-optic tether to the surface to permit control of the holocamera and associated environmental sensors. The image volume is a 63 mm diameter cylinder of variable length (from 100 to 680 mm) yielding image volumes of 312-2119 cm³. Holograms are reconstructed in the laboratory using a helium–neon laser and corrected for axial shrinkage. Images of particles in the hologram are recorded using a CCD camera and digitized with a frame-grabber. Targets are then identified manually. The images collected with the holocamera are remarkably clear and the system can resolve small features in the 10 μ m size range. Particle velocities can also be estimated by pulsing the laser at short time intervals. The holocamera has been employed operationally in East Sound, WA, to examine distributions of particles around thin-layers and in the Straits of Georgia, Canada (Malkiel, Alquaddoomi, & Katz, 1999). During



Plate 36. Holographic and bioluminescent detection systems. (A–C) The holocamera system mounted on the JSL submersible. The large rectangle on the opposite side of the JSL (right image) is part of the ISIT bioluminescence camera system (E. Malkiel, E. Widder, J. Katz, photos). (D) HOLOMAR in situ holographic camera (J. Watson, photo). (E) ISIT bioluminescence detector system with a circular excitation frame mounted on the JSL (E. Widder, photo).

these operations, the sample volume was 732 ml and the reconstructed images had resolutions ranging from 10 to 20 μ m for spherical particles and 3 μ m for linear particles that lay within 100 mm of the film. The most recent operations were in the Gulf of Maine during June–July 2000 using the Johnson–Sealink submersible. During these deployments both the holocamera and the intensified silicon-intensified target (ISIT) bioluminescence measurement system (Kocak, Lobo, & Widder, 1999) (Plate 36E) were deployed together on the submersible (J. Katz, personal communication) Further refinements to the system are planned, including conversion to off-axis holography and incorporation of the particle image velocimetry (PIV) analysis. The PIV (Zhang, Tao, & Katz, 1997) utilizes double exposures separated by 20 μ s to estimate velocity vectors for individual particles. Laboratory studies with PIV in an off-axis holography mode resulted in an order-of-magnitude increase in the number of resolved particles detected and a reduction in the minimum size of resolved particles to 3 μ m (Katz et al., 1999).

Watson and colleagues at Aberdeen University have developed an in situ holographic system called HOLOMAR (Hobson & Watson, 1999; Hobson, Lampitt, Rogerson, Watson, Fang & Krantz, 2000; Watson et al., 2000) (Plate 36D). This instrument can collect either on- or off-axis holograms of volumes of water up to 100,000 cm³. The instrument is large (~3 MT) and up to 45 separate images can be acquired during each deployment to depths of 100 m. A large pressure housing contains the laser, power supply, control electronics, optical components and photographic plate holders. Two arms protrude from one end of the housing and provide a direct optical path for collection of in-line holograms while a recessed optical port allows collection of off-axis holograms.

The optical imaging systems described thus far have utilized active illumination systems. Many zooplankton produce or induce the production of bioluminescent light that can be detected with sensitive CCD cameras. Kocak et al. (1999) developed a method to quantify the distribution, abundance and identities of bioluminescent zooplankton. Their submarine-mounted system consists of an ISIT video camera mounted on the Johnson SeaLink manned submersible, aimed forward at a 1m diameter transect screen (Plate 36E). Bioluminescent organisms are mechanically-stimulated to luminesce when they encounter the screen and these flashes are recorded on the camera. Quantitative samples of plankton are collected during horizontal transects using a suction pump system and flow meter system connected to series of sample storage containers that are rotated into and out of the flow.

3.4.3. Particle detection systems

Particle detection systems refer to non-image-forming devices that utilize interruption of an electrical current or a light beam to detect and estimate the size of a passing particle. The operating principles and history of some of these systems have been reviewed by Sprules et al. (1992). Boyd and Johnson (1969) appear to have developed the first in situ particle counting and sizing system which was initially called the electronic zooplankton counting device (EZCD) and was subsequently referred to as the in situ zooplankton detecting device (Boyd, 1973) (Plate 37A, B, C). This system was based on a modified Coulter Counter conceptualized by Maddux and Kanwisher (1965). Like the Coulter Counter, the EZCD measured the voltage across two pairs of electrodes within a tube containing seawater. As zooplankton passed through the tube past the electrodes, they displaced electrolytes and altered the voltage across the electrodes. This voltage transient was amplified and converted to an FM signal that was transmitted to a ship via a conducting tow cable, where it was detected and processed by a PDP-8/LINC computer. The device was mounted in a modified Icelandic high-speed plankton net with a reduced intake that was designed to minimize multiple particles from passing through the detector simultaneously. The net was also equipped with pressure and temperature sensors and a flowmeter. Calibration was achieved by passing glass beads of known mass through the detector and regressing the amplitude of the voltage signal against bead mass. Real-time plots of particle size versus frequency, and integrated biomass and biomass versus size were possible with this system. The EZCD was used to quantify biomass distributions in North Atlantic surface waters and in tow-yo mode down to 300 m to quantify small-scale relationships between zooplankton



Plate 37. Electronic and optical particle counting systems. (A–C) The Boyd Particle Counter circa 1972 (Wiebe, photos). (D) An OPC (M. Zhou, photo). (E) An OPC on an aquashuttle undulating vehicle (S. Cummings, photo).

distributions and thermal microstructure (Boyd, 1973). A shipboard version of the device was connected to a continuously-pumped stream of water and employed to analyze spatial heterogeneity of zooplankton in surface waters in relation to chlorophyll fluorescence and temperature (Maddux & Kanwisher, 1965). Herman and Dauphinee (1980) developed another conductive zooplankton counter, which they deployed aboard a Batfish towed vehicle. Their electronic zooplankton counter consisted of a self-cleaning net equipped with an oscillatory mechanism designed to prevent clogging. This net concentrated and channeled zooplankton into a tube containing electrodes. After passage through the detector cell, zooplankton were retained within a sample bag for later examination. The detector cell estimated the transit velocity through the cell by measuring the time of the voltage anomaly at two successive pairs of electrodes. The length of the particle was estimated from the duration of the voltage anomaly at one pair of electrodes and the magnitude of the voltage anomaly provided an estimate of the volume of the particle. Circuitry was incorporated to distinguish the passage of particles from voltage anomalies associated with thermohaline changes. System calibration began with repeated passes of non-conductive beads of known geometries through the cell. Each particle was sampled 200 times to estimate the error distributions of length and volume measurements. Sampling errors were approximately normally distributed around the mean length and volume and were higher for smaller particles. Similar tests were conducted with live zooplankton whose dimensions had been measured and the system appeared to have similar error distributions for plastic beads and for live zooplankton. The EZCD was used operationally to quantify the distributions of zooplankton off the coast of Peru in 1977 when the Batfish was tow-yo'd for 30 km between the surface and 70 m. A shipboard version of the counter was developed for use with an along-track pumping system.

A second group of particle detectors utilized photodetectors rather than changes in voltage. The optoelectronic plankton sizer (Cooke, Terhune, Ford, & Bell, 1970) was a laboratory-based system designed to automate the measurement of preserved plankton samples. Samples were poured into a reservoir from which they flowed through a device that constrained particle orientation and passed a light source that projected the particles silhouettes onto an array of photosensors. The OEPS produced estimates of the number of individuals in seven size classes. Beyond the initial system description by Cooke et al., (1970) the system does not appear to have been used operationally.

Another system that utilized interruption of a light source to size and count plankton was the HIAC particle size analyzer. This device was originally designed for chemical analysis (Sprules et al., 1992) and was modified at the Lowestoft Laboratory during the late 1970s for plankton counting (Tungate & Reynolds, 1980). The HIAC was a shipboard or laboratory-based device that employed a collimated light beam and a photodiode detector. Water samples were prefiltered and then passed through a photo detector. As particles passed through the light beam, they reduced the light intensity striking the photodiode and generated a voltage pulse that was proportional to the cross-sectional area of the target. The system counted particles into twelve size classes, and could be equipped with different sensors designed to quantify particles within certain size ranges between 1 and 9000 μ m.

The OPC was developed during the mid-1980s (Herman, 1988) (Plates 37D, 37E and 38A) and the currently available commercial instrument is based on a design by Herman (1992). This instrument measures changes in the intensity of a light beam that occur when a particle crosses the beam. A series of six high-intensity, LEDs produce 640 nm light that is focused into a 4 mm wide×20 mm high sheet. This sheet is projected across a 22 cm wide tunnel through which water flows. Light intensity attenuation caused by the passage of a particle across the light sheet is detected and counted. The size of a particle is determined by measuring the magnitude of the change in light intensity. The OPC bins data into 4096 electronic size-classes from 0.25 to 20 mm (Herman, 1992) at rates of up to 200 Hz (Currie, Claerboudt, & Roff, 1998). Laboratory studies conducted by Herman (1992) demonstrated that the OPC can produce reliable estimates of abundances of precision microspheres ranging in diameter from 0.38 to 15.8 mm.

The OPC is a commercially available instrument, manufactured by Focal Technologies Inc. which has been broadly adopted by the oceanographic community because it is relatively inexpensive and easy to use. Both in situ (OPC-1T) and laboratory models (OPC-1L) are available with the primary difference being the reduced 2 cm path-length of the OPC-1L. The OPC-1T has been mounted on a variety of towed platforms (e.g. Sameoto, Cochrane, & Herman, 1993; Currie et al., 1998; Sprules, Jin, Herman, & Stockwell, 1998), while the OPC-1L has been employed in shore-based or shipboard applications (e.g. Beaulieu, Mullin, Tang, Pyne, King, & Twining, 1999; Woodd-Walker, Gallienne, Robins, 2000; Zhang, Roman, Sanford, Adolf, Lascara, & Burgett, 2000). The OPC has also been incorporated into a shipboard device called the continuous underway fish egg sampling system (CUFES — section 3.4.2) which enumerates the distribution and abundance of fish eggs in surface waters (Checkley, Ortner, Settle, & Cummings, 1997).



Plate 38. Variants of the OPC. (A) An OPC mounted on a SCANFISH undulating vehicle (M. Zhou, photo). (B) A diagram of the laser OPC (Herman et al., 1998). (C) A diagram of the laser OPC mounted within the MVP fish (Brooke Ocean Technology). (D) The MVP's multi-sensor free-fall fish is prepared for deployment (Brooke Ocean Technology).

In spite of the prevalence of OPC systems in current use, interpretation of OPC data remains a subject of some controversy (Wieland, Petersen, & Schnack, 1997; Heath, Dunn, Fraser, Hay, & Madden, 1999; Halliday, Coombs, & Smith, 2001). The OPC produces equivalent spherical diameter (ESD)-based, sizefrequency data and cannot directly provide information on the species composition of particles. Identities of particles must be inferred using information from concurrent net samples or other techniques. Potential sources of error that may influence the OPC's size-frequency distributions include non-spherical geometries of particles, differences in relative transparency of targets, and coincident detection of large numbers of particles (Herman, 1992). These issues have resulted in the development of a more sophisticated version of the OPC called the laser OPC (LOPC) (Herman et al., 1998) (Plate 38B). The LOPC contains a larger intake tunnel (7 cm×7 cm) within which, a 1 mm thick×35 mm high laser sheet (670 nm) passes twice to provide complete coverage of the 7 cm high intake tunnel. The returning beam passes through an interference filter and falls on a 35 element photodiode array. Data from the photodiode detector are digitized at 1 MHz. A 12-bit analog-digital converter and improved beam sensitivity have reduced the lower detection threshold to particles as small as 50 µm. The high sampling frequency and sensitivity of the laser sheet allow the system to provide information about the shapes of particles as they pass through detector because small particles traversing the beam will produce five to six measurements which can be used to estimate particle shape. The LOPC has been incorporated into the moving vessel profiler (MVP) which is designed

to collect hydrographic and biological information from a series of vertical casts collected at high frequency from a moving vessel (Plate 38C, D). The MVP was developed by the Bedford Institute of Oceanography and available as a commercial instrument through Brooke Ocean Technology, Inc.

3.4.4. Optical instruments for non-quantitative studies

Nishizawa, Fukuda, and Inoue (1954) from Japan collected still photographs of live zooplankton from within a diving chamber using a collection box of clear plastic (15 cm high×20 cm wide×5 cm thick), which was placed in front of, and outside an undersea observation chamber called the Kuroshio-Go. The collection box could be opened and closed to collect a sample of water and plankton. What appears to be a collimated beam of light was projected into the chamber from a 300 W mercury vapor lamp operating at a frequency of 50 Hz and a pulse length of 0.01 s. The contents of the box were photographed with a Focabell camera (Orion Camera, Tokyo). A variety of particles and plankton (including copepods and chaetognaths) were photographed within the chamber at depths ranging from 10 to 75 m. The pulsed light source provided a means of estimating the swimming velocities of plankton by measuring the distance between successive multiple images; they estimated the swimming velocity of a copepod at 12 cm per second with resting intervals of 0.02 s.

Edgerton and Hoadley (1955) developed a 35 mm repeating-flash, shutterless deep-sea camera and this system formed the basis of a photographic profiling system deployed by Johnson, Backus, Hersey, and Owen (1956) to investigate the composition of the deep-scattering layer (Plate 39A). A strobe was oriented nearly parallel to the camera so that targets located in-front of the camera at an unspecified distance were illuminated. The camera was equipped with either a 50 mm lens $(20^{\circ}\times30^{\circ}$ field of view) or a 35 mm lens $(30^{\circ}\times40^{\circ}$ field of view). Their profiler was coupled with an ship-mounted, down-looking echosounding system that was designed to collect concurrent acoustic and optical measurements of mid-water scatterers. Their intent was to trigger the camera when the echosounder operator detected strong acoustic targets, however the substantially greater volume of the acoustic beam at depth meant that ~40% of all photographic images contained no targets. They were successful in collecting images of larger zooplankton such as salps and micronekton that appeared to be associated with strong acoustic returns.

Investigations of the nature of the deep-scattering layer were refined in 1956 when Backus and Barnes (1957) replaced the 35 mm still camera with an underwater television system. Their television system was similar to the gear used by Barnes (1953) for benthic studies. The camera was aimed forward and illumination was provided by a pair of 2 kW lights. A canvas shroud could be placed over the framework of the system so that the flow of water past the camera was reduced which improved the quality of images of zooplankton as they passed by the camera window. The camera was used in conjunction with echosounders which were either a surface-mounted down-looking 12 kHz Edo UQN-1B or a pair of transmit-receive 34 kHz Edo UQN-1B transducers that were mounted on the camera frame and was aimed at a point 2.1 m in front of the television camera's optical axis. Their optical system was capable of resolving small zooplanktors down to *C. finmarchicus*-sized copepods.

At approximately the same period that the deep scattering layer was being studied with television, Schröder (1961) deployed an underwater television system in the Bodensee (Lake Constance) of Germany to ground-truth the freshwater zooplankton composition of sound scattering layers (Plate 39B). Schröder's camera system was manufactured by Grundig, Fuerth (Bavaria), and IBAK, Kiel and produced a black and white image that corresponded to the European Television standard, which was presumably the PAL with a resolution of 625 lines and a frequency of 50 Hz. The television camera faced forward and downward at an angle of 20°. A pair of 1000 W incandescent lamps, each producing 19 000 lumens were mounted on two lateral arms that projected forward on either side of the of the camera. The lamps faced each other and produced a continuous region of illumination that was oriented perpendicularly to the axis of the camera at a distance of 30 cm in front of the lens. This dark-field illumination was satisfactory and according to Schröder, "The plankton lit up brightly and stood out so against the dark background clearly". Schröder



Plate 39. Early versions of underwater cameras and television systems. (A) A underwater camera system used by Johnson et al. (1956) to ground truth the composition of the deep scattering layer (photo from DSR 3). (B) An underwater television system used by Schröder (1961) in the Bodensee (Photo Archive fur Hydriobiologie Supplement 25).

suspended the camera from a pair of small boats powered by a single outboard engine. The boats contained a generator, controller, monitor, a drum containing 105 m of cable and other hardware. During deployments the vessels moved forward at a slow speed (0.2 m s^{-1}) and the camera system recorded the presence of a variety of small zooplanktors down to 1 mm in length.

The ecoSCOPE (Kils, 1992) is an optical video-endoscope that enables direct observation of predatorprey interactions between juvenile fish and zooplankton. It is a small, free-drifting system tracked by SONAR. One endoscope projects a thin sheet of light to illuminate the prey (e.g. copepods, tintinnids, etc.), and a second endoscope records the dynamics of predator/prey encounters and water motions from a distance of 4 cm. Endoscopes penetrate into the volume in which the fish would respond to large objects (30 cm sphere), but they have no apparent effect on behavior. Infrared shuttered LED arrays and infrared or ultraviolet XENON flashes — synchronized to the CCD arrays — build up the light sheet to minimize avoidance. Multi-flash operation allows for evaluation of extremely fast processes. The tips of the endoscopes are camouflaged with silvery sides and dark dorsals. The ecoSCOPE has been operated from an ROV, from the keel of a sailing vessel, and in towed and moored modes, but the best recordings of predator/prey interactions have come from free-drifting deployments, when the instrument was hovering within schools of feeding juvenile herring. Direct readings from the ecoSCOPE or other high magnification in situ imaging systems are difficult to assess by the eye, because of the motion of the optical system. A software package called dynIMAGE (Kils, 1992) animates sequential images by referencing a floating particle selected by the operator and shifting the sequential images to hold the reference particle stationary. As a result, when viewing the compensated animations, the fish and its prey remain in the middle of the viewing field.

The CritterCam (Strickler & Hwang, 2000) is a laboratory and field instrument designed to image zooplankton. The instrument utilizes Schlieren optics and spatial matched filtering to document zooplankton behavior in laboratory tanks. The laboratory instrument has been adapted for in situ operations near a nuclear power plant intake off Kenting, Taiwan (Strickler & Hwang 2000). The power supply, video recorders, and monitors were attached via an umbilical cable to the underwater optics housed in pressure cases. This system imaged a 27×22 mm zone of water at a distance of 50 mm and was capable of resolving objects of 15 μ m or larger. This approach has been incorporated into a quantitative sampler called ZOO-CAM (Zooplankton Camera) currently being developed by G. Paffenhöfer and colleagues (G. Paffenhöfer, personal communication). ZOOCAM is a profiling instrument that utilizes a 1000 pixel×1000 pixel digital camera in conjunction with Schlieren optics to resolve particles down to 20 μ m. The instrument will be lowered at 5 cm s⁻¹ and a large intake funnel concentrates zooplankton by a factor of ~100 into an imaging chamber 50 mm×15 mm thick.

Optical sensors can provide valuable ground-truthing for acoustical sensors. To this end, Jaffe, Ohman, and Roberts (1998) mounted a megapixel digital still camera on their FishTV sonar array (Jaffe, Reuss, McGehee, & Chandran, 1995) and named the resulting system the optical–acoustical submersible imaging system (OASIS) (Plate 40A, D). The digital camera is a 1524×1024 pixel black and white instrument coupled to a red-filtered strobe providing illumination at ~90° to the plane of the camera. The direction of the FishTV sonar beam is angled between the camera and strobe (~45° relative to the plane of either) and the camera is triggered to capture an image of a target within the sonar beams when target strength (TS) exceeds –90 dB. Interestingly, this approach is very similar to that used by Johnson et al. (1956) who attempted to trigger their camera when an echosounder operator detected a target of sufficient intensity. While Jaffe et al. (1998) used acoustic returns to trigger their optics, Warren, Stanton, Benfield, Wiebe, Chu and Sutor (2001) employed an analog video camera to aim an acoustic array at individual zooplankton. The array of transmit-and-receive pairs of transducers operating at 24 and 120 kHz was mounted on the front of a MAXRover ROV which was guided toward individual siphonophore colonies, euphausiids, and other zooplankton taxa. The focal points of the transducer pairs were co-located with the center of the field of view of the video camera. When animals were centered the video field, the targets were interrogated



Plate 40. Acoustic systems in various configurations. (A) Fish TV (Jaffe et al., 1995). (B,C) TAPS (Holliday & Pieper, 1995). (D) OASIS (Jaffe et al., 1998). E) A MOCNESS with a dual-beam acoustic system and video camera circa 1994 (Greene et al., 1998, Wiebe, photo).

with multiple pings for TS estimation. The video camera provided individual orientation data in addition to targeting information.
3.5. High-frequency acoustics

High-frequency acoustics (38–1000 kHz and higher) provides the foundation for another class of tools to study zooplankton (Wiebe & Greene, 1994; Foote & Stanton, 2000). A short background on the use of high frequency acoustics is presented here to set the stage for discussion about multi-sensor systems; a more compete discussion of acoustical methods is presented by Foote and Stanton (2000). Haury (1982) compared acoustical tools with other sampling systems with respect to frequency of sampling, ease of analysis of the samples, time required to make an observation, and types of physical and biological gradients and variability that may be examined. With bottles and nets, frequency of sampling is low, analysis is relatively hard, and time required to analyze a sample is large; it is thus difficult to examine strong sharp gradients. Photographic and video systems provide improvements and acoustics can provide very high frequency measurements. With acoustics, the analysis problem is relatively easy per observation, and strong gradients can be observed over short spatial distances. There is, however, a diminution in the resolution and quality of some kinds of information obtained as the tools become more technologically sophisticated. With bottles and nets, planktonic individuals can be identified, staged, and counted, and their physiological and biochemical rates can be measured. With only an optical image on film or video, many fundamental biological measurements can not be made. With acoustics, estimates of the biomass, numbers, and size of the zooplankton targets ensonified can be made, but this is generally not a trivial task (Wiebe, Stanton, Benfield, Mountain, & Greene, 1997). The technology is not currently available to identify and discriminate species directly, although there are some promising developments that may give some better resolution, first, perhaps, at a higher taxonomic level (Martin, Stanton, Wiebe, & Lynch, 1996; Traykovski, Stanton, Wiebe, & Lynch, 1998).

There are two fundamental measurements: volume backscattering (integration of the energy return from all individuals in a given ensonified volume, i.e. echo integration) and TS (echo strength from an individual). Depending upon the construction of the echo sounder and transducers, either or both of these measurements can be obtained. With a single-beam transducer, only volume backscattering can be determined directly. A given return cannot be used to discriminate individual size, although statistical procedures have been developed to provide estimates of the animal assemblage size distribution using the data from single-beam transducers (Clay, 1983; Stanton, 1985a,b). The ancillary use of the acoustic Doppler current profiler (ADCP) to measure volume backscattering is receiving increasing attention because of its wide-spread use to measure ocean currents from ships and moorings. With recent advances in hardware configuration and software, more quantitative results are now possible.

With a series of single-beam transducers operating at different frequencies (38 kHz to 10 MHz), it is possible to extract estimates of animal size distribution in addition to volume backscattering (Greenlaw & Johnson, 1983). Holliday and Pieper (1989) have developed this technique. Using a number of transducers operating at different frequencies, the acoustic volume backscatter is measured at each frequency. TAPS (Tracor acoustic profiling system) is one system that has been designed specifically to utilize this approach (Holliday & Pieper, 1995) (Plate 40B, C). This information, coupled with a theoretical model of how sound at different frequencies backscatters from individual zooplankton, enables the determination of what the animal size distribution must have been to have produced the observed backscatter. This is called the 'inverse problem'. The number of size categories that can be discriminated is one less than the number of frequencies (i.e. transducers). A problem with this technique is that, as currently used, a single model of backscattering from the plankton is employed (usually a fluid sphere model). Yet, often two or more models are needed to characterize the scattering characteristics of the individuals in the ensonified volume (Stanton et al., 1994; Stanton, Chu, & Wiebe, 1998). In addition, the number of size categories may be substantially more than the number of frequencies. Thus, the inverse solution is usually under-determined and requires a computationally intensive search to find a global solution that has a globally minimized error associated with it. Some discussion of these problems is provided by Horne and Jech (1999).

Multi-beam acoustical systems provide a direct means of determining individual TS. The two current designs are dual-beam and split beam; both provide a hardware solution to the problem of TS determination. In the case of dual-beam systems (Ehrenberg, 1974; Traynor & Ehrenberg, 1979), there are two or more ceramic elements which form narrow and wide beams. The beam widths are usually constructed so that the wide beam has between two-and-a-half to three-times the width of the narrow beam. Typical beams range between 3°/8° and 6°/15°. Sound is emitted by the narrow beam and both the narrow and a wide beams receive the return. The difference between the narrow and wide beam voltages provides information about where in the beam the target resides, called the off-axis angle. With the measurement of the off-axis angle, the TS can be corrected to what it would have been had the individual had been on-axis. The TS of an animal that is detected with both beams can be estimated directly with a precision determined largely by the sensitivity and calibration of the system. Dual-beam systems have been constructed that operate at frequencies from 38 to 1000 kHz.

Split-beam acoustical systems (Ehrenberg, 1979) divide a beam into four 90° sectors. Both the intensity and the phase of the returning echo are measured for each sector. Differences in phase are used to compute the exact location of an individual in the beam. The off-axis angle is used to correct the TS. Split-beam systems have been constructed that operate at frequencies from 38 to 420 kHz. There is some difficulty in constructing higher frequency split-beam systems. Information from both types of multi-beam systems also can be used to do target tracking. The split-beam system has the advantage that it provides the bearing of an individual as well as off-axis angle.

The utility of acoustic systems is derived principally from their capability to operate with high ping rates and precision range-gating. This enables high resolution vertical and horizontal data to be acquired along a trackline or from a mooring. Mapping of planktonic distributions on a wide range of space and time scales is becoming possible because of the continued development of acoustic systems.

The interdependence of sound frequency, the minimum detectable target size, and the range of operation strongly affects deployment and sampling strategies. This is often illustrated by reference to ka (where $k=2\pi/\lambda$ and λ (wavelength)=c/f (c=sound speed ~1500 m s⁻¹ and f=frequency), and a=radius of sphere or a cylinder depending upon the model used for the scatterer). If an individual is small relative to the wavelength of the sound (i.e. $ka \ll 1.0$), either no echo or a very small echo, relative to its size, will be recorded in the echo sounder. With higher frequencies, smaller animals can be quantitatively detected. Thus, with 120 kHz, an individual ~10 mm can be detected; with 420 kHz, the minimum size is ~3 mm; with 720 kHz, minimum size is ~1.5 mm. However, with increased size resolution, there is a decreased range of operation. At 120 kHz, echo integration can be conducted to ~200 m; at 420 kHz, to ~80 m; and at 720 kHz to ~30 m from the transducer. This fundamental limitation puts strong constraints on how the instrumentation can be configured and how it can be used to analyze animal distributions in the water column. A related problem involves the interaction between size resolution, as a function of range, and the noise of the system. As the sound propagates away from the transducer, the size range of animals that can be detected is reduced. This is because with distance, the noise threshold increases and echo returns from smaller individuals will fall below this threshold. Furthermore, with increasing distance from the transducer, the ensonified volume increases, thus, increasing the probability that a return is from more than one individual. These biases must be taken into consideration when processing and interpreting acoustic data.

Accurate interpretation of acoustic backscattering data also requires knowledge of the sound speed contrast (i.e. the ratio of the sound speed in zooplankton to that in the water) and density contrast (i.e. the ratio of the density of zooplankton to that of the water). These are referred to as the 'material acoustic properties' of live marine organisms. Material properties of zooplankton are poorly known. Also they depend on the spatial and temporal distributions of the oceanographic parameters such as temperature and pressure (Chu, Wiebe, & Copley, 2000). For fluid-like weakly-scattering marine animals (i.e. copepods, euphausiids, gelatinous species, etc), small variations in sound speed and density can result in substantial variation in the measured volume-scattering strength. The lack of in situ information about these properties significantly limits interpretation of acoustic data in terms of zooplankton abundance and/or biomass estimates.

4. The current state of plankton sampling systems

Collecting systems designed to provide a physical sample of zooplankton can be traced back to 19th century devices. Some of these, still being used today along with collecting systems based on contemporary technology, are being used by investigators carrying out a wide variety of ocean research and survey programs. Zooplankton samplers in use today reflect the fact that no single collection system adequately samples all zooplankton. Non-opening/closing nets, such as the WP2 (Fraser, 1966; UNESCO, 1968) (Plate 2A), modified Juday (Aksnes et al., 1983), and Bongo (Posgay et al., 1980) (Plate 2D,E), are still used in large ocean surveys (e.g., CalCOFI, Northwest Atlantic continental shelf surveys). Simple, double-messenger opening/closing nets similar to those developed by Hoyle (1889); Leavitt (1935) (Plate 6A), Clarke and Bumpus (1939, 1950) (Plate 8A), and others are still manufactured and used. The Multinet (Weikert et al., 1981) (Plate 31A), RMT 1+8 (Dimmler et al., 1990) (Plate 28A), BIONESS (Sameoto et al., 1979, 1980) (Plate 30C), and MOCNESS (Wiebe et al., 1976, 1985) (Plates 28D and 29) are widely used multiple-net systems that carry additional sensors to measure other water properties. Plankton pumps are also being used, especially to collect the smaller micro-zooplankton (Powlick, John, & Blake, 1991).

4.1. Integration of multi-sensor systems

The need and desire for more rapid methods to count and size zooplankton in situ has lead to the development of the impressive array of acoustic, optical, and physical sensors described above. Each of these systems has limitations in range, resolution, and interpretation when used alone. The advent of towing cables with optical fibers, which enable high-speed, high band-width, two-way data communication, and electrical conductors, which provide power, have enabled the development of towed systems in which different sensors have been merged into multi-sensor systems. High speed computers complete the package and the result is access to data in realtime while the instrument package is deployed.

4.1.1. Winch controlled towed systems

The MOCNESS has been equipped with a high frequency acoustic system for forward or sideways range-gated viewing (Wiebe & Greene, 1994; Greene et al., 1998) (Plate 40E). Initially, the acoustic system (420 and 1000 kHz) was operated with power and data telemetry handled on a separate cable deployed along-side the conducting cable used to tow the MOCNESS. Access to electro-optical cable enabled the complete integration of a dual-beam acoustical system with the MOCNESS (Wiebe & Greene, 1994; Greene et al., 1998). Copper conductors supplied power to the underwater electronics and glass fibers provided the path for data telemetry: one for the acoustics and one for the MOCNESS environmental sensing package and control module. A training mechanism that allowed hemispherical positioning of the two transducers was mounted on the top frame of the MOCNESS and was controlled by the MOCNESS software. A video camera was also mounted on the top frame during field studies in the Gulf of Maine and VHS recordings were made of the plankton approaching the net made visible by an underwater lighting system. These images provided a qualitative indication of the larger zooplankton present, but were not of high enough resolution for quantitative work.

In addition to the normal suite of sensors, an EG&G Edgerton model 205 camera and a flash light was mounted on the top of a modified MOCNESS and on the top of BIONESS. In both cases the camera was aimed to take black and white photographs ~ 2 m in front of the net mouth (Sameoto et al., 1980). The camera was triggered from the deck of the ship. Animals the size of euphausiids were recognizable, but

species identification was not possible. A 120 kHz echosounder deployed in a small v-fin towed body provided volume backscattering data concurrent with the acquisition of net collections and photographs. The BIONESS has also been equipped with an OPC, video lighting system, and used in conjunction with an echosounder in Emerald Basin on the Scotian Shelf off Nova Scotia (Sameoto et al., 1993).

The bio-optical multi-frequency acoustical and physical environmental recorder — BIOMAPER-II, a significantly enhanced version over its prototype (BIOMAPER – Wiebe et al., 1997; Austin, Arthur, Torkelson, Wiebe, & Stanton, 1998; Wiebe, Stanton, Greene, Benfield, Austin, & Warren, 1999; Wiebe et al. 2002), was developed in 1996 to conduct high-speed, large-area surveys of zooplankton and environmental property distributions (Plate 41A–E). The vehicle has generally been towed from the starboard side of medium sized oceanographic research vessels, such as the 54.5 m R/V *Oceanus*. It is operated over a wide range of towing speeds up to 10 kts. Most scientific missions require continuous 'tow-yo' operations, during which the winch operator constantly spools tether out, then in, so that the vehicle travels through the entire water column in a slow zig-zag fashion. The maximum operating depth of the system is 300 m. The average tow speed is 4–6 kts depending on the depth of the vehicle.

BIOMAPER-II has a free-flooded open-frame architecture with an outer skin in the form of easily removable flat plastic panels (Wiebe et al., 1999, 2002) (Plate 41A). It weighs ~2000 lb in air and 1200 lb in water, and has a length of 3.78 m. Mounted inside are a multi-frequency sonar (up-looking and downlooking pairs of transducers operating at 5 frequencies: 43, 120, 200, 420 and 1000 kHz), an environmental sensor package (CTD, fluorometer, transmissometer), and several other bio-optical sensors (down- and upwelling spectral radiometers, spectrally matched attenuation and absorption meters) (Plate 41E). A VPR system is mounted above and just forward of the nose piece (Plate 41B). On early cruises a single camera was deployed and more recently two have been used. The lower four acoustical frequencies involve split beam technology and are able to make TS and echo integration measurements. A 20 ft (6.1 m) shipping container van, specifically modified to become the at-sea laboratory space for command and control of BIOMAPER II, holds the electronic equipment for real-time data processing and analysis (Plate 41C).

4.1.2. Undulating towed bodies

Since the development of the Undulating Oceanographic Recorder (Bruce & Aiken, 1975) (Plate 19C), various vehicles have been built of relatively light weight and with control surfaces to enable them to actively change their vertical position without changing the towing wire length. SeaSoar, for example, is one that has been equipped with optical (VPR and OPC) and/or acoustical (TAPS — Holliday & Pieper, 1995) instrumentation for zooplankton data collection. The SeaSoar has been used with an OPC in a large scale survey in the California Current (Huntley, Zhou, & Nordhausen, 1995), with TAPS in JGOFS studies in the Arabian Sea (McGehee & Jaffe, 1994; Lee, Jones, Brink & Fischer, 2000) or with both a VPR and TAPS for GLOBEC studies on the southern flank of Georges Bank (C. Lee, personal communication). GLOBEC studies off the west coast of the USA are also using a SeaSoar with an OPC.

4.1.3. Tethered self-propelled ROVs and DSRVs

ROVs have been equipped with acoustical and video systems to study zooplankton. A SeaRover ROV was equipped with the same dual-beam acoustic system and environmental sensors used on the MOCNESS for work in the Arctic under an ice camp, in sound scattering layers in Puget sound, and over seamounts off Southern California (Greene & Wiebe, 1990, 1991) (Plate 42A). This ROV, rated to 300 m, has two horizontal thrusters, one vertical thruster, and one lateral thruster providing speeds up to 3 kts. It had a color video camera and lighting suite with pan and tilt capability. A VPR rigged to provide 3D images of plankton and an environmental sensor package (temperature, conductivity, pressure, fluorescence) were mounted on the front of the ROV JASON to examine the micro-scale behavior of individual zooplankton (Gallager, Yamazaki, & Davis, 2003) (Plate 42D). JASON is a mid-sized, powerful ROV that has a length of 220 cm, a width of 110 cm and a height of 120 cm, and weighs 2000 kg in air. This same VPR and



Plate 41. BIOMAPER II — a multi-sensor platform for zooplankton studies. (A) Schematic drawing of BIOMAPER-II. (B) The BIOMAPER-II VPR. (C) The BIOMAPER-II van for data acquisition. (D) BIOMAPER-II being launched from R/V Endeavor circa 1999. (E) The ac9s in BIOMAPER-II being displayed.

environmental sensing system were also deployed on the much smaller SeaRover ROV to study the distribution, abundance, and behavior of small zooplankton being fed upon by endangered Right whales in Cape Cod Bay, MA during spring of 2000 (S. Gallager, personal communication) (Plate 42C, E).

Jaffe et al. (1995) used Fish TV (FTV), a realtime 3D imaging sonar operating at 445 kHz, on a Phantom IV ROV and were able to track individuals the size of euphausiids. As described above (section 3.4.4),



Plate 42. ROVs used to deploy optical and acoustic sensors. (A) The SeaRover with acoustics and video circa 1989 (Wiebe, photos).(B) The Acoustical Array and video on the Maxi-Rover ROV circa 1998 (Wiebe, photo). (C, E) A 3D-Stereo VPR on the SeaRover ROV circa 2000 (S. Gallager, photos). (D) A 3D-Stereo VPR on ROV Jason circa 1995 (P. Alatalo, photo).

Warren et al. (2001) used a combination of acoustics and video on the front of a MAXRover ROV to track siphonophores and other zooplankton, and to determine their TSs in situ (Plate 42B).

A completely different style of tethered, but autonomous vehicle is the AVPPO (Thwaites et al., 1998) which was described briefly in section 3.4.2 above (Plate 34C). In this system, a buoyant twin-hulled vehicle which carries a two-camera VPR, environmental sensors (temperature, conductivity, pressure,

downwelling light, fluorescence, beam-transmittance, flow), and engineering sensors (pitch, roll), is attached to a Kevlar-reinforced electro-mechanical cable and winch system. This assembly is mounted in a bottom lander with trawl protection and deployed on the seafloor at depths up to 100 m. A typical cycle has the master controller 'wake up' at a scheduled time, turn on the sensors and begin the winch payout to enable the vehicle to float to the sea surface at 30 cm s⁻¹. At the surface, the sensors are turned off and the winch reels the cable back in at 15 cm s⁻¹. Cycle intervals can vary from 1 to 24 h. Environmental data are logged on a computer hard disk and video data stored on a SVHS tape. This system has undergone successful deployments in 80 meters of water on Georges Bank (Thwaites et al., 1998).

Dual-beam acoustics (420 and 1000 kHz) have also been deployed from the DSRV Johnson Sea-Link to study euphausiids, siphonophores, and other zooplankton in the submarine canyons off Georges Bank and Southern New England, and in the Gulf of Maine (Greene, Wiebe, Burczynski, & Youngbluth, 1988). In these studies, video pictures were taken of the animals in the vicinity of the transducers, collections of zooplankton were made with a pumping system mounted on the front of the DSRV, and environmental measurements (CTD, fluorescence, beam transmittance) were made. A bioluminescence detector has also been deployed with this suite of instruments on the Johnson Sea-Link (Plate 36E) and when used in conjunction with a dual-beam acoustic system has enabled small-scale distributions of gelatinous zooplankton and euphausiids to be mapped out (Widder, Greene, & Youngbluth, 1992). This same bioluminescence detector was also used on dives made in Monterey Canyon off the central California coast with the single-person submersible Deep Rover (Widder et al., 1989).

4.2. The evolutionary history of zooplankton sampling systems

The history of development of quantitative zooplankton collecting systems, which in many respects began with Hensen (1895), was vigorous in the late 19th and early 20th century (Fig. 6). Non-openingclosing nets, opening closing nets, high-speed samplers and planktobenthos net systems all had their start in this era and one of the enabling technologies was the wide-spread use of wire rope for towing the nets (Table 1). Most opening-closing net systems were messenger-based. The pace of development slackened during the period of World War I and only partially picked up in the 1920s and 1930s during which the existing tools underwent modifications and improvements, but few new samplers were introduced. The one outstanding exception was the CPR which Hardy (1926b) developed in the 1920s. It has seen continued use and improvement up to the present. The 1940s, the period of World War II, also resulted in a cessation in the entry of new devices. Few papers appeared during this time introducing new instruments to the field.

Revitalization of the development of new mechanically-based instruments occurred during the 1950s and 1960s. A new lineage of high-speed samplers, the Gulf series, began in the 1950s and numerous variants developed in the 1960s and 1970s. In addition, net systems specifically designed to collect neuston first appeared in the late 1950s. It was during the 1960s that many focused field and laboratory tank experiments were carried to investigate the hydrodynamics of nets, and much of our current knowledge concerning net design and construction criteria was developed (Smith, Counts, & Clutter, 1968; UNESCO, 1968). The advent of reliable electrical conducting cables and electrically-based control systems during this same period gave rise first to a variety of cod-end samplers and then to the precursors of the acoustically and electronically-controlled multi-net systems and environmental sensors which appeared in the 1970s (Table 1). The newer electronically-based collecting systems did not, however, replace the older non-opening closing or messenger based opening/closing systems. Refinements of systems from all categories were described well into the 1990s.

The decade of the 1970s saw a succession of multi-net systems based on the Bé MPS and on the Tucker trawl. With the micro-computer, the 1980s saw the development of sophisticated control and data logging electronics for these systems (Table 1). Acoustical telemetry, which suffers from low band-width, continues to be used where conducting cable is not available. Now, however, it is usually supplemented with battery-



Fig. 6. A composite time line showing the boxes outlining the individual systems in Figs 1–5. Introductions of new classes of samplers often coincided with the availability of new technologies (i.e., closing cod-end systems, multiple net systems, and electronic/optical systems; Table 1). An exception may the development of neuston net systems.

Table 1 Some enabling technology milestones

Timeframe	Technology
Late 1800s	Wire rope and winches
1950s, 1960s	Electrified cables and release mechanisms
1960s, 1970s	Transistorized electronics and acoustic telemetry
1970s, 1980s	Micro-computers
1980s, 1990s	Electro-optical cable and advanced optical-acoustical components
Beyond 2000	Miniaturized components, ultra high storage capacity, lower power components, longer battery life, higher telemetry rates

powered data logging systems that enable high-resolution data to be collected from accompanying environmental and engineering sensors (e.g. ARIES — Dunn et al., 1993a).

In the 1990s, acoustic and optical technologies gave rise to sensor systems that either have complemented multiple net systems or have been used free-standing without nets (Table 1). While they have not yet replaced nets, it is only a matter of time before much of the work in collecting the basic information on the distribution and abundance of zooplankton species will be possible without the use of nets.

86

4.3. Intercomparisons of sampling efficiency and selectivity of zooplankton sampling systems

The diversity of sampling systems that have evolved since Hensen's net reflect technological advances, the ingenuity of their developers, and the multiplicity of applications for which they were developed. The developers of new samplers recognized that no single system was a perfect sampling device, each was endowed with strengths and weaknesses, and that there was always room for improvement. Parallel with the development of sampling devices, has been the accumulation of a body of research on the selectivity and relative performance of different gear. As new systems replace older ones, it has become essential to quantify the relative efficiencies of each. This has been particularly important for long time-series where adoption of new sampling gear could introduce artifacts in zooplankton community distribution and abundance trends (e.g. Ohman & Smith, 1995) and for evaluation of the performance of new systems using benchmarks from well-tested gears (e.g. Checkley et al., 1997).

The literature on gear selectivity and intercomparisons is almost as diverse as that describing the development of new samplers and a review of such data is beyond the scope of this paper. We have identified a broad range of citations dealing with such research and this literature search is summarized in Table 2. The search is by no means exhaustive, but we hope that it will provide a starting point for those interested in evaluating the performance of one or more of systems described in this text.

5. Future developments

Although "...the practice of towing a net through the water to capture and concentrate organisms in its path, or recovering a volume of water intact in a bottle complete with its population of organisms and complement of dissolved constituents, is likely to remain in use for the foreseeable future" (Dunn et al., 1993a), the future promises vastly increased application of remote sensing techniques and sensor development. Realtime data telemetry, processing, and display show a steady pattern of advancement, even as quantities of data gathered grow exponentially (Table 1).

5.1. Realtime 4D data acquisition and visualization

Tethered sensor systems such as the BIOMAPER II now have the capability of sampling very large amounts of data from diverse sensors in realtime. The challenge resulting from this capability lies in making proper use of the data. Three-dimensional (space) and four-dimensional visualization (space and time) of biological and acoustic data are also an increasingly important aspect of data processing (Wiebe, Davis, & Greene, 1992). For a number of research programs today, the development of an image of the spatial arrangement of organisms is but the first step in efforts to study and understand their relationships to each other and to their environment. Thus, there is need for realtime 3D and 4D images. When data are collected to create 3D images, however, the information is commingled in space and time, since synoptic highfrequency acoustical images over large ocean areas are not yet feasible. One problem is that the fluid field that is being ensonified is moving (i.e. current/flow). Another is that the animals are moving relative to the water. Techniques to track the water movements and to remove the effects of water motion in the process of reconstructing the 3D distribution of the organisms are being advanced (Skjoldal, Wiebe, & Foote, 2000; McGillicuddy et al., 2001). Devices to track the motion of the animals are now becoming available (especially for relatively large ones). Recent studies of blue crabs with tiny transponders have revealed the intricate motions of these animals independent of the water motions in which they were living (Niezgoda, Benfield, & Sisak, 2003). Such devices will continue to be miniaturized and perhaps soon will enable tracking studies of zooplankton.

Table 2

Literature survey of gear comparison studies. Each published study has been assigned one or two alphabetic characters. Alphabetic characters within cells intersected by two different sampler codes indicate the citation code(s) for studies that compared those two samplers. Studies at the intersection of cells assigned to the same gear type are comparisons of variants of the same gear or different mesh sizes on the same gear. The citations that correspond the each letter code appear on the following page. Refer to the literature-cited section for the full citation.

	WP2 Net	Water Bottles	VPR	U-Tow	Tucker Trawl	Rectangular Midwater Trawl	Pump Systems	Other Nets	Optical Plankton Counter	Norpac Net	Neuston Nets	Hansen Net	MOCNESS	Miller High- Speed Sampler	Marutoku B Net	MAFF Guildline Sampler	LHPR	Light Traps	Juday Net	Isaacs-Kidd Midwater Trawl	Indian Ocean Standard Net	Ichthyoplankton Recorder	High-Frequency Acoustics	Hensen Egg Net	Gulf VII Pro Sampler	Gulf III Sampler	CPR	Clarke-Bumpus	CalCOFI Net	Bongo Nets	BIONESS	Bé Net	Adriatic Flankton Sampler
Adriatic Plankton Sampler																			-												Ħ		KK
Bé Net																												1		JJ		(†	
BIONESS									X			\vdash	AN															+			+		
Bongo Nets	O,AE			AE	K,AD	AC	AE	O,AG	CC		0							K	0	J				0 BB		B,E,AC) K	E	YY	A,E,J			
CalCOFI Net					1.12				-																	10,10,1			QQ	<u>, , , , , , , , , , , , , , , , , , , </u>			
Clarke-Bumpus Sampler																			AP		AP					E		AI					
Continuous Plankton Recorder																	С															(T	
Gulf III Sampler						AC		DD					DD							AC						N		1				Ē	
Gulf VII Pro Sampler																UU												1				(†	
Hensen Egg Net	O,AA							0				\square							O	xx								1			\square		
High-Frequency Acoustics													T,II						Ar									1	+			rt	_
Ichthyoplankton Recorder								NN																							+		
Indian Ocean Standard Net												<u> </u>							AP									+					
Isaacs-Kidd Midwater Trawl	XX					AC		AB												FF													
Juday Net	0	TT						H,O											SS												+	(
Light Traps, Various Designs											Y			U																			
Longhurst-Hardy Plankton Recorder						F	G		S,V			\square	G				V											\top			Ħ	(†	_
MAFF Guildline Sampler																	112																
Marutoku B Net										OO,PP																		+			Ħ	m	_
Miller High-Speed Sampler	AE						AE																										
MOCNESS	R		D				G,AO	DD AH	Ι			\square																			\square	(†	
Hansen Net	Z							-01																									
Neuston Nets					К							\square																1				(†	
Norpac Net								VV	нн	ww																		1					
Optical Plankton Counter	LL				Ι			I																								(
Other nets		AM			AL		EE,	P,ZZ																									
Pump Systems	RR						IVIIVI																							-	+	(
Rectangular Midwater Trawl																												\top	1				
Tucker Trawl					AL																							1					
U-Tow	М																															ſŤ	
Video Plankton Recorder																															\square	T	
Water Bottles																																Π	
WP2 Net	GG																																

5.2. Autonomous vehicles

The first proposed use of an autonomous vehicle for biological surveys was by Aron (1962). He described the self-propelled research vehicle developed by the Applied Physics Laboratory in Seattle, WA, which was a 51 cm diameter×309 cm long autonomous vehicle (a modified MK 38) equipped with a non-opening/closing Clarke–Bumpus Sampler (Plate 43A). He also described plans to install a modified CPR to take discrete samples and a suite of environmental sensors. In spite of this early awareness of their

A,	Anderson and Warren (1991)	HH,	Kawamura (1989)	AP,	Tranter (1963)
B,	Arbault and Lecroix (1975)	II,	Kirsch et al. (2000)	AQ,	Williams et al. (1983)
С,	Batten et al. (1999)	JJ,	Kloppmann (1990)	AR,	Zenitani (1998)
D,	Benfield et al. (1996)	KK,	Kršinic & Lucic (1994)		
Е,	Bjorke et al. (1974)	LL,	Labat et al. (2002)		
F,	Bone (1986)	MM,	Leithiser et al. (1979)		
G,	Brander and Thompson (1989)	NN,	Lenz et al. (1995)		
H,	Calbet et al. (2001)	ОО,	Matsuoka (1995a)		
I,	Checkley et al. (1997)	PP,	Matsuoka (1995b)		
J,	Clarke (1983)	QQ,	McGowan and Fraundorf (1966)		
Κ,	Choat et al. (1993)	RR,	Moehlenberg (1987)		
L,	Colton et al. (1980)	SS,	Murav'ev and Kanaeva (1985)		
М,	Cook and Hays (2001)	TT,	Musaeva and Nezlin (1995)		
N,	Corten (1990)	UU,	Nash et al. (1998)		
О,	Dicenta et al. (1976)	VV,	Nemoto (1980)		
P,	Esnal et al. (1997)	WW,	Nishiyama et al. (1987)		
Q,	Gal et al. (1999)	XX,	Oeberst et al. (1981)		
R,	Goesaeter et al. (2000)	YY,	Ohman and Smith (1995)		
S,	Grant et al. (2000)	ZZ,	Oozeki (2000)		
Т,	Greene et al. (1998)	AB,	Pearcy (1980)		
U,	Gregory and Powles (1988)	AC,	Pearcy et al. (1983)		
V,	Halliday et al. (2001)	AD,	Pepin (1993)		
W,	Hays (1994)	AE,	Pillar (1984)		
Х,	Herman et al. (1993)	AF,	Pogodin (1980)		
Υ,	Hernandez and Lindquist (1999)	AG,	Posgay and Marak (1980)		
Z,	Hernroth (1987)	AH,	Potter et al. (1990)		
AA,	Herra (1986)	AI,	Rossi and Ferrari (1975)		
BB,	Herra and Grimm (1984)	AJ,	Schnack (1974)		
CC,	Huntley et al. (1995)	AK,	Schnack et al. (1998)		
DD,	Huse et al. (1996)	AL,	Shima and Bailey (1994)		
EE,	Icanberry and Richardson (1973)	AM,	Shushkina et al. (1980)		
FF,	Kajihara et al. (1988)	AN,	Skjoldal et al. (1993)		
GG,	Kankaala (1984)	AO,	Solemdal and Ellertsen (1984)		

potential as physical and biological samplers, autonomous self-propelled vehicles have only recently begun to be used widely to gather oceanographic data.

The remote environmental measuring units (REMUS) are a new class of small AUVs which can carry an impressive array of environmental sensors (von Alt, Allen, Austin, & Stokey, 1994) (Plate 43C). The standard vehicle is 18 cm in diameter and 114 cm long and has a normal operating speed of 1–4 kts. Sensors include an upward- and downward-looking ADCP, a CTD, an optical backscattering sensor, a fluorometer, and a 600 kHz side scan sonar (Glenn, Haidvogel, Schofield, Oscar, & von Alt, 1998). One REMUS has been equipped with a suite of sensors to enable turbulence measurements. Plans are underway to equip REMUS with a VPR (Haystead, 2000). The AUV can be deployed to navigate within a transponder net using ultra short baseline (USBL), long baseline techniques (LBL — Stokey & Austin, 1999), or relative to a single or series of transducers using the relative acoustic tracking system (RATS — Austin & Stokey, 1998). A bottom-mounted docking station has been developed to enable REMUS to complete a survey mission, and then return to the station where it downloads the acquired data, uploads new instructions, recharges its batteries, and waits for the time to start the next survey (Stokey et al., 1997; Purcell et al., 1998).

Another class of autonomous vehicles is epitomized by the autonomous benthic explorer (ABE) (Yoerger,



Plate 43. Autonomous vehicles which will soon be used to study zooplankton distributions. (A) The self-propelled research vehicle with envisioned plankton recorder (Aron, 1962). (B, D) The ABE (A. T. Deuster, photos). (C) The AUV 'REMUS' out for a test deployment (T. Kleindinst, photo). (E) The AUV 'Autosub1' (Fernandes & Brierley, 1999); photo from autosub web site).

Bradley, Walden, & Cormier, 2000) (Plate 43 B, D), This vehicle consists of three open-frame bodies. Flotation is in the two upper housings and the electronics, sensors, and batteries are in the lower housing. Seven thrusters and three propellers enable it to move in any direction. ABE is equipped with precise navigation and control systems that enable it to descend to a worksite, navigate preset tracklines or terrain-

follow, and find a docking station and dock. It is normally configured with a CTD, magnetometer, echosounder (for bathymetry), and a monochrome stereo electronic imaging CCD camera. It has a maximum range of ~50 km using rechargeable gelled lead acid, or longer using more advanced battery types, and it can work in depths up to 5000 m. Most of its deployments to date have been focused on seafloor studies, but it could easily be equipped with acoustical or optical sensors to measure zooplankton distribution and abundance.

A much larger AUV which has been employed for biological studies is the Autosub-1 (Fernandes & Brierley, 1999) (Plate 43E). It is an AUV which is ~90 cm in diameter and 680 cm long that has a 500 m depth capability and an endurance of ~32 h at 2.6 kts. The AUV carries a gyrocompass, ADCP, an echosounder, and acoustic telemetry and surface radio electronics. It can be programmed to run a geographically based course using GPS surface positions and dead reckoning. The echosounder was equipped with 38 and 120 kHz transducers that could be mounted either facing up or down, and has initially been used for surveys of herring schools in the sea off western Scotland. It has recently been used in under ice surveys of krill in the Antarctic.

The autonomous Lagrangian circulation explorer (Davis et al., 1992c) and the more recently developed Profiling ALACE floats, which carry temperature and conductivity probes, are vertically-migrating neutrally-buoyant drifters that track the movements of water at depths between the surface and 1000-2000 m depth. The ALACE floats are 17 cm in diameter×107 cm tall with a damping disk near the top with a diameter of 35 cm. By adjusting their buoyancy, they move between the programmed depth and the sea surface where they transmit data via the ARGOS satellite system. The PALACE floats create profiles of water properties on their journeys to and from the sea surface (Plate 44A, B). A typical cycle has the float at depth for 25 days, an ascent to the surface in ~ 1 h, a 24 h period for data telemetry and surface tracking, and 2 h return to depth (Davis, 1998). Present battery power and usage provides for ~70 cycles over a 5year time period. Hundreds to thousands of the PALACE floats will be deployed over the next few years and it is expected that they and other similar vehicles will become a mainstay in the global ocean observing system (GOOS). A next generation of neutrally buoyant floats is represented by an autonomous glider named SPRAY (Sherman, Davis, Owens, & Valdes, 2001) (Plate 44C, D). This 183 cm long vehicle has wings and an internal weight control system that enables it to nose down or up and turn by rolling. Altitude is controlled by altering buoyancy. SPRAY will be able to sail along specific preprogrammed tracklines. A next step in their development is to provide biological instrumentation to complement the physical sensors.

5.3. In situ species identification

High-resolution optical systems, such as the VPR, combined with computer-based identification programs can now provide higher level taxon identifications in near-realtime. Improved resolution of the imaging systems and better image analysis software will make it possible to more accurately identify individuals and some species identification will become routine. Yet, even under the best of laboratory conditions, the adults of some zooplankton species are difficult to identify, and juvenile and larval forms may be morphologically indistinguishable. Classification of species using acoustic signatures is less well developed and it now seems unlikely that the technology to develop species-specific acoustic signatures will be developed soon. The improved optical technologies for local identification of zooplankton, together with the technologies for near- to far-field, frequency-dependent acoustic backscattering and TS measurements, and finally combined with models will, however, enable realtime prediction of the spatial distribution of zooplankton biomass, numbers, and size distribution in the water column.

Molecularly-based species identification is also likely to make significant strides in the next decade (Bucklin, 1998). Molecular characters are being used to identify meroplanktonic larvae of sessile invertebrates (Bell & Grassle, 1992; Medeiros-Bergen, Olson, Conroy, & Kocher, 1995) and stages of zooplankton that are difficult to distinguish (Bucklin, Bentley, & Franzen, 1998; Bucklin, 2000; Bucklin, Guarnieri,



Plate 44. New autonomous vehicles which may provide the means for large-scale synoptic mapping of zooplankton distribution. (A, B) The autonomous drifter 'Solo' (Niiler, 2000). (C, D) The autonomous underwater glider 'Spray' (Sherman et al., 2001, W. B. Owens, photo).

McGuillicudy, & Hill, 2001). A basic requirement for implementation is the genetic characterization of the world's zooplankton species. Species identification will require DNA sequence data for selected genes which discriminate even the most closely related species. Efforts to create such genetic databases are underway. It is now conceivable that this information will enable simultaneous analysis, identification and quantification of all species occurring in a zooplankton sample. Such molecular analysis could be done using freshly collected or appropriately-preserved zooplankton samples as conceptualized by Bucklin (1998) in describing "the flow-injection, identification, and sorting system (FIISS): a remote, automatable system to detect, identify, sort, and collect small marine organisms". Miniaturization of the molecular processes (Cheng et al., 1998) may eventually permit autonomous collection and analysis in near realtime.

Early in this 21st century, we can expect to see genetic detectors such as FIISS that can be deployed on towed vehicles which can survey the water column, detect the presence of a species, and estimate its abundance in a particular depth strata. These would be combined with optical, acoustic, and other environmental sensors to provide a full spectrum biological profile of the water column. Until the need for ground truthing is eliminated, the suite of sensors would be deployed on net systems or their use coordinated with net system collections, as is presently done. Ultimately, such devices could be put on AUVs and the successors to ALACE and PALACE float systems, such as SPRAY, for deployment throughout the worlds oceans to study the physical structure of the water column and to provide near realtime data on the distribution and abundance of zooplankton.

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Appendix A

Author	Type or Name of net/sampler	Specifications
Hensen (1887); Jenkin (1901); Wimpenny	ns Hensen Egg Net	38 cm diameter mouth (40 cm long conical mouth piece); 100 cm diameter conical net mouth. 144 cm
(1937)		long net of No. 20 silk (Plate I A, B)
Chun (1888, 1903)	Chun-Peterson Net	A vertical net lowered closed, propellor activated opening and closing.
Hoyle (1889)	opening/closing Net	61 cm diameter conical net (muslin or silk) – no other dimensions given – Proposed electrical activation to open/close net. (Plate 5 C)

94	P.H. Wiebe, M.C. Benfield / Progr	ress in Oceanography 56 (2003) 7–136
Hensen (1895)	Planktonbenthos Sampler	A eight wheeled carriage-like sled with a net mounted in between the third and fourth pairs of wheels. (Plate 22 A)
Apstein (1896); Dakin (1908)	Apstein Net	14 cm diameter mouth (20 cm long conical mouth piece) 40 cm diameter conical net mouth. 100 cm long net of No. 20 silk. Dakin (1908) also describes a 'butterfly' closing mechanism for this net
Fowler (1898)	'Mid-water' Net	11.4 cm x 11.4 cm rectangular net mouth frame which was hinged at the central axis. It was equipped with a silk net (9.8 or 15.7 meshes per cm) which was enclosed by a similar net made from mosquito netting. This net was sent down closed, opened by a messenger and closed by a second one. Designed for vertical towing.
Bruce (1904)	Scotia Closing Plankton Net	Essentially like the Nansen net.
Apstein (1906)	High Speed Sampler	A cylindrical tube with ~2 cm diameter mouth opening expanding to 4 cm diameter in the main body with a filtering surface at the rear. Overall length ~20 cm (Plate 13 A).
Zacharias (1907)	High Speed Sampler	A cylindrical tube similar to Apstein's ~3 cm diameter mouth opening expanding to 8 cm diameter main body with baffles for different towing speeds and a filtering surface at the rear. Overall length 42 cm (Plate 13 B).
Monti (1910)	High Speed Sampler	A cylindrical tube modified from Zacharias with a 3–4 cm diameter mouth opening expanding to 10–12 cm diameter main body and a filtering cone leading to a stopcock at the rear. Overall length 50 cm (Plate 13 C).
Buchanan-Wollaston (1911)	Wollaston Pop-down Net	55 cm net opening diameter 34 cm long made of canvas; 25 cm diameter conical section 68 cm long made of silk netting (no size given). (Plate 10 B).
Kofoid (1911a,b, 1912)	Horizontal Self-closing Net	37 cm net diameter. Conical silk bolting cloth net (nos. 12 to 20) about 200 cm long. Two hinged jaws in the mouth of the net swing forward and downward. Each is activated by a messenger to open then close the net mouth. Used at the end to a cable for horizontal/oblique towing (Plate 5D).
Bigelow (1913)	Horizontal Opening/Closing Net	A hinged ring to which a net with 75 cm diameter mouth was attached. System sent down with ring closed and opened with a messenger. A second messenger released the ring and a draw-string closed the net off.
Nansen (1915)	Vertical Closing-net Horizontal Closing-net (with current meter to measure flow)	35 to 100 cm net diameter (but up to 300 cm for Murray & Hjort Expedition of 1910); 50 cm cylindrical portion of canvas; 150 cm long conical section of silk (no size given) (Plate 5 A).

Juday (1916)	Juday Net	25 cm diameter mouth opening with 33 cm long canvas cone expanding to 30 cm diameter, followed by a conical net 70 cm long made of No 20 silk bolting cloth (Plate 1 C). A closing net with simple messenger release also described; 12 cm diameter mouth opening with 40 cm long canvas cone expanding to 17 cm, followed by a 47 cm long conical net with the same mesh
Ostenfeld and Jespersen (1924)	International Standard Net (ICES)	50 cm diameter mouth with 60 cm cylindrical portion of 1 cm mesh, 200 cm conical section of silk (No. 25 or No. 3). This net used for both vertical and horizontal closing tows (based on Nansen net). A unique way to avoid ship motion described using two davits and a counter balancing weight (Plate 1 D).
Russell (1925)	Closing Net Mechanism	A description of a single messenger tripping mechanism to close a net being towed horizontally.
Hardy (1926b, 1936a); Glover (1953)	Standard Plankton Indicator (high-speed sampler)	Originally 10.1 cm diameter mouth opening expanding to 17.8 cm diameter main body. Overall length 91.4 cm. In modified form with 3.8 cm diameter aperture opening,, 7.6 cm diameter filter disc, 56 cm overall length, and with depressor and stabilizing fins. Normal towing speed 8 kts (Plate 13 D.E).
Hardy (1926b, 1936c) Glover (1962)	The Continuous Plankton Recorder	1.27 cm on side square mouth opening (originally 10.1 cm diameter) high-speed (12 to 17 kts) towed body collecting plankton on gauze (22.9 cm wide and 23.6 meshes per cm) rolls. The body is 50 cm wide x 50 cm tall x 100 cm long. A propellor drives the rollers winding up the gauze. The system is normally towed at 10 m depth at speeds up to 20 kts (Plate 19 A, B).
Russell (1928)	Epi-benthic Plankton Net	122 cm wide x 30 cm tall rectangular mouth. 240 cm length net made of 'stramin'. Net is mounted in an Agassiz trawl frame (Plate 22 B).
Kemp et al. (1929); Marr (1938)	N50, N70, N100, N 200, N450 Nets	All cylinder-cone nets that were towed either vertically, horizontally or obliquely depending upon size, and all with closing capability. N50– 50 cm diameter cylinder 66 cm long made of canvas; cone 65 cm long of silk netting of 78 meshes per cm. N70 cylinder 0.64 cm mesh 53 cm long; cone with two sections one 96.5 cm long with 15.74 threads per cm, and the other 134.6 cm long with 29.1 threads per cm. N50 and N70 (similar in size and mesh to Hjort net (Murray and Hjort, 1912) (Plate 1 E). N100– 100 cm diameter cylinder 1.27 cm mesh 107 cm long; cone with two sections one 107 cm long with 4 mm mesh, and the other 213 cm long

		with 5.9 meshes per cm or stramin. N200– 200 cm diameter cylinder 2.54 cm mesh 213 cm long; cone with two sections one 198 cm long with 7 mm mesh, and the other 396 cm long with 4 mm mesh. N450– 450 cm diameter mouth opening and a cylinder-cone net with four sections. Cylinder 3.8 cm mesh 457 cm long; Cone 1371 cm long with three equal length sections with 1.27 cm mesh, 0.7 cm mesh, and 0.7 cm mesh with 0.4 cm mesh liner respectively. Used either as open net or with a messenger device that closed the net about half way back to the cod-end while still allowing the net ring to tow normally. Depth recording instrument used on the net.
Jenkin (1931)	Double Releasing Mechanism	A description of a double messenger tripping mechanism to open and close a net being towed horizontally at the end of a towing cable. Also described is a wire angle indicator to be used to determine the depth of the net using wire angle and meters of wire out.
Beauchamp (1932)	Planktonbenthos Dredge	A simple pair of U-shaped runners were connected by two cross struts which supported a net which collected animals living just above the bottom. No opening/closing mechanism was present.
Leavitt (1935, 1938)	Opening/Closing Net System	100, 150, and 200 cm diameter nets made of scrim, silk, and stramin respectively. Net dimensions not given (Plate 6 A).
Hart (1935)	Closing Net Design	A rod of wood or pipe is outfitted with a combination wire clamp and closing release at the top and a pair of snap hooks at the bottom, one to secure the device to the wire and one to secure the bottom portion of the net. Attached to the rod is a net with a bridle which inserts into the release latch. Midway along the pipe is a second snap hook which is attached to the mid section of the net. Multiples of these units may be attached to the wire at various depth intervals as the wire is lowered vertically into the water. Plankton collections are made as the nets are hauled up until a messenger hitting the release lets the bridle go, thus closing the net (Plate 5B).
Henderson et al. (1936); Glover (1953)	Miniature Plankton Indicator	This indicator had a body length of 33 cm, a diameter of 3.8 cm, an aperture diameter of 1.27 cm, a filter disc of 2.54 cm in diameter and was towed at about 2 knots (Plate 13 F).
Pierce (1937)	High-speed Plankton Collector	7 cm mouth opening of front cone which was 16.5 cm long. 17.8 cm diameter cylinder body which was 25.4 cm long. 7 cm conical coarse silk net 16.5

Fry (1937)	High-speed Metal Plankton Net	cm long with small jar cod-end. 10.2 cm diameter mouth opening expanding to 25.4 cm followed by a mesh cone (15.7 meshes per cm) and a cod-end. Overall length 152 cm. Towed with 3 part chain bridle at speeds up to 10 kts (Plate 14 C)
Erdmann (1937)	High-speed Collector	~4.5 cm diameter mouth expanding to 12 cm with overall length of 64 cm. Has an opening/closing mechanism (Plate 14 D)
Van Cleve (1937)	Electrical Plankton-Net Closing Device	A solenoid activated double release mechanism controlled electrically from the surface used to open and close a 100 cm diameter ring net. The electrical cable was attached to the towing cable at 50 to 100 m intervals.
Clarke and Bumpus (1939, 1950)	Clarke-Bumpus Plankton Sampler	12.7 cm diameter mouth opening with cylindrical tube 16.0 cm long. Tube equipped with flat plate which pivots to open or close the flow through the tube and a flowmeter. 61 cm long conical net is attached to the rear of the tube (Plate 8 A).
Wheeler (1941)	Parachute Net	275 cm diameter parachute opening tapering over a distance of 350 cm to a 100 cm diameter mosquito netting net. Free fall to bottom with concrete weights, released by salt block dissolution, and floated backwards to surface with gasoline float (Plate 11 B)
Ahlstrom (1948)	CalCOFI Net	100 cm diameter ring net about 5 m in length with No. 30 xxx grit gauze (a grade of silk bolting cloth). Netting changed to 505 m Nitex mesh and then to 333 m mesh (Plate 2 C).
Smith and Ahlstrom (1948)	High-speed Collector	2.54 cm diameter mouth expanding to 5.08 cm (brass), cylindrical net 5.08 cm and 25.4 cm long made of No. 56xxx grit gauze, and a bucket. Towed at 9 knots.
Bossanyi (1951)	Epi-benthic Plankton Sampler	~91 cm x 61 cm rectangular mouth with net about 213 cm long. Netting with 15.7 meshes per cm. Able of open/close mouth opening (Plate 22 C).
Gauld and Beganal (1951)	High-speed Tow Net	46 cm diameter mouth opening with 15 cm long calico collar, 94 cm long silk net (10.2 meshes per cm), and 12 cm diameter x 17 cm long sleeve with ring sewn in at end. The tail of the net is flipped inward and bridles attached to the ring are attached to the front of the net. A three-part bridle tows the net at speeds up to 7 kts. Design taken from Sheard (1941) (Plate 15 A).
Tucker (1951)	The Tucker Trawl (non- opening/closing)	183 cm x 183 cm flexible rectangular net mouth 914 cm long net with 1.8 cm stretched mesh for first 457 cm and 1.3 cm mesh for last 457 cm. 152 cm of coarse plankton or muslin netting lined the

Tonolli (1951)	The Plankton-Bar	end of the net. System equipped with mechanical time/depth recorder (Plate 4 A, B). A method for continuous sampling plankton from several depths simultaneously using a combination
		of ~ 18 cm diameter nets with 38 meshes per cm and a pumping system. Five nets with equidistant spacing on a towing wire were normally used (Plate 11 D).
Arnold (1952)	Gulf I-A High Speed Sampler	7.6 cm diameter inside cylinder net 91 cm long of No. 10 screen (0.038 cm mesh). Equipped with flowmeter. Towed at \sim 9 kts (Plate 15 C).
Gehringer (1952b)	Gulf III High Speed Sampler	40.7 cm diameter nose piece entrance into an 50.2 cm diameter cylinder 152 cm long made of 0.152 cm monel metal mesh. 49.5 cm diameter inside conical net 137 cm long of No. 10 screen (0.038 cm mesh ~ No. 1 silk). Equipped with flowmeter. Towed at ~ 5+ kts. Also used with 20.3 cm nose cone (Plate 15 D).
Isaacs and Kidd (1953)	The Isaacs-Kidd Midwater Trawl	A trawl with a pentagonal mouth opening and a dihedral depressor vane as part of the mouth opening. The original IKMTs were 10 foot (304 cm), and 15 foot (457 cm) at the mouth. The 10 foot IKMT net was 31 feet (9.45 m) in length (Plate 3 D).
Wickstead (1953)	Mechanically Opening/Closing Epi- benthic Plankton Sled	61 cm x 30 cm rectangular mouth opening : length of net or mesh size not given (Plate 22 D).
Langford (1953)	Toronto Trap (Plankton pump)	In situ pump with No.20 silk mesh with flowmeter. For lakes
Motoda (1953)	Cod-end Sampler	15.5 cm diameter mouth opening and 35.5 cm long attached to 57 cm diameter net 200 cm long with bolting cloth 42.5 meshes per inch in upper 120 cm and 56.5 meshes per inch in lower 80 cm (Plate 25 A).
	High-speed Successive Plankton Sampler	10 cm diameter and 100 cm in length. Tapered nose with two 2-cm openings. Body of cylinder has multiple sections 1.5 cm diameter x 18 cm long to store samples. Equipped with depth/flowmeter. Collects samples at ~ 8 kts.
Barnes (1953)	A Closing Net	A hemispherical metal cowling is mounted in front of a net ring with an opening sized so that a closing lid can be accommodated when the net is open. A Nansen messenger closing mechanism is used to release the spring loaded closing lid which pivots over the net mouth. No dimensions given for net size or mesh (Plate 8 C).
Glover (1953)	Small Plankton Sampler	This is a small high-speed sampler (similar to Hardy's Standard Plankton Indicator and the

		Miniature Plankton Indicator) with a 1.9 cm diameter aperture opening, 3.2 cm diameter internal net and 8.9 cm long, and a 30.5 cm overall length (Plate 14 A).
Nishizawa et al. (1954).	In situ Photography of Zooplankton From A Diving Chamber	A clear plastic collection box (15 cm high x 20 cm wide x 5 cm thick) could be opened and closed to collect a sample of water with its constituent plankton. Contents illuminated by a 300 W lamp and photographed with a camera. Multiple exposures allowed swimming velocity estimates.
Slack (1955)	Horizontal Opening/Closing Plankton Net	14.0 cm diameter mouth opening with framework25.4 cm long. With an internal flowmeter.
Cassie (1956)	High-Speed Nets	Model 1: a brass cylinder 6 cm diameter and 6 cm long with bridle attachment lugs had a 180 cm bolting cloth net (16 or 30 meshes per cm) attached to the back (Plate 18 A). Model 2: Same as model 1 except system shorter (90 cm) and net made out of brass gauze with 16 meshes per cm and two metal rods (struts) connected the brass cylinder to the cod-end bucket. Model 3: Same as model 2 except shorter (60 cm) and four metal rods (struts) connected the brass cylinder to the cod-end bucket. All towed from the stern of the vessel at ~ 8 kts on a 40 m tow line.
Currie and Foxton (1956)	N70 V Net (Discovery Net) (described by Kemp et al. (1929)	A version of the Nansen net. 70 cm diameter mouth opening with 3 nearly cylindrical net sections and a final conical section. Section 1 with .63 cm mesh, section 2 canvas for closing rope, section 3 made of silk with 40 meshes per inch (15.7 meshes per 1 cm), and section 4 made of silk with 74 meshes per inch (29.1 meshes per 1 cm)
Johnson et al. (1956)	In situ Photographic Ground-truthing Of The Deep-scattering Layer	35 mm shutterless camera illuminated by a strobe. Camera coupled to a ship-mounted, down-looking echosounder (Plate 39 A).
Backus and Barnes (1957)	In situ Television System	Underwater TV coupled with illumination from a pair of 2kW lights combined with either a down- looking 34 kHz echosounder or a colocated 34 kHz echosounder with the acoustical focal point near the TV's center of focus.
Currie and Foxton (1957)	Modified N70 Net	A modified version of the Nansen net with a large depth-flowmeter mounted mid-way down the middle of the cylinder portion of the net.
Motoda (1957)	North Pacific Standard Net (Norpac Net)	45 cm mouth diameter with a conical net length of 180 cm (mesh 0.33 mm – GG54) (Plate 1 F).
Collier (1957)	Gulf II High Speed Sampler	A shipboard pump drew water from near the keel of the vessel and it was delivered to a circular pan divided into 8 parts each of which had a filter to

100	P.H. Wiebe, M.C. Benfield / Progr	ess in Oceanography 56 (2003) 7–136
Ahlstrom (1958)	Isaacs Sampler (High- speed Sampler)	catch the plankton. The Sampling interval for a filter was 1 hour. Filters (#1 bolting silk) were replaced every 8 hours. This system was developed as a substitute for CPR 2.5 cm mouth opening expanding to a diameter of 7.6 cm; overall length of 130 cm. Plankton filter is a cylinder of Monel metal mesh (23 mesh per cm) ~5.2 cm in diameter and 36 cm long. System equipped with a flowmeter and depth sensor (from
Bary et al. (1958)	Bary Catcher High-speed	bathythermograph) and a recording unit utilizing clear 35 mm acetate film. Can be towed up 10 kts. Can be put anywhere on cable and multiple units can be towed simultaneously (Plate 15 B) 22.9 cm diameter mouth opening: behind closing
Dary et al. (1956)	Plankton Sampler	value, tube chamber is 19.5 cm diameter. 213 cm overall length of outer fiberglass shell. Two metal nets can be used, one with 15.70 meshes per cm and one with 3.9 meshes per cm. Has depth- flowmeter (like that of Currie and Foxton, 1957) in the tail. Towed up to 10 kts. More than one unit can be attached to the wire. Can be used for vertical or horizontal towing (Plate 18 B, C).
Arnold (1959)	Gulf V Plankton Sampler	41 cm diameter mouth opening with frame 130 cm long. Conical Monel mesh net with 30 meshes per cm. An unencased and scaled down version of the Gulf III described by Gehringer (1952a) (Plate 16 A)
Zaitsev (1959, 1970)	NS (Neuston Net)	60 cm x 20 cm rectangular mouth aperture with net 250 cm long with plastic foam floats 20 cm x 10 cm x 4 cm attached to sides of metal net frame. Used from drifting or anchored vessel (Plate 20 A).
Bé et al. (1959); Bé, (1962)	Multiple Plankton Sampler; Bathypelagic plankton Sampler	50 cm x 50 cm opening with nets of 0.2 mm mesh 300 cm long (50 cm nylon cloth collar; 240 cm netting, 10 cm nylon cloth for cod-end attachment). First described as a vertically towed system using messengers to open and close three nets. A depth- flowmeter readings continuous recorded on smoked glass cylinder. Then modified to do horizontal or oblique towing using a pressure actuated device to open and close nets a preselected depths (MPS 0– 100, 100–250 m, and 250–500 m; BPS 500–1000 m). Also built with 100 cm x 100 cm mouth opening (Plate 9 A, B, C).
Hempel (1960)	HAI (modified Gulf III)	Entrance of 18 cm diameter and net mesh of 0.4mm. Towed at 6 kts (Plate 16 C).
Yamazi (1960)	Pump System with Multiple Sample Collection System	A submersible pump mounted in a circular frame work. Flow from the pump is directed to a flat disc to which 16 to 24 small net cod-ends are attached.

		A ratchet mechanisms rotates the disk and enables the changing of the nets into the path of the flow. System has temperature and light sensors.
Jaschnov (1961)	High-speed Vertical Plankton Net	Rectangular mouth opening. Closed-like Juday net Used No. 38 silk. Speeds up to 2.8 m/sec (5+ kts)
Schröder (1961)	Towed, Underwater Television System	Forward-looking Grudig/IBAK TV camera coupled to orthagonally-oriented pair of 1000 W lamps located 30 cm in front of TV (Plate 39 B).
Zaitsev (1961, 1970)	PNS (Neuston Net)	A five stage sampling frame with a height of 100 cm and width of 60 cm in which five 60 cm x 20 cm rectangular mouth aperture nets are stacked. Nets and frame flotation similar to that described by Zaitsev (1959). Used from drifting or anchored vessel.
Paquette et al. (1961)	Enlarged Clarke–Bumpus Sampler	25.4 cm diameter mouth opening with cylindrical tube 12.7 cm long. Tube equipped with flat plate which pivots to open or close the flow through the tube and a TSK flowmeter. 107 cm long conical net is attached to the rear of the tube. (No mesh size given)
Miller (1961)	Modified Small Hardy Plankton Sampler	This is a small high-speed sampler (modified from that described by Glover (1953) with 10.1cm diameter aperture opening on a body tube 14 cm internal diameter and a 61cm overall length. Attached to the back of the tube is a 91 cm long nylon net of three meshes (0.947 mm, 0.526 mm, and 0.264 mm). Multiple units used on the towing wire at speeds of 7 to 8 kts with a multiplane kit otter depressor on bottom of wire (Plate 14 B).
Blackburn and Reith (1962)	Micronketon Net	152 cm x 152 cm rectangular mouth opening net attached to metal tube frame with Isaacs depressors attached to bottom corners. Net was 579 cm long made of 5.5 x 2.5 mm rectangular nylon mesh. Towed at speeds of 5 kts. A bathythermograph attached to the top frame member provide a temperature-depth trace for a tow. Not ordinarily used with a flowmeter (Plate 4 C. D).
Yentsch et al. (1962)	Opening/Closing Devices For Plankton Nets	Pressure activated open/closing device for Clarke- Bumpus sampler, a midwater pressure piston release system for ring nets, and a Squib-operated open- closing mechanism for use with cod-end sampler (12.7 cm diameter and 51 cm long described (Plate 25 C).
	Enlarged Clarke–Bumpus Sampler	An enlarged (jumbo) version of the Clarke-Bumpus Sampler with a 30 cm diameter mouth opening and 183 cm long net (Plate 8 B). A pressure potentiometer in a SS case and attached to a conducting cable described for determining the

102	P.H. Wiebe, M.C. Benfield / Progress in Oceanography 56 (2003) 7–136	
Aron (1962)	Self-Propelled Research Vehicle	depth of the end of a net tow wire. A 51 cm diameter x 309 cm long autonomous vehicle equipped with a non-opening/closing Clarke- Bumpus Sampler. (Described are plans to install a modified CPR which would take discrete samples
Williamson (1962, 1963)	Automatic High-speed Plankton Sampler	and a suite of environmental sensors) (Plate 43 A). A sampler that has a series of 21 nets attached to the bottom of rectangular 'trap doors' which are sequentially closed by means of a cam/screw assembly driven by a ships log (propeller). Each net is about 6.35 cm long and made of nylon cloth with 23.6 meshes per cm. The body of the device is 29.2 cm tall x 14 cm wide x 114 cm long not including the side fins. The aperture is 1.9 cm x 1.9 cm Effective sampling speeds 5 to 11 knots and sample length is 1 to 20 km. More than one sampler can be
Nakai (1962)	Marutoku	used on the towing wire (Plate 18 D). 45 cm diameter mouth opening with cylinder/cone design – similar to International Standard Net (MTA) – sometimes rigged as Nansen closing net. Cylinder coarse mesh; conical section 80cm silk mesh netting. MTB– similar to above, but with flowmeter (Plate 3 A, B).
	Marunaka	60 cm diameter mouth opening cylinder/cone design. Cylinder coarse mesh (3.3 cm) 33 cm long. Conical portion silk net 150 cm long. Can accommodate flowmeter. Sometimes rigged as
	Maruchi (conical nets)	Nansen closing net. Variants listed as MNA, MNB. 130 cm diameter mouth opening with 450 cm long net. A series of variants MCA MCE
	Marudai	250 cm diameter mouth opening with 800 cm long net. A series of variants designed to sample
	Kitahara	megaplankton and nekton (MDA, MDB, PMD). 24 cm diameter mouth opening for head piece and 45 cm diameter conical net 80 cm long. A Hensen style net (KT)
Fish and Snodgrass (1962)	Scripps-Narragansett High-speed Multiple Plankton Sampler	50 cm diameter mouth opening Gulf III sampler with a circular disk holding five cod-end metal mesh buckets. The disk is rotated to open and close the buckets by electrical commands from the surface transmitted on a double conductor towing cable. Net depth, flowmeter readings, filtered volume are recorded (Plate 16 B)
Currie (1962) Foxton (1963)	Foxton Two-chamber Cod-end	Modification to IKMT to allow pressure actuated depth separated collections by two part cod-end (Plate 25 D).
Frolander and Pratt (1962)	Bottom Skimmer	A double runner sled 46 cm wide x 23 cm tall x 132 cm long with a roller on the forward lower

		cross strut, sheet lead attached to the bottom near the front, and a pair of metal float balls snap- hooked to the top to keep sled right-side-up. Inside was mounted a Clarke-Bumpus cylinder and net (63.5 cm length. Towed at speeds of 1–2 kt (Plate 23 C).
Grice (1962)	Automatic Multiple Net Plankton Sampler	The conning-tower (sail) on the nuclear submarine, SEADRAGON, was equipped with a 9 cm diameter intake pipe that led to a sampler with a revolving circular ring with 24 positions to which nets could be attached. The nets, made of 0.223 mm Nitex nylon mesh, were 1.9 cm in diameter x 30.5 cm long. Nets were placed on alternate openings and a battery powered timer and motor rotated the nets into and out of position to collect a sample on a two hour schedule. Sampling schedules of 0.5, 6 or 12 hours were also possible. There was no flow meter (Plate 12 A).
Ishida (1963, 1964)	Streamer Plankton Sampler	45 cm diameter mouth opening with a closing door and a metal cylinder 45 cm long to which is attached a net of 5 meters length. The sampler sinks with closing door open flushing the net. When halted attached line lifted, the door closes and end of net is closed capturing a 600 liter sample (Plate 10 E).
Willis (1963)	Neuston Net	17.8 cm x 3.8 cm rectangular mouth opening of net 67.3 cm long (netting nylon with 78.7 meshes/cm). Normally towed while ship drifting at 1 kt (Plate 20 C).
Currie (1963)	Indian Ocean Standard Net	113 cm diameter mouth with 3 cylinder sections 70 cm (12.5 mm mesh), 30 cm (sail cloth, and 100 cm (0.330 mm nylon mesh) and a conical section 300 cm (0.333 mm mesh). No closing mechanism used in standard haul. Flowmeter use recommended. Based on the Discovery N 100 net. Used during the Indian Ocean Expedition of the 1960s (Plate 1 G).
Clarke (1964)	Clarke Jet Net High-speed Plankton Sampler	12 cm diameter mouth opening with an overall length of 125 cm. Uses nylon netting with 0.44 mm mesh. Towing speeds up to 10.5 kts (Plate 18 E).
Pearcy and Hubbard (1964)	IKMT with MPS Cod-end	A 1.8 m IKMT fitted with a scaled down version of the Bé (1962) MPS with 3 nets attached to the back of the trawl. A pressure-release system controls the opening/closing of the cod-end nets (Plate 26 B).
Aron et al. (1964)	Discrete Depth Plankton Sampler (DDPS)	Cod-end sampler used with IKMT or a 1-m diameter net with underwater electronics to sample depth and temperature operated with single conductor cable. Mark III had 10 or 15 cm diameter opening and four catch chambers (Plate 26 A).

Wlodek and Szwa	High-speed Plankton	Dimensions in Polish.
(1964); Omori (1965)	ORI Nets	160 cm diameter mouth opening. ORI-C net with 2 cylinder sections with lengths of 70 cm (1.97 mm mesh), and 70 cm (sail cloth), and 2 conical sections 450 cm (1.97 mm mesh) and 150 cm (.33 mm mesh). Equipped for a Motoda (1959) double releasing mechanism. ORI-200 has same form and all 1.97 mesh, and OIR-33 made from GG 54 silk natting (Plota 6 P)
Clutter (1965)	Epi-benthic Plankton Sampler	32 cm x 32 cm rectangular mouth opening net attached to a metal box frame work which was 37 cm tall x 37 cm wide x 30 cm long. The net was about 30 cm long had 0.333 mm nylon mesh. The system was lowered to the seafloor where an anchor attached to the net frame by a spool of line became fixed. The net was towed at ~1.5 kts away from the anchor until the line was fully extended whereupon it triggered a choke rope closing the net. Distance covered by the sampler was about 10 m. A scaled up version with 70.1 cm x 70.1 cm mouth opening also described (Plate 23 A)
David (1965)	Neuston Net	30 cm x 15 cm rectangular mouth opening with net 365 cm in length (21.3 meshes to cm). Normally towed at 5–6 kts (Plate 20 D)
Bieri and Newbury (1966)	Booby-II (neuston Net)	Wooden frame 63 cm wide x 16.5 cm tall x 121 cm long with a pair of Otter board fins extending down 58.5 cm below the top. Styrofoam plastic used for floatation. Inside the wooden frame is a metal framework to support a 63 cm x 20 cm rectangular net 100 cm long (number 54 nylon grit gauze). Towed at 1 to 3 kts from the bow of a vessel with bridle attached to the forward side of the frame so that it rides out away from the vessel (Plate 20 B).
McGowan and Brown (1966)	Opening/Closing Bongo Net	A pair of circular hoops (70 cm diameter joined by a central axial which was clamped to a cable. A Dacron cloth 'door' covered each mouth opening which when released by a messenger, folded into the net mouth. The nets were 71 cm in diameter, had a non-filtering collar section 84 cm long and a conical net 420 cm long with 0.505 mm mesh. A flowmeter was present and after a set number of revolutions, caused the nets to be released from the hoops; choke ropes closed them (Plate 9 D).
Longhurst et al. (1966)	Longhurst-Hardy Plankton Recorder (LHPR)	50 cm diameter net mounted in a towing frame. Attached to the cod-end of the net was a plankton recorder box with two rolls of gauze that were spooled onto a single spool after cutting across a

P.H. Wiebe, M.C. Benfield / Progress in Oceanography 56 (2003) 7-136

104

		tunnel through which water and plankton flowed out of the back of the net. The take-up spool with the plankton sandwiched between the two strips of gauze was advanced in discrete steps (15 seconds to 60 seconds) by an electronics package on the tow frame. Data on pressure and temperature and flow counts were logged on an internal recorder in the pressure case. Normally towed at 1.5 to 2.5 kts and collected ~ 100 samples (Plate 26 C).
Jossi (1966)	ICITA Plankton Net	100 cm diameter mouth opening with a conical net with a short (18cm) section of canvas and a 330 cm length section of 0.281 mm Nitex nylon mesh. Used with a flowmeter. The standard net used during the International Cooperative Investigations of the Tropical Atlantic (Plate 2 B).
Fraser (1966); UNESCO Working Party 2 (1968)	WP2 Net	57 cm diameter mouth opening (0.25 m^2) cylinder (95 cm length)/cone (166 cm length) net made with nylon mesh (0.2 mm). A flowmeter is mounted offset in the mouth. For vertical tows. A recommended standard net for collecting 0.2 mm to ~ 10 mm zooplankton (Plate 2 A).
Kinzer (1966)	Opening/Closing Mechanism For HAI (a high-speed plankton sampler)	A modified Gulf III sampler was equipped with a hemispherical nose cone and the mouth opening (22 cm diameter) was adjusted to accommodate a closing lid. One messenger is used to cause the lid of move aside opening the mouth of the sampler; a second messenger is used to move the lid back over the mouth opening at the end of the tow (Plate 16 D).
Knox (1966)	Laboratory-based Holographic System	On-axis holograms of live plankton recorded on film emulsion with a ruby laser and reproduced with an He-Ne laser.
Beverton and Tungate (1967)	Multiple High-speed Plankton Sampler (Lowestoft Sampler)	30.5 to 48.5 cm diameter nose cone aperture with 76.6 cm diameter body and 244 cm in length (a modified Gulf III sampler). Conical netting of nylon mesh of 0.270, 0.305, or 0.420 mm or Monel metal mesh of 0.270, 0.42, 0.560 mm. Has two auxiliary samplers with nose cones of 5 to 9 cm diameter and main body 16.5 cm diameter ($0.061 - 0.270$ cm mesh). An additional phytoplankton or water sampler has an aperture of 0.1 cm and a body diameter of 11.5 cm. Flowmeter mounted in nose cone (Plate 17 A).
Macer (1967)	Bottom Plankton Sampler	\sim 30 cm x 20 cm mouth opening, but net dimensions or mesh used not given (Plate 23 B).
Danielssen and Tveite (1968)	Neuston Sampler	A framework supports five rectangular nets with mesh sizes ranging from 0.150 to 0.500 mm. A flowmeter is used.

106	P.H. Wiebe, M.C. Benfield / Progr	ress in Oceanography 56 (2003) 7–136
Emery (1968)	Diver Tow Net	30 cm diameter ring net with 0.183 mm mesh towed by diver.
Omori (1969)	Bottom Plankton Sampler	70 x 70 cm rectangular mouth opening net is attached to a sled made of iron (75 cm wide x 90 cm long x 25 cm tall) with a plastic runner on the bottom. The net of 2.0 mm mesh is 350 cm long. A finer mesh netting (330 m) was used to line the posterior 150 cm to retain smaller zooplankton. The system is equipped with a messenger operated closing mechanism and a flow meter.
Sameoto and Jaroszynski (1969)	Neuston Sampler	102 cm x 102 cm rectangular mouth opening aluminum box frame 152 cm long equipped with foam floatation on top, a pair of fins on the side, and a fin on the bottom. Attached to the back was a net 104 cm x 104 cm at the mouth and 927 cm long made from 0.308 mm nylon mesh. A two-part towing bridle was attached to one side and the sampler kited out away from the side of the vessel beyond the ships wake. Towing speeds 8 to 11kts (Plate 20 E).
Knox and Brooks (1969) Nellen and Hempel (1969)	Laboratory-based Holographic System 'Nackthai' (naked shark)	Based on Knox's (1966) system modified to use 35 mm film and animated. A modified Gulf V sampler with a 20 cm diameter nose cone aperture expanding to 38 cm diameter over length of 53 cm. Attached to back of cone is a net 120 cm long. Frame work in which net supported 45 cm x 45 cm x 190 cm long. Overall sampler length 243 cm. A comparison was made between the Hai and the Nackthai samplers which showed the Nackthai filtered more water and caught significantly more plankton and fish a result attributed to its non-encased net (Plate 16 F)
Davis and Barham (1969)	Opening/Closing Tucker Trawl	Used timing clocks to open and close the Tucker trawl mouth. Net design modified from that described by Tucker (1951) so that first 500 cm of the net mesh was 1.1 cm Marlon netting and last 200 cm was 0.33 mm nylon mesh. A depth- telemetering pinger used to monitor net depth during tow and a depth-time recorder used to make alternate record (Plate 9 E).
Clarke (1969)	Tucker Style Opening/Closing Trawl (RMT 8)	283 cm x 400 cm rectangular flexible mouth opening with 5 mm mesh net 1188 cm long. Net mouth is opened and closed acoustically. Pinger used to determine depth.
Boyd and Johnson (1969)	In situ Zooplankton Detecting Device	A modified Coulter Counter that measured the voltage across two pairs of electrodes within a tube containing seawater. Mounted in a modified Icelandic high-speed plankton net with a reduced

		intake. A voltage transient induced by passage of zooplankton through cell was amplified and converted to an FM signal that was transmitted to a ship via a conductive tow cable where it was detected and processed by a PDP-8/LINC computer (Plate 37 A, B, C).
Cooke et al. (1970)	Opto-Electronic Plankton Sizer	Laboratory based system that projected the silhouettes of preserved zooplankton on to an array of photosensors and estimated of the number of individuals in seven size classes
Zaitsev (1970)	MNT (Neuston trawl)	An elliptical metal frame 100 cm wide x 50 cm tall with a net 400 cm long made of netting with Nos. $21-23$ meshes. Two plastic foam floats (25 cm x 12 cm x 8 cm) are attached to each side of the net frame. Net towed in a circle at about 4 kts.
Johannes et al. (1970)	Fixed In-current Plankton Net	A pair of 50 cm diameter nets made from number 10 gauze were mounted side by side in a rectangular frame with an extender rod to support the net cod-ends horizontally . The nets and frame were attached 100 cm above the bottom to a wire extending from an anchor stand to a surface float. The nets were free to rotate so that they always faced into the flow (Plate 24 B).
Grice and Hülsemann (1970)	DSRV Alvin Net #1	A pair of nets were mounted onto the front of DSRV Alvin for collecting planktobenthos at great depths. The mouth openings were 'D' shaped and hinged so that on descent and ascent of the submersible, the nets could be turned back away from the flow and would not filter. The Alvin arm was used by the pilot to open and close the net. The nets had 0.233 mm mesh (Plate 23 D).
Motoda (1971)	MTD Horizontal Net	56 cm diameter cylinder (80 cm length and cone (110 cm length) net mounted on wire with a triangular framework so that up to 10 can be towed simultaneously. With closing system that invert forward portion of the net and draws mid-net section tight. A flowmeter can provide approximate volumes filtered. Mesh size not given (Plate 8 D).
Rakusa-Suszczewski, (1972)	Umbrella Net	A pair of nets attached to an umbrella-like support. The system was deployed down a 12 cm ice hole and expanded below the undersurface of the ice. A circular motion caused the nets to scrap the undersurface of the ice and collect organisms in the water just below it. There was no flow meter or a description of the net specifications.
Grice (1972)	DSRV Alvin Net #2	A pair of nets were attached to a pair of rectangular frames 61 cm wide x 31 cm tall which each had a metal door hinged at the top. The Alvin arm was

		used by the pilot to open and close the door. The nets were positioned about 20 cm above the bottom. The nets had 0.239 mm mesh. Normal 'pushing' speed was 1 kt (Plate 23 E).
Murphy and Clutter (1972)	Plankton Purse Seine	A miniature purse seine 3048 cm long x 640 cm tall with netting of 0.333 mm nylon mesh (Plate 12 C).
Hempel and Weikert (1972)	Modified David Neuston Net	A pair of vertically stacked nets with 30 cm x 15 cm rectangular mouth opening and 0.3 or 0.5 mm mesh (Plate 21 B).
Miller (1973)	Surface Plankton Push Net (neuston Net)	A pair of rectangular nets (0.505 mm nylon mesh) each 60 cm x 60 cm mouth opening and ~420 cm long are positioned side by side in a framework that is mounted in front of a small catamaran boat that pushes the frame through the water at ~ 2.6 kts. Samples are removed from the nets through a well in the catamaran floor. Flow is measured with a TSK flowmeter modified to electronically record flow counts (Plate 21 E).
Hopkins et al. (1973)	Messenger-operated Tucker Trawl	180 cm x 180 cm rectangular mouth opening Tucker trawl with a double messenger activated release mechanism made by GO. Net is made from 1.1 cm mesh for first 500 cm and 0.33 mm nylon mesh for last 2 meters. Flow measured with a TSK flowmeter and a time-depth recorder is used to log net trajectory. Also used with trawl with 180 cm x 360 cm mouth opening. Tow speeds generally are between 2and 2.5 kts (Plate 6 C).
Stewart et al. (1973)	Laboratory-based Holographic System	Laboratory holography modified for off-axis recording with shorter pulse length to capture high resolution images of moving copepods.
Baker et al. (1973)	The N.I.O. Combination Net (RMT 1+8)	A combination 100 cm x 141 cm rectangular flexible mouth opening net and one with a 283 cm x 400 cm mouth opening, one above the other on the same towing framework. The 8-m ² as described by Clarke (1969). The 1-m ² was 423 cm long and had 0.32 mm nylon mesh. Data telemetry improved to include temperature and flow. Descriptions of scaled up versions of the RMT 8 to 25-m ² and 90- m ² mouth openings provided (Plate 28 A).
Porter (1973)	Diver-pushed Net	50 cm diameter ring net 200 cm long with 0.12 mm mesh pushed by a diver
Lockwood (1974)	Modified Gulf V	50 cm diameter mouth opening x 213 cm long with a nose cone; netting 24.6 mesh per cm; two flowmeters. Based on Beverton and Tungate (1967) sampler. Towed at about 3 kts (Plate 17 B).
Frost and McCrone (1974)	Multiple Net Trawl (modified Tucker trawl)	100 cm x 141 cm rectangular flexible mouth opening with 0.33 mm nylon mesh nets 6 meters

		long. Originally with 5 nets and increased to 9 nets. (Also a 200 cm x 282 cm mouth opening trawl with 5 nets of 6.35 mm stretch mesh). System powered electrically on conducting wire and controlled from surface. Monitored depth, angle, and flowmeter revolutions (Plate 28 C).
Brown (1975)	Opening/Closing IKMT	A IKMT was outfitted with a 'flap' of material that extended from the net mouth to the back end of the net and a 3-stage cod-end. At the start of a haul the flap was down and animals collect in stage 1 of the cod-end. A timer released the flap which rode to the top of the net and animals collected in the stage II cod-end. A second timer release caused the stage II cod-end to be pursed and it was replaced with the stage III cod-end.
	Bongo Style Vertical Closing Net.	An open pair of 50 cm diameter circular net hoops were mounted on each end of a 150 cm wide cross- strut which was attached to a towing cable. Nets were attached to the bottom of the hoops and their cod-ends were attached to a spreader bar which was also attached to the wire. The nets were lowered to a maximum depth to haul and then during the haul back to the surface, a messenger was used to close the nets either by releasing the hoops so that they turned 90— or by releasing the nets which fell back and were pursed by throttling lines attached to the cross-strut. A non-opening/closing variant of this net, the CalVET net, was described by (Smith et al., 1985) (Plate 10 A).
Bruce and Aiken (1975)	Undulating Oceanographic Recorder (UOR)	A streamlined encased towed body 98 cm wide x 75 cm tall x 156 cm long and weighing 180 kg. Undulates between 7 and 15 to 70 meters (wave length 3 to 30 km) at towing speeds of 7 to 15 knots. A 1.9 cm aperture leads to a tunnel and plankton are collected on gauze rolls (15.2 cm wide silk with 0.3 mm mesh) using the same mechanism as used in the Hardy CPR1. The UOR carries sensors to measure temperature, salinity, and pressure; data logged internally at 30 observations per minute. A propeller drives the rollers winding up the gauze and provides the power for the electronics. System has about a 12 hour towing duration (Plate 19 C).
Wiebe et al. (1976, 1985)	MOCNESS (modified Tucker trawl)	100 cm x 141 cm rigid mouth opening with nine 0.333 mm nylon mesh nets 6 meters long. System powered electrically on conducting wire and originally controlled from surface deck unit and

		now computer controlled. Sensors include pressure, temperature, conductivity, fluorometer, transmissometer, oxygen, and light. Versions include systems with 1/4, 1, 2, 4, 10 and 20 m ² mouth openings all using the same release mechanisms, sensors, and compute logging and controls (Plates 28 D; 29 A-D).
Sameoto and Jaroszynski (1976)	Octagon Net	75 cm diameter iron channel octagon mouth opening which was attached to the towing wire with stainless steel snap swivels and held from sliding down by a stop on the wire. Used with a net made of 1 mm nylon mesh and towed at speeds up to 7 kts (Plate 3 C).
	Messenger-operated Tucker Trawl	A 100 cm x 100 cm and a 400 cm x 400 cm rectangular mouth opening Tucker trawl with a double messenger activated release mechanism. Net is made from coarse mesh. Flow measured with a digital flowmeter. A depressor plate is mounted on bottom net bar. Tow speeds generally are between 2 and 4 kts (Plate 6 D).
	Modified Opening/Closing Bongo Net	75 cm diameter reinforced ring held to the wire by the same method as the Octagon Net. The net had a double messenger release mechanism with the first messenger releasing a dacron cloth door blocking the net mouth and the second one releasing the net
Haury et al. (1976),	Modified LHPR	To cm diameter net of three lengths (230, 300, 370 cm) were mounted in a towing frame. The modified recorder box had a mesh area to mouth opening ratio of 2.9 as opposed to <1.0 for previous designs and the orientation of the gauze across the recorder box tunnels was horizontal instead of vertical. The modified design reduced or eliminated many of the problems observed in earlier designs. Data on pressure and temperature and flow counts were logged on an internal recorder in the pressure case. Normally towed at 1.5 to 2.5 kts and collected ~ 100 samples (Plate 26 E).
Sameoto et al. (1977)	Multiple Plankton Sampler Based On MOCNESS And N.I.O. Nets	100 cm x 100 cm mouth opening with 10 nets (0.243 mm mesh). Net length not given. Non-rigid mouth opening with net bars similar in design to MOCNESS that slide down cables. A depressor is mounted below the bottom net bar. System powered electrically on conducting wire and controlled from surface deck unit. Data logging included depth, roll, pitch, and temperature. A non-telemetering flowmeter was mounted in each net (Plate 30 A).
Ellertsen (1977)	A Neuston Net	Six stacked nets two with 10 cm tall x 25 cm wide rectangular mouth opening and four with 20 cm tall

		x 25 cm wide mouths. Nets 100 cm long made of 0.2 mm nylon mesh. Pontoons made of fiberglass covered Styrofoam 10 x 15 x 100 cm. A flowmeter can be used (Plate 21 C).
Bourdillon et al. (1978)	Opening/Closing Mechanism For Plankton Nets	A double messenger system to allow ring net to be sent down closed, opened at depth, and then closed again by a second messenger (Plate 7 A)
Porche (1978)	High-speed Multiple Sampler	In french – appears to have 4 nets and one intake. Nets appear to rotate into water flow position to collect sample
Clayton and Pavlou (1978)	Modified Juday (1916) Net To Avoid Surface Chemical Contamination Of Sample.	75 cm diameter cylinder (120 cm length and cone (290 cm length) net (Nitex mesh size not given) with a cylinder skirt 380 cm long to enclose net mesh. Net ring and netting enclosed in nylon utility cloth and tied with a release line that is pulled free after the net is underwater. A messenger used to close net (Plate 7 B, C).
Fukuchi et al. (1979)	NIPR-I Sampler	A cylinder (24 cm x 57.5 cm) contains a motor driven propellor and a flow meter. Water is pushed into a net (20 cm diameter x 50 cm length with 100 m mesh attached to the rear end of the cylinder The system is used to sample under sea ice to depth of 10 m.
Ortner et al. (1979)	Laboratory Silhouette Photography Of Preserved Zooplankton	Sample poured on to a sheet of photographic emulsion and exposed to a flash creating a negative image of the sample that could be counted and measured under a microscope.
Sameoto, Jaroszynski and Fraser (1979, 1980)	BIONESS	100 cm x 100 cm mouth opening with 10 nets. System powered electrically on conducting wire and controlled from surface deck unit. Data logging included depth, roll, pitch, flowmeter revolutions, and temperature, and conductivity. There is also a 1/4 m system. This system has basic design similarities to that of Bé (1962) MPS system (Plate 30 C, D).
Roe and Shale (1979)	Multiple Rectangular Midwater Trawl (RMT 1+8)	A combination multiple plankton and nekton collecting system with three 1-m ² and three 8-m ² with pair of nets opened and closed by acoustic command. Also transmitted acoustically are depth and flow. (A modification of system described by Baker et al., 1973) (Plate 28 B)
Rützler et al. (1980)	Horizontal Plankton Sampler (HOPLASA)	18.5 cm diameter x 40 cm long plexiglass cylinder houses an electric motor and propeller assembly and a flow meter. Attached to the back is a net 80 cm long made with 0.25 mm nylon mesh. The device which creates its own current flow through the net is intended for plankton collection on or near the bottom of coral reefs (Plate 24 C)

Herman and Dauphinee (1980)	Electronic Zooplankton Counter	An electronic detector that used voltage anomalies induced by particle transit through a conductive cell to estimate length and volume of particles. A self- cleaning net concentrated and then channeled
Tungate (1980)	Hiac Particle Size Analyzer	Shipboard or laboratory-based device that employed a collimated light beam and photodiode detector to generate a voltage pulse that was proportional to the cross-sectional area of the target that impinged on the beam. The system counted particles into twelve size classes and could be equipped with different sensors designed to quantify particles within certain size ranges between 1-9000 —m
Posgay and Marak (1980)	MARMAP Bongo Net	A non-opening closing descendant of the McGowan/Brown Bongo net. A pair of circular hoops (61 cm in diameter and 30 cm long) are joined by a central yoke which is clamped to the towing cable. The nets are 61 cm in diameter and have cylindrical section 147 cm long and a conical section 153 cm long. Mesh sizes from 0.1 to 0.5 mm have been used, but normally 0.333 mm is used. A flowmeter is present in each hoop (Plate 2 D. E).
Wishner (1980)	Deep-Tow Net System	Three rectangular mouth opening nets ~ 30 cm wide x 44 cm tall and 130 cm long mounted on a metal framework attached to the bottom of the Deep-Tow Instrument (Spiess et al., 1973). The unobstructed nets were opened/closed by surface command transmitted via conducting cable to a release mechanism (Plate 24 A).
Griffiths et al. (1980)	Collapsible RMT 1+8	System described by Baker (1973) was modified to enable handling off smaller vessels without a crane using 'Kelly's eyes' and chain rather than link wire.
Weikert and John (1981)	Modified MPS	A modified version of the Bé MPS net with a rectangular sampler box 50 cm x 50 cm on a side and 60 cm deep equipped with 5 nets (0.3 mm mesh) each 250 cm long. Nets are opened and closed electronically through conducting cable and pressure is monitored. No flowmeter used (Plate 31 A, B).
Schram et al. (1981)	Neuston Sampler Mini- neuston Net	A framework supports five 50 cm x 20 cm mouth opening rectangular nets each 125 cm long with mesh sizes ranging from 0.150 to 0.500 mm. Frame equipped with a flowmeter is used (Plate 21 D). A similar system, but with three nets as above.
Brown and Cheng (1981)	Manta Net	A rectangular framework 100 cm wide by 20 cm tall with a pair of wings that ride the sea surface and a pair of paravanes to guide the net away from

112

		the ship. Attached to the frame was a Bongo Net (240 cm circumference) with 505 um mesh. A 100 kg weight was used to hold the asymmetrical bridle down below the surface so that the mouth opening was relatively free of towing lines. Equipped with a flow meter (Plate 21 A).
Ortner et al. (1981)	Camera Net System	35 mm still camera with a high-capacity film magazine in front of the cod-end of a conical 70 cm diameter, 0.202 mm mesh plankton net attached to a rigid frame. This system provided in situ silhouette photography of zooplankton as they passed into the cod-end of a plankton net at intervals separated by less than 1 m (Plate 33 C).
Reeve (1981)	Reeve Net	A very large acrylic cylindrical cod-end (30 liters) attached to a simple ring net or a paired net system (with 75 cm diameter nets) to collect fragile gelatinous animals (with 17-liter cod-ends). Also describes a pressure activated mechanism to enable the nets to 'float' up the wire to the surface without being affected by the motion of the vessel (Plate 3 E, F).
Heron (1982)	Free fall Plankton Net	Mouth opening – a modified WP2 cylinder-cone closing net (mesh not specified) which is allowed to free-fall and then is 'strangled' shut and retrieved. (Plate 10C)
Teul and Knauer (1982)	A Cowl for Opening/Closing Plankton Nets	A canvas cowl is attached to the cod-end bucket of a double messenger opening/closing ring net. It is large enough to enclose the net and net ring and the pursing cowl line is released by the first messenger. The second messenger closes the net (Plate 7 D).
Milligan and Riches (1983)	MAFF/Guildline High- speed Samplers	Modified (Lowestoft Sampler (Beverton et al., 1967)–itself a modified Gulf III sampler) which has a 40 cm diameter conical nose cone aperture with 76.6 cm diameter body 275 cm long. A second system has a 20 cm diameter nose cone aperture with a 53.3 cm diameter body that is 275 cm long. These systems have a Guildline CTD sensor unit with oxygen, pH, and digital flowmeter as additional probes with telemetry through a conducting cable. (MAFF stands for Ministry of Agriculture, Fisheries, and Food)
Aksnes and Magnesen (1983)	Modified Juday Net	A pair of Juday nets with 40 cm diameter mouth openings were mounted on a frame 50 cm apart. Mesh of nets 0.18 mm. Towed vertically.
Williams et al. (1983)	Double LHPR	A modified version of the LHPR (Longhurst et al., 1966). An unenclosed Lowestoft Sampler (Beverton et al., 1967), 130 cm high x 92 cm wide x 357 cm long and with a 35.6 cm expanding to 76 cm

Lippincott and Thomas (1983)	Neuston Net	diameter nose cone was used with a recorder box (with 0.28 mm nylon mesh gauze) attached to the cod-end of a main net. A second recorder box was attached to the end of 0.053 mm polyester mesh net. The mouth of this net was attached to a nose cone with 2.6 and 5.1 diameter mouth openings expanding to 7.7 cm. System acoustically (IOS) telemeters depth, flow, and temperature. System also carries a chlorophyll sensor with recorder system. Nose cones of both nets have doors that are shut when system deployed and can be opened remotely. Designed to tow up to 6 kts (Plate 27 A). 128 cm wide x 30 cm tall rectangular mouth opening with 260 cm long net with 0.351 mm nylon mesh. A TSK flowmeter is mounted in the lower portion of the net mouth. Lobster buoy floats
Honjo et al. (1984)	Large Amorphous Aggregates (LAA) Camera	provide buoyancy. Profiling system incorporating a 35 mm camera and a 106 x 106 x 0.1 cm light sheet provided by a pair of strobes and a Fresnel lens. Camera axis orthogonal to plane of light sheet. Sampling rate 0.05 Hz
O'Hara (1984)	O'Hara Automatic Plankton Sampler	Patterned after the CPR, and LHPR, this sampler has two rolls of plankton mesh (0.457 mm Nitex nylon). One roll crosses a tunnel down stream of the inlet through which water is drawn by an 2 HP outboard battery powered motor and is taken up with a second spool. The second roll is also wound up on the take-up spool to sandwich the plankton. The second spool is in a formalin filled chamber. Gauze is stepped into the tunnel to collect plankton being drawn through the sampler. A preset number of flow meter counts determines length of filtering for each sample. A unit can collect 12 samples over a 30 minute period (Plate 32 A)
Kozasa (1984)	Gimbal Ring Zooplankton Sampler	A double gimbaled frame 100 cm tall x 65.5 cm wide supports a ring net 30 cm in diameter. A bridle is attached to the top of the frame and a weight to the bottom so the net mouth is free of obstructions. No description of net length or mesh size given.
Kimmerer (1984)	Improvement For Opening/Closing Plankton Nets	A modification different from that described by Teul and Knauer (1982) to improve performance of double messenger opening/closing net which involves making second bridle and to tow net backwards while deploying. First messenger allows net to reverse 180 degrees to make collection, second messenger closes net. Also described is a
Bone (1986)	Large LHPR	drogue to keep net streaming properly and a flowmeter stop for a GO meter (Plate 7 E). A modified version of the LHPR (Longhurst et al., 1966). A tubular frame 185 cm high x 125 cm wide x 640 cm long and with a 81 cm expanding to 100 cm diameter nose cone was used with a recorder box (with 1.55 mm nylon mesh gauze) attached to the cod-end of a conical net 300 cm long with same mesh. The mouth of the recorder box is equipped with an opening/closing unit which shunts water flowing through the net to the open sea when closed and into the recorder when open. System acoustically (IOS) telemeters depth, flow, and temperature and controls recorder box opening/closing unit. Underwater electronics record temperature, depth, flow, and controls gauze advance. Designed to tow up to 4 kts (Plate 27 B)
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Walker and Davies (1986)	Lowestoft Frame Trawl	advance. Designed to tow up to 4 kts (Flate 27 B). 142 cm x 142 cm rectangular mouth opening trawl with a rigid mouth frame and nets 747.5 cm long of 5.0 cm mesh. Uses a TSK flowmeter converted to a digital counter unit and conducting cable to power depth and temperature sensors. Data recorded on a surface chart recorder. Normally towed at 3 kts. A 100 cm x 100 cm mouth opening trawl with a net length of 475 cm also described. Mainly for small pelagic fish capture. Not opening/closing (Plate 4 F).
Nester (1987)	Horizontal Ichthyoplankton Tow-net System	A 50 cm diameter circular net ring is mounted in a 53 cm x 53 cm rectangular frame. Net is a cylinder- cone with 0.333 mm nylon mesh. Tow bridle attached to spreader bar to keep net opening clear of bridle and depressor attached to bottom of frame. Has two flowmeters one inside net and one outside. Usually towed at 3 kts. Mainly for larval fish. Similar to Blackburn and Keith (1962) system. Not opening/closing.
Macaulay and Daly (1987)	English Umbrella Net	A rectangular net 200 cm on a side and 300 cm long made from 0.22 mm nylon mesh is designed to fit through a hole in an ice flow closed, and open once underneath. A messenger is used to close the mouth opening at a specific depth prior to retrieval though the ice (Plate 11 C).
Herman (1988)	Optical Plankton Counter	3 cm x 22 cm rectangular mouth opening. A parallel beam 2 cm x 2 cm x 22 cm crosses perpendicular to the flow of water through the system. Animals passing through the beam are counted and sized. System used stand-alone or with a net in front or on other collecting systems (pumps

Plummet Net

and nets) as additional sensor (Plates 37 D, E; 38 A. B).

100 cm diameter mouth with a lead weighted net ring and net with 0.571 mm mesh. For downward collecting, the net was lowered by the cod-end to a pre-determined depth and a messenger used to release the cod-end attachment and draw tight a he net (Plate 10 D). fishing, vertical, rectangular mouth ed to two bars that s along parallel m is used to opened close it as it The net ~ 180 cm ariety of mesh 1600 mm Nitex. munication). the attached to the om a shock cord. wo bridles, one ame and the other The net frame ving the second net etrieval is begun. outh opening with e from five sets of ont and fine mesh at esh, 400 cm of 5.1 sh, 300 cm of 1.3 mesh). There are p spreader bar and goes to separate on bottom spreader n transferred to top ain taken by lower 5). **BIONESS**. Uses monitor depth, nction and to of the nets. An resent to log depth, her parameters. (dimensions not 224 cm x 224 cm n long. Tow speeds

		choke collar near the mouth of th Another version of a downward-1 closing plummet net has a 1-m ² to opening with a net that is attached run along a pair of net bar glides sides. A double messenger system the net as it falls to depth and to reaches the bottom of the haul. This in length has been used with a ver- sizes; 0.163 mm, 0.560 mm, and According to Daly (personal com- first messenger releases a bridle a opening net bar under tension from The second messenger releases to attached to the back of the net fr attached to the closing net bar. The assumes a vertical position, allow bar to fall, closing the net, and re-
Enzenhofer and Hume (1989)	A Closing Midwater Trawl	300 cm x 700 cm rectangular mo net 1800 cm in length. Net made mesh with coarse mesh at the fro the back (600 cm of 10.2 cm me cm mesh, 300 cm of 1.9 cm mes cm mesh and 200 cm of 0.3 cm two towing cables one for the to one for the bottom. Each cable g winch. Net lowered with tension so that net is closed. Tension the spreader to open net. Tension ag spreader to close net (Plate 12 B
Dunn et al. (1989, 1993)	OCEAN (Opening Closing Environmental Acoustic Net	Rectangular net design similar to an acoustic telemetry system to r battery voltage, flow, and net fur control the opening and closing o underwater data logger is also pr conductivity, temperature and oth OCEAN system carries four nets given).
	LOCHNESS (Large Opening Closing High- speed Sampling System)	LOCHNESS carries 5 nets with 2 mouth opening $(5-m^2) \times 1400$ cm up to 6 kts (Plate 31 D, E).

Hovekamp (1989);

Daly (personal

communication)

Kršinic (1990)	Adriatic Plankton Sampler	A 50 cm diameter cylindrical sampler sent to depth with the cylinder net (0.25 mm mesh) closed and upside down (cod-end facing upward). A messenger releases the bottom margin of cylinder allowing it to drop open (115 cm length) and at the same time closing half circle doors. A second messenger releases the first support bridle and the sampler turns right side up. Sampler collects about 250 liters of water (Plate 11 A)
Froese et al. (1990); Lenz et al. (1995)	The Ichthyoplankton Recorder (IR): Under Water Cod-end Video System	CCD-Camera with 384 x 256 pixels and 90 mm macro lens as a cod-end unit mounted in a un- encased Gulf III sampler. An LED strobe light (66 nm wavelength) with 50 2.5- μ s flashes per second. System has an induction flowmeter and a sensor package to measure pressure, temperature, conductivity, dissolved oxygen, and light. Video and environmental data telemetered via conducting cable to the ship for recording, processing, and display (Plate 33 A).
Dimmler and Klindt (1990)	New Electronic For The RMT 1+8	This is a PC controlled unit with an underwater electronics unit connected by conducting cable. Nets are opened and closed by command at the surface. Sensors include pressure, temperature, conductivity, tilt-angle of net mouth, flow from two flowmeters and data acquisition rate is 4 times per second. Data processing and display occurs in realtime.
Doherty and Butman (1990); Garland (2000)	Moored, Automated, Serial, Zooplankton Pump (MASZP)	A self-contained pump and plankton collection system based on the LHPR mechanisms which can be deployed on a mooring or bottom tripod. The system is mounted in a metal frame 91 cm in diameter and 200 cm tall with water able to flow into the pump tunnel entrance (5 cm diameter) from all horizontal directions. Two strips of plankton gause (0.1 mm mesh) on supply spools cut across the intake tunnel and are wound onto the take-up spool at discrete intervals while the pump is running. Sample volume measured by pump displacement and pump revolutions. Sampling controlled by battery powered PC controller and data logger. Sampling can be based on time, an external event, or both, and can collect either 40 1000-liter samples or 80 500-liter samples. An electro-magnetic current meter is used with the sampler (Plate 32 C, D).
Sconfietti and Cantonati (1990)	A Neuston Net	A 40 cm diameter net (60 cm long) is attached at the front and rear to a polyurethane float by rods extending down below the float with the top of net about 12 cm below the surface. (Plate 20 F)

Lewis and Heckl (1991)	Moorable, Automated Plankton Sampler	Patterned after the CPR, LHPR and O'Hara (1984) sampler, a series of ten small nets (12.5 cm x 16 cm in diameter and 13 cm in length) made with 0.253 mm Nitex nylon mesh and having a inner collar are sewn into a 20 cm wide vinyl belt. The belt with nets starts on one spool crosses a tunnel down stream of the inlet through which water is drawn by an 2 HP outboard battery powered motor and is taken up with a second spool. The second spool is in a formalin filled chamber. Nets are stepped into the tunnel to collect plankton being drawn through the sampler. An electronics package turns the system on and off and logs flow. Several 'net boxes' can be put in series to increase the number of samples collected (Plate 32 B).
Terazaki (1991)	The Ocean Research Institute Vertical Muliple Plankton Sampler (ORI- VMPS)	100 cm x 100 cm rectangular mouth opening multiple net system that can be equipped with 4 to 10 nets 510 cm long with 0.33 mm nylon mesh. Nets are opened/closed by surface commands down transmitted via conduction cable to an underwater unit (Plate 31 C).
Davis et al. (1992)	The Video Plankton Recorder	A set of four video cameras, strobe light, and underwater electronics package to control underwater environmental sensors and the video system. Unit has a surface control and data logging and image processing system and is attached to the underwater unit by electro-optical conducting cable. System records at 60 fields per second (Plate 34 A- D).
Gorsky et al. (1992)	Underwater Video Profiler (UVP)	Video camera sampling at 25 Hz aimed at a collimated 19.2 x 14.3 x 1.5 cm light sheet that is either continuous or strobed. Orientation of camera orthogonal to light sheet. Internal data recording on Hi-8 video tape (PAL system) with post-processing incorporation a frame-grabber and image processing software (Plate 35 D).
Bergström et al. (1992)	ROV-mounted Video Camera	Color video camera mounted on the front of an ROV aimed at an area defined by a frame. Sample distance along survey transects measured by a flowmeter
Kils (1992)	EcoSCOPE	Pair of optical endoscopes used for observations of zooplankton and fish predators. Illumination from LED arrays or xenon flashes coupled with a CCD.
Dunn et al. (1993).	Autosampling And Recording Instrumental Environmental Sampler (ARIES)	A stretched version of the Lowestoft modified Gulf III (similar to Williams et al., (1983) LHPR frame) was used to mount three sampling systems. The nose cone had a 35.6 cm diameter opening expanding to 76 cm diameter. Instead of an LHPR

		box, a 2000 cm long by 16 cm wide belt was outfitted with 110 6-cm diameter cod-ends with 0.2 mm mesh. A drive motor periodically incremented the belt moving the nets from a feed spool into a position to collect a sample at the back of the net and then onto a take-up spool. Water samples were collected with 60 250- ml bottles mounted in a carousel similar to a conventional rosette sampler. A data logger recorded temperature, conductivity, pressure, flow, and sampling events at rates between 1 second and 60 minutes. User selected plankton and water sampling rates were 1 to 60 minutes. An acoustical telemetry system transmitted depth for realtime monitoring of the system. Towing speed is 4–5 kts (Plate 27 C)
Burd and Thompson (1993)	Rosette Controlled Tucker Trawl system	100 cm x 140 cm rectangular mouth opening frame frame with 7 nets made with 0.33 mm mesh. A rosette release mechanism was used to open and close nets by commands from the ship via conducting cable. The frame carried pressure, temperature, conductivity, transmissometer sensors. Flow past the frame was measured with an ADCP (Plate 30 B).
Motoda (1994)	Modified Norpac Net	45 cm diameter circular mouth opening with cylinder 65 cm and 130 cm cone mesh (0.35 mm). Equipped with a flowmeter. Also there is a description of a self-closing cod-end box which has two net bags to collect the catch. The net is sent down vertically and when towed horizontally, a counter balance weight opens one net bag. When the net is brought to the surface vertically, the weight shifts closing the one and opening the other net bag (Plate 25 B).
Wiebe (1994); Greene (1998)	DBAD-MOCNESS	A $1-m^2$ MOCNESS was equipped with a dual-beam echosounder and dual-axis training mechanism for the transducers. An electro-optical cable was used data telemetry (Plate 40 E).
Holliday (1995)	TAPS	The Tracor Acoustical Profiling System, a four transducer array operating at frequencies 265 kHz, 420 kHz, 1.1 MHz, and 3 MHz that provides backscattering data at a range of 2-3 m. (Plate 40 B,C)
Jaffeet al. (1995)	Fish TV (FTV)	A realtime 3D imaging sonar consisting of two groups of eight rectangular transducers operated at 445 kHz with one set transmitting and the other receiving. 8 x 8 x 512 spatial positions are imaged as fast as five times per second; depth of field is 3.8 m. The FTV was deployed on a Phantom IV ROV

Chacklay Ir. at al	CUEES With Machine	and was able to track individuals the size of euphausiids (Plate 40 A).
(1997)	Vision System	illuminated by in-line strobe to image pre- concentrated samples of eggs flowing through seawater feed. Machine vision to detect, identify and count eggs.
Jaffe et al. (1998)	Optical-Acoustic Submersible Imaging System (OASIS)	A 3D acoustical imaging system (Fish TV – 445 kHz), a CCD camera (1524 x 1024 pixel resolution) with strobe illumination, and a pair of current meters are mounted in frame. When the sonar system (creating an $8.8,512$ image at a maximum of 4 frames per second) detects an object, the camera takes a picture of it (Plate 40 D).
Nash et al. (1998)	Gulf VII/Pro Net And Maff/Guildline High- Speed Samplers.	An un-encased frame 275 cm long and 76 cm in diameter with a conical nose cone. (There are smaller and larger variants of the frame and nose cone). Standard mouth opening is 40 cm diameter. Pronet is a conical net with 0.28 mm nylon mesh is 230 cm long. Both systems are equipped with a pressure, temperature, conductivity sensor, and flowmetering package for transmission to ship via conducting cable or logged internally. Other environmental sensors can be accommodated. Data scanned/recorded twice per second. Routinely towed at 5 kts and up to 7 kts (Plate 17 C).
Kim and Mullineaux (1998)	Wishner Deep-Tow Net System Adapted For Use on Alvin	Three rectangular mouth opening nets \sim 30 cm wide x 44 cm tall and 130 cm long mounted on a metal framework attached to the front instrument basket of DSRV Alvin. Sequential opening and closing of the nets done by the pilot using the manipulator arm.
Tiselius (1998)	In situ Video Camera	Low cost single camera video system illuminated by a synchronized strobe with optional on-board CTD. Data telemetered to surface via conductive cable (Plate 33 B).
Herman et al. (1998)	Laser Optical Plankton Counter (LOPC)	Optical plankton counter utilizing a laser sheet, high-speed 1MHz 12 bit analog-digital detector capable of collecting particle size and shape data for zooplankton down to 50 μ m (Plate 38 C, D).
Katz et al. (1999)	Holocamera	An in-situ, internally-recording in-line holographic camera that records on a film emulsion (Plate 36A, B, C).
Kocak et al. (1999)	ISIT	Intensified Silicon-Intensified Target (ISIT) video camera (Plate 36 B, E).
Samson et al., (2001)	Shadowed Image Particle Profiling and Evaluation Recorder (SIPPER)	Laser line-scanning system designed to image and quantify large and small zooplankton at high resolutions. Mounted on towed High Resolution

		Sampler (HRS) and AUV vehicles (Plate 35 C).
Benfield (2000)	Zooplankton Visualization And Imaging System	Zooplankton profiling system equipped with a 2048 x 2048 pixel digital camera, structured strobed light
	(ZOOVIS)	sheet and CTD linked to surface acquisition
		hardware and software via an electro-optical cable (Plate 35 B).
Watson et al. (2000)	HOLOCAM	An in situ holographic system that can collect on-
		or off-axis holograms of volumes of water up to 10^5 cm ³ (Plate 36 D).
Strickler and Hwang	In situ CritterCam	Video recorder utilizing Schlieren optics and spatial
(2000)		matched filtering for observation of zooplankton behavior.
Wiebe et al. (1999;	BIOMAPER-II	An integrated instrument platform for coupled
2002)		biological and physical measurements that has a 5
		trequency split-beam acoustic system, a VPR
		bio-Ontical system. An electro-ontical towing cable
		is used for two-way data communications and the
		system can be towyo'd to depths of 300 m (Plate
		41 A-E).

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