Zooplankton sampling

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In this series:

Zooplankton sampling

Preface

Ever since the early days of plankton research, estimating the abundance of plankton organisms has been one of the most crucial and difficult problems. While the need was felt to compare indices of the abundance of certain groups of plankton organisms or of total plankton biomass and to study their variations in space and time, accuracy of those attempts was seriously hampered both by patchiness in plankton distribution and by uncertainties with regard to efficiency and selectivity of the various types of plankton gear. The increasing number of international expeditions with ships of various nations during recent years called for uniformity in sampling devices and techniques. The introduction of the Indian Ocean Standard Net for the International Indian Ocean Expedition was a very successful step in that direction (Currie, 1963).

Following its own earlier attempts (Künné, 1929, 1933) the International Council for the Exploration of the Sea (ICES) set up in 1961 a sub-committee to look into the possibilities of standardization of zooplankton sampling. At about the same time the Scientific Committee on Oceanic Research (SCOR) of the International Council of Scientific Unions and the United States National Academy of Sciences Committee on Oceanography (NASCO) became engaged in similar activities. A joint working group of scientists nominated by ICES, SCOR and Unesco was then established in January 1964, consisting of four small working parties each of them dealing with zooplankton organisms of a certain size range, thus splitting the zooplankton into four groups which are more or less uniform with regard to the sampling devices employed for their collection. Under the over-all chairmanship of Dr. J. H. Fraser (Aberdeen) the four working parties produced reports and recommendations on the use of nets and other devices already in existence, and in certain cases they also proposed the introduction of new nets. A preliminary report of the working group and its four working parties was published in SCOR *Proceedings*, Vol. 2, 1966. Dr. Fraser has also published in 1966 a brief account of the activities of the group.

In the course of the discussions, particularly within Working Party 3 on larger zooplankton, the need was felt for an intensive survey of the present state of knowledge regarding the technological aspects of plankton nets, their hydrodynamics, efficiency, and selectivity. The sponsoring organizations of the working group accepted therefore the invitation of the Australian Commonwealth Scientific and

Industrial Research Organization to hold a Symposium on the Hydrodynamics of Zooplankton Sampling in Sydney with Mr. D. J. Tranter as chairman. Thanks to financial contributions coming from the three co-sponsoring organizations and from national sources, world-wide participation to the symposium was ensured and a considerable number of papers on various aspects of sampling methodology were presented.

Instead of publishing these papers in full, it was decided to bring together the results of the papers, and the discussions on them, as well as relevant parts of the reports of the four working parties, into a manual consisting of review papers, each dealing with a major topic of sampling methodology. Unesco agreed to publish the manual in its series Monographs on Oceanographic Methodology.

Unesco expresses its thanks and appreciation to Mr. D. J. Tranter as editor of 'Reviews on Zooplankton Sampling Methods' and to the authors of the review papers for their valuable and speedy collaboration in preparing Part I of this volume, and to Dr. J. H. Fraser for editing the report of the Working Group on Standardization of Zooplankton Sampling Methods at Sea (Part II). It is hoped that this volume will serve as a guide to plankton workers in many parts of the world and also as the basis for further development of more reliable methods for estimating zooplankton abundance in the sea.

The scientific opinions expressed in the review papers are those of the authors and should not be interpreted as the views of Unesco.

Contents

Part I

Reviews on zooplankton sampling methods

Edited by D. J. Tranter

This series of reviews had its origin in the Symposium on the Hydrodynamics of Zooplankton Sampling, held at Sydney in February 1966. By then, the major problems of sampling methodology had been identified, and the symposium discussions were centred about those questions. Dr. G. Hempel, then of the Unesco Office of Oceanography, proposed that a series of reviews be written by participants at the symposium and be published as a Unesco Monograph on Oceanographic Methodology.

The various authors have collaborated at all stages of the preparation of these reviews and have sought the advice and criticism of a wider body of planktologists. This assistance is gratefully acknowledged, as is also the support of ICES, SCOR, and Unesco.

An attempt has been made to adopt a uniform terminology (see page 123). This has often had an arbitrary basis, the responsibility for which rests with the editor rather than with the authors. The references cited are to be found in the bibliography (pages 126-44) which contains also other references pertinent to plankton sampling. Asterisked (*) references denote information presented at the Sydney Symposium.

D. J. TRANTER

The history of plankton sampling

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This very brief reference to history is intended to show how plankton sampling has been evolving from its early beginnings towards more accurate methods, what problems have arisen, and some attempts to solve them. It is not intended as a survey of all these attempts, nor is it a list of methods as this can be obtained from the bibliography. For more detailed reviews of the earlier methods see Jenkins (190 1), Dakin (1908), Steuer (1911), and Künné (1933). More recent reviews are those by Linger (1960), on macroplankton methods, and Omaly (1966). The methods are

still very much in the process of evolution and we can expect many new
developments
in the future.

Plankton sampling by nets started less than 150 years ago and it is therefore very much in its infancy compared, for example, to fishing operations. In 1828 a surgeon, Dr. J. Vaughan Thompson, made a plankton net to sample crab and barnacle larvae. Darwin used a small net on the *Beagle,* and in 1844 Müller used a small-meshed conical net to catch a host of minute creatures, and this resulted in a great deal of publicity. His net was just a simple cone attached to a rigid ring which could be operated by hand from a pole, or it could be fixed by bridles to a single towing warp. Such simple nets (Fig. 1*a*) can end by continuing the mesh to a pointed tip or they can end in a detachable jar, bucket, or bag.

When one considers the vast wealth of unknown life revealed by these simple methods, and that this apparatus gave, for all who used it, a life's work in describing the abundance of new species, both plants and animals, it is not really surprising that further development of the gear was at first slow. This simple tool was the foundation of our knowledge of plankton, and without the laborious taxonomic background given to us by the last two or three generations, we could not have progressed along the more sophisticated lines we are thinking about today. The very simplicity of this gear has such advantages that it will probably never cease to be used.

Plankton was soon realized to be more than a systematist's treasure trove, and because it had such significance in the productivity of the sea and the food chains therein, planktologists wanted to know how to relate the number of organisms found to the volume of water filtered, their distribution in depth, space and time, and their daily, seasonal, and annual variations. Development of the gear was gradual to begin with but its tempo increased, partly because of the increased
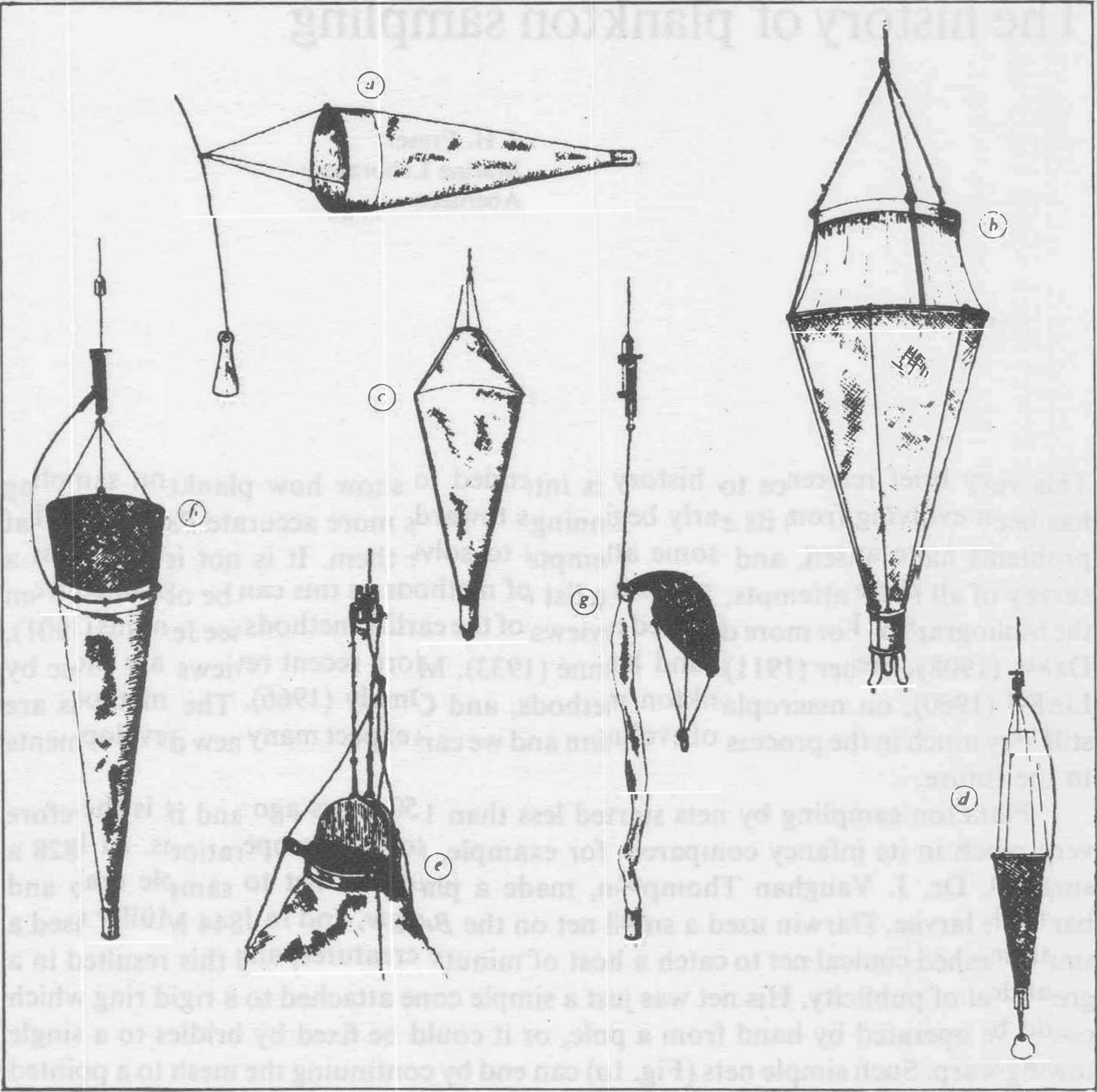
Figure 1
a   Simple conical tow-net.
b   Hensen net.
c   Apstein net.
d   Juday net.
e   Apstein net with semi-circular closing lids.
f   Nansen closing net open.
g   Nansen net closed.

realization of the importance of quantitative work, and partly because of the increase in the number of people studying the subject.

The desire for so much comprehensive quantitative knowledge brought with it a whole host of sampling problems. Questions arose concerning mesh size and material, the volume of water filtered, closing devices, measurement of the depth of sampling, speed of tow, avoidance, and escapement. Each of these problems has been considered and reconsidered for a hundred years and we are still not satisfied. However, new techniques of underwater diving and photography, and the use of test tanks, have given us new tools and we are now stepping away from

the ideas of gadget-minded biologists and asking more advice from the acknowledged experts in hydrodynamics and engineering. This is giving the evolution of plankton sampling a new impetus.

MESH SIZE AND MATERIAL

Plankton varies from about 2 μ to 1 m in diameter, for which size range there is no one mesh size remotely suitable—nor even for a reduced range of 200 μ to 10 mm. A range is needed, both in mesh size and in amount of water filtered, and so samplers vary from water-bottles to young fish trawls. One difficulty has been that organisms smaller than a given mesh size go through the meshes in an unknown and variable quantity dependent on their shape, protuberances, activity, elasticity, and the amount of clogging. How much easier it would be to sample plankton if it consisted only of smooth spherical balls!

The smallest organisms are collected with a net of the smallest possible mesh width, or on a filter using a sample from a water-bottle. There will always be losses at the lower end of the size range, and clogging problems. For slightly larger organisms No. 3 gauze (approximately 60 meshes to the inch, mesh width approximately 0.25 mm) became common practice by tradition—but is it the best? Used in a big net, filtering enough water to sample the relatively scarcer but bigger organisms of approximately 3 mm or more, this gauze gives a sample so overburdened with micro-plankton that it is difficult to sort out the ones required. The same principle applies to the next largest series, and so on. One needs to filter relatively small amounts of water through a fine gauze, more water through a medium gauze, and a vast quantity through a coarse gauze. The material used, to be satisfactory, must have clear-cut meshes of constant size, and in general the larger the ratio of area of mesh aperture to the area of the strands used the better—subject to adequate strength, which in turn depends on the support given to each strand, and on the speed of tow. The quantities of material used for plankton sampling are relatively small so that costs can only be kept reasonable by using material already being produced for commercial purposes. Bolting silk, manufactured for sifting flour, became generally adopted, but it suffers from two major faults: it can shrink and it can rot. Synthetic fibres such as nylon, perlon, etc., are not so susceptible to these faults and they are becoming more widely used now. The development of such fibres with a variety of characteristics of strength, flexibility, elasticity, etc., has become an important influence in the evolution of plankton sampling.

The method of extracting the catch from the net has varied considerably. Where the catch was not meant to be maintained alive, the simple continuation of the net to a cod-end was a reasonably satisfactory method for small nets. In larger nets it was more convenient to have the cod-end in the form of a detachable bag, and this is still regarded as satisfactory for many purposes. However, to maintain the catch in as good a condition as possible, the bag is replaced by a detachable bucket in which the catch is retained in a limited amount of sea-water. The catch could be run off through a small tap—which is easily clogged—or the bucket can

be removed and the catch tipped out. The amount of water retained in the bucket depends on the siting of gauze filter windows. As these readily clog in areas where the plankton is rich, many varieties of bucket have been invented. Permanent gauze windows need frequent thorough cleaning and replaceable windows have distinct advantages. In one design (Tregouboff and Rose, 1957) these are fitted to the ends of projections near the top of the bucket.

VOLUME FILTERED

One of the first essentials in quantitative plankton sampling was to know the volume of water filtered. It might be better, even now, to use the word 'guess' instead of 'know', though the guess-work has vastly improved from the original simple calculations based on length of tow and area of mouth. Clogging of the meshes introduces an error into this calculation, and reduces the effective mesh size so that a smaller and smaller size range of plankton is retained as clogging continues. One of the earliest responses was to increase the amount of filtering area—with its attendant increased difficulties of handling, and extricating the catch. An alternative was to reduce the area of the mouth by a non-filtering cone as Hensen (1895) did (Fig. 1b). Apstein truncated his cone even further (Fig. 1c), and Juday (1916) made his cone about the same size and taper as the net itself (Fig. 1d). All these gave improvements but the answer was still guess-work, particularly because the filtration efficiency depended on an unknown variable factor: clogging.

The need for flowmeters became evident. These are in the process of evolution, having developed from the earliest designs of Nansen (1915) and Harvey (1934) to the sophisticated instruments of today (see Chapter 6). The main lines of advance have been in reducing fragility without interfering with free-running, and in recording depth together with volume filtered (Currie and Foxton, 1957). The earlier results were improvements on guess-work rather than accurate measurements. Later work showed that the siting of the meter was critical. If one encloses the whole sampling apparatus inside a container, as in the Gulf III (Fig. 2a; Gehringer, 1952), and measures the outflow beyond the net, a more accurate register might be expected to be given. However, the best site for the meter must be based on a study of the flow patterns, which may not be evenly distributed even in the tail.

The accuracy of measuring volume filtered has been determined by comparison with pump samples (Gibbons and Fraser, 1937b; Barnes, 1949a; Aron, 1958b; O'Connell and Leong, 1963). The water can be measured either on the deck of the ship—which means complicated piping if anything other than very small volumes is required—or in situ using a submersible pump, with its electrical hazards. It is not known how well the active organisms avoid the currents produced at the mouth of the pump. Avoidance is further complicated by the rise and fall due to unpredictable movement of the ship at the surface.
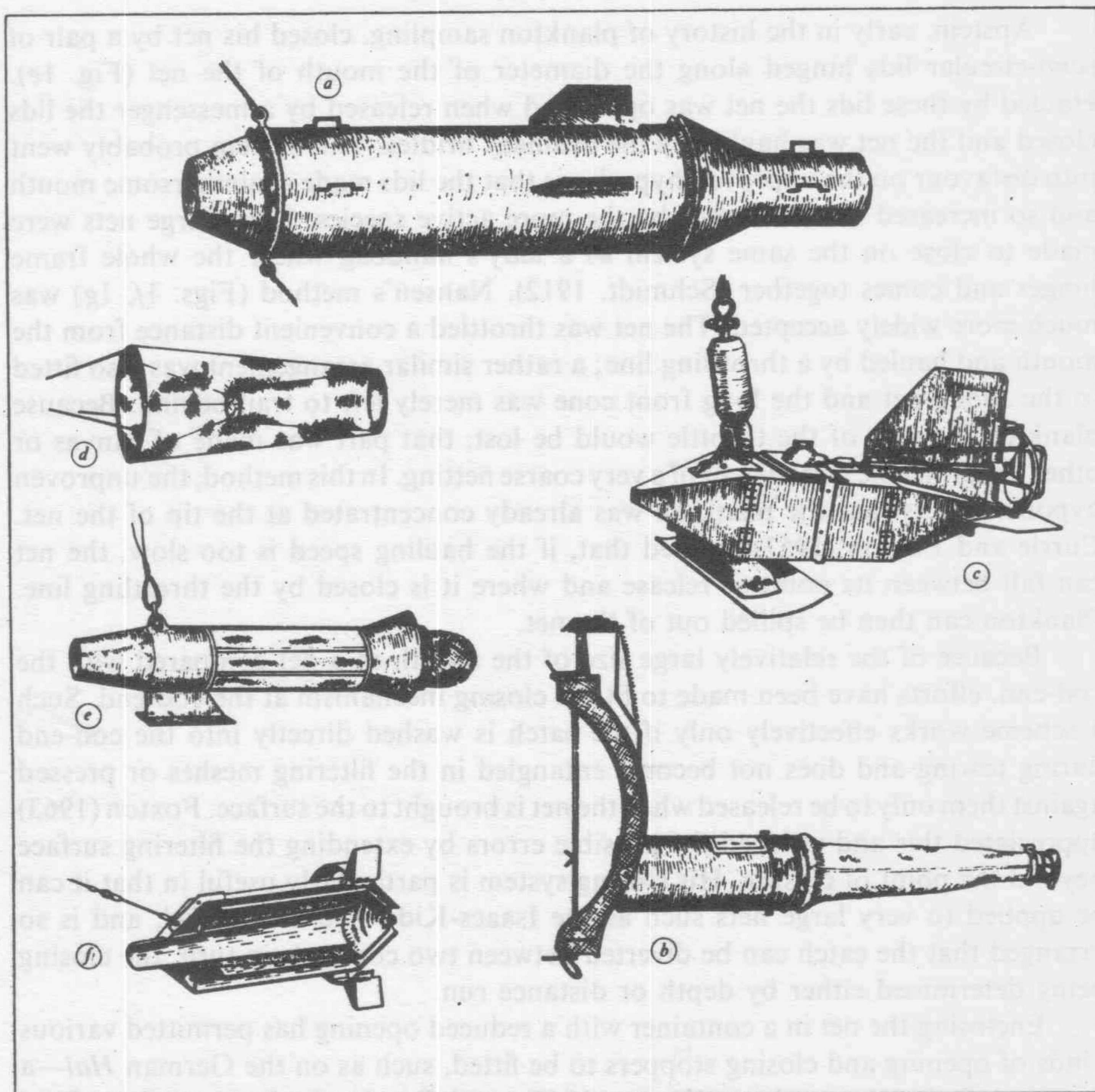
Figure 2
a Gulf III sampler.
b Clarke-Bumpus sampler.
c Hardy continuous plankton recorder.
d Sheard high-speed sampler.
e Icelandic plankton sampler.
f Clarke Jet net (section).

CLOSING NETS

Samples are frequently taken vertically to give a measure of the plankton under one square metre of surface. Where the depth is insufficient for a good sample, an oblique haul, which is merely an extended vertical haul, is used. The more extended the haul the less serious will be the effect of patchiness, though it is never completely removed. Because biologists wanted to sample the strata in which they were interested without getting the catches contaminated from other layers, they invented closing nets in all sorts of patterns. Nets descending tail first should not collect plankton on the way down, and they can therefore be left open during descent and closed only after hauling the required distance.

Apstein, early in the history of plankton sampling, closed his net by a pair of semi-circular lids hinged along the diameter of the mouth of the net (Fig. 1e). Hauled by these lids the net was open, and when released by a messenger the lids closed and the net was hauled by the ordinary bridles. This system probably went into disfavour on the unproven hypothesis that the lids made a cumbersome mouth and so increased the avoidance by the more active species. Some large nets were made to close on the same system as a lady's handbag where the whole frame hinges and comes together (Schmidt, 1912). Nansen's method (Figs. 1f, 1g) was much more widely accepted. The net was throttled a convenient distance from the mouth and hauled by a throttling line; a rather similar arrangement was also fitted to the Juday net and the long front cone was merely left to trail behind. Because plankton in front of the throttle would be lost, that part was made of canvas or other impermeable material, or of a very coarse netting. In this method, the unproven hypothesis was that the plankton was already concentrated at the tip of the net. Currie and Foxton (1957) showed that, if the hauling speed is too slow, the net can fall between its point of release and where it is closed by the throttling line. Plankton can then be spilled out of the net.

Because of the relatively large size of the mouth of a net compared with the cod-end, efforts have been made to fit the closing mechanism at the cod-end. Such a scheme works effectively only if the catch is washed directly into the cod-end during towing and does not become entangled in the filtering meshes or pressed against them only to be released when the net is brought to the surface. Foxton (1963) appreciated this and reduced the possible errors by extending the filtering surface beyond the point of closure. His closing system is particularly useful in that it can be applied to very large nets such as the Isaacs-Kidd midwater trawl, and is so arranged that the catch can be diverted between two cod-ends in turn, the closing being determined either by depth or distance run.

Enclosing the net in a container with a reduced opening has permitted various kinds of opening and closing stoppers to be fitted, such as on the German *Hai*—a modified Gulf III sampler—(Kinzer, 1962), and Bary's plankton catcher (Bary *et al.*, 1958). Before these developments, Clarke and Bumpus built their quantitative net (Fig. 2b) in which the canvas cylinder was replaced by a metal one into which the closing disc, a rotating butterfly valve, is fitted and operated by a messenger through a rather large external frame. This sampler is considered too small by a number of workers and larger variations have been introduced (Paquette, Scott and Sund, 1961).

To sample the whole vertical column by single closing nets meant taking a series of hauls. This is time-consuming and subject to the additional error introduced by ship's drift during the time interval. This led to the development of multi-depth sampling equipment, notably the Bé net (Bé, 1962a) and Motoda's design (Motoda, 1963), to take several discrete samples at one haul. A parallel evolution of equipment to sample in horizontal space, where distances to be traversed are so much greater, also occurred. The most noteworthy of these is undoubtedly the Hardy continuous plankton recorder (Hardy, 1936a, 1939; Glover, 1962) shown in Figure 2c; this takes a continuous ribbon of plankton over set distances in an instrument designed to be towed by commercial ships. Originally designed to operate at 10 m below

the surface, this instrument is in the process of further evolution. Longhurst *et al.* (1966) have developed a sampling system using the Hardy continuous recorder principle, but taking serial samples instead of a continuous ribbon, and Williamson (1963) has designed a simpler and lighter instrument for taking a series of discrete samples from a small research vessel.

The fact that there are so many designs is an indication that none of those yet produced is really 100 per cent satisfactory.

DEPTH OF SAMPLING

How to find out when the net has reached a desired depth is a problem that has its own history of development. Sometimes it does not matter within rather loose limits but sometimes it matters very much indeed. For 'vertical' tows it is simple to measure the length of wire out, but usually there is a drift of one sort or another and the wire is not vertical. Its angle can be measured and an allowance made for this, but we can only guess the angle of the wire we cannot see. Similarly, with horizontal or oblique hauls, the wire angle above the surface can be measured but the angle the wire assumes below water may be very different.

Often in the past nets have been operated at guess-work depths, and probably many will continue to be so operated in the future. These remarks do not apply to nets operating on contact with the sea floor (Bossanyi, 1951; Wickstead, 1953; Clutter, 1965), nor to surface nets like David's neuston net (David, 1965).

At midwater level the development of suitable techniques has continued along three lines:

1. From the Kelvin tube, which gives the maximum depth, to the modern depth flowmeter which produces a picture of the track of the net. This information is available only after the net has been retrieved.
2. Telemetering systems which pass back the data to the ship either electrically through a cored cable or by sound impulses transmitted through the water and picked up by a towed microphone. When the correct depth is reached the opening and closing system can be operated electrically from the ship (Van Cleve, 1937), or by using sound at controlled frequency to initiate triggering mechanisms.
3. Apparatus which opens and closes the gear at predetermined depths such as Yentsch's pressure-actuated pistons which cut various thicknesses of wire (Yentsch, Grice and Hart, 1962), or Rose's electromagnetic devices operated by preset manometers (Rose, 1948). The latter method uses watertight batteries and seems very cumbersome.

SPEED OF TOW, AVOIDANCE, AND ESCAPEMENT

Speed of tow affects the composition of the catch by changing the avoidance and escapement (see Chapters 4 and 5). In the past, the speed of tow has usually been a compromise between the desired speed and the strain which the gear can withstand.

One way to permit faster hauls is to reduce the size of the mouth opening. For many years now the Hardy continuous plankton recorder (Fig. 2c) and the plankton indicator (Glover, 1961) have been successful at the normal speeds of commercial ships and fishing vessels. Because they have only a small entrance, and a small, well-supported filtering area, they have given very successful results, even with quite large organisms like euphausiids. The Sheard net (Sheard, 1941) was a high-speed sampler made by bringing back the open cod-end of the net towards the mouth (Fig. 2d). The ability of the net to withstand the high towing speeds was in part due to the double support given to the fibres.

Turbulence in front of the net, created by the towing bridles, can be avoided by towing from the top of the net and attaching a paravane or depressor below, as with the Hardy plankton indicator and continuous recorder, the Gulf III (Gehringer, 1952) and its modifications, the Bary catcher (Bary et al., 1958) and the Jet net (Clarke, 1964).

A paravane net is also towed from the top only, but its mouth is not kept at right angles to the direction of tow and as we do not really know its angle we cannot calculate the effective mouth area. With the modern tendency to enclose the net in a rigid outer case, the water flow over the tube itself will tend to keep the mouth opening properly opposed. Such a sampler can also be fitted with stabilizing fins, although these have to be quite large to be effective. With a rigid outer casing the net can be better supported internally and, because it is protected, a metal gauze can be used. This does not shrink or loosen its meshes though it does clog. High-speed nets now tend to be mostly of the enclosed type and as a rule they are easier to handle than the free type, and easier to monitor. High-speed sampling in its simplest form is probably best illustrated by the Icelandic plankton sampler (Fig. 2e). However, this takes quite a small sample and, although excellent for certain purposes, has not yet found general favour.

The design of these nets is going through a stage of evolution and still leaves a lot to be desired in removing the guess-work, especially with respect to filtration efficiency, and ensuring the smooth passage of water through the whole of the filtering area. The Jet net (Clarke, 1964) is an advance along these lines, although the ease of handling and removal of the sample could be improved. This net is shown in Figure 2f.

We have come a long way since the days of Dr. Vaughan Thompson and Johannes Müller, but there are a great number of problems yet to solve. Solving them takes time and money and it must be remembered that some laboratories have less resources than others, not only for designing and testing but also for purchase, use, and maintenance of costly equipment. Biologists have tried to be as economical as possible in the design of their equipment, but it is now time for more consideration to be given to comparing the relative expense of more efficient sampling gear compared with running costs of ships, laboratories, and the salaries of scientific staff.

I will end this chapter with a quotation from the recent paper of Aron, Ahlstrom, Bé, Bary, and Clarke (1965): 'Problems associated with variation of time and space among pelagic organisms are already difficult enough to evaluate without imposing additional complexity through the inadequate understanding of the sampling tools.'

2

Plankton gauze

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INTRODUCTION

The gauze used in plankton nets influences not only the size of the plankton caught, but also filtration efficiency, drag, clogging, mesh velocity, and the condition of the catch. There are few published works examining the properties of plankton gauze (Kofoid, 1897b; Wiborg, 1948; Saville, 1958) but the recent results of Hagmeier[*][1] and Heron[*] are relevant to this question.

CHARACTERISTICS OF PLANKTON GAUZE

For effective sampling, plankton gauze should have the following properties.

The meshes should be square and the mesh aperture uniform. The material of the strands should be stiff enough to resist bending or stretching, but flexible enough to allow self-cleaning action (see Chapter 3). The nature of the weave should prevent strands from sliding out of place and should prevent the meshes from distorting diagonally. The porosity should not change when the net is immersed in sea-water. The gauze should resist clogging and allow complete removal of material after use. The material of the strand should not abrade easily. It should resist degradation by sunlight and by chemicals used in cleaning.

The gauzes used in plankton nets are almost exclusively those developed for flour milling and screen printing. They are usually made of nylon or silk. Less commonly used materials are polyesters and the polyamide perlon. General industrial screening gauzes, made of monel metal alloy or stainless steel, are used for rigid nets. Metal and most synthetic gauzes have monofilament strands. Silk and some nylon gauzes have multifilament strands.

Construction

Both the warp and the weft of 'plain weave' (Fig. 1a) are single strands. The weft of 'locking weave' (Figs. 1b and 1c) is usually a single strand, while in the warp double and single strands alternate. There are two types of locking weave. In the monofilament type (Fig. 1b), the warp has double strands alternating in direction

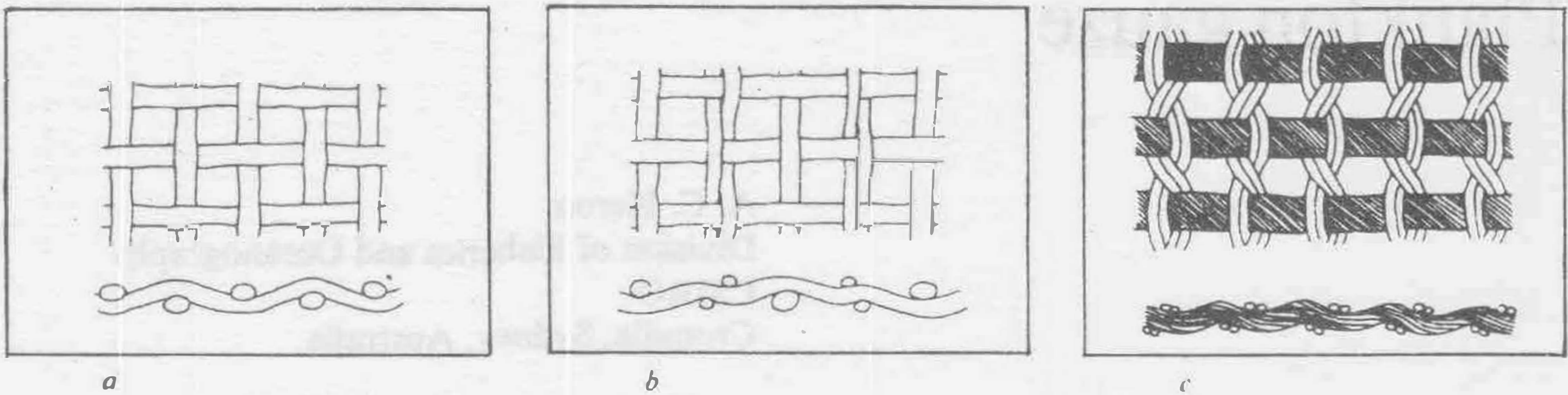1. Asterisked (*) references denote information presented at the Sydney Symposium.

Figure 1

→ weft direction	Major types of weave used in plankton gauzes.
↑ warp direction	Plan views and vertical sections.
	a Plain weave.
	b Simple locking weave—monofilament.
	c Twist locking weave—multifilament.

in the vertical plane. This locks the weft strands from moving along the warp. In the multifilament type (Fig. 1*c*), the warp has double strands which cross each other and alternate on each side of the weft strands ('twist' weave).

Mesh width

The mesh width is the most important measurement affecting the size selection of plankton. Definitions of mesh width and porosity, the other important measurement affecting size selection of plankton, are given in the Terminology of this review (page 123). The specification 'meshes per inch' is of limited usefulness, and should be used only as a supplement to mesh width.

Table 1 and Figure 2 show that some materials vary widely in mesh width and shape. The more widely spaced are the peaks for warp and weft measurements (Fig. 2), the more rectangular is the shape of the hole.

TABLE 1. Comparison of measurements of mesh width with manufacturers' specifications (sample size: 100 meshes)

Brand	Mesh type	Mesh width (μ)		
		Manufacturer	Sample mean	Standard deviation
Nytal 7P[1]	Nylon monofilament, plain	200	197	32
Nytal 7xxx[1]	Nylon monofilament, plain	200	187	45
St. Martins 7N[2]	Nylon monofilament, plain	190	191	22
Fuji 7Nxxx[3]	Nylon monofilament, locking	193	195	34
Nytal 7[1]	Nylon monofilament, locking	200	188	36
Nitex 202[4]	Nylon monofilament, locking	202	199	20
St. Martins 7N[2]	Nylon multifilament, twist	195	186	39
Estal Mono P.E.[1]	Nylon monofilament, plain	200	210	22
Monodur[5]	Perlon monofilament, plain	200	224	69
Pylene[3]	Polyethylene monofilament, plain	202	220	169

1. Swiss Silk Bolting Cloth Manufacturing Co. Ltd., 9425 Thal, St. Gallen, Switzerland.
2. Henry Simon (Australia) Ltd., Simon House, Francis Street, Glebe, N.S.W., Australia. Henry Simon Ltd., Cheadle Heath, Stockport, England.
3. Nippon-Nakano Bolting Cloth Co. Ltd., Tokyo, Yofuku-Kaikan Building, Tokyo, Japan.
4. Tobler, Ernst & Traber, Inc., 71 Murray Street, New York 7, N.Y., U.S.A.
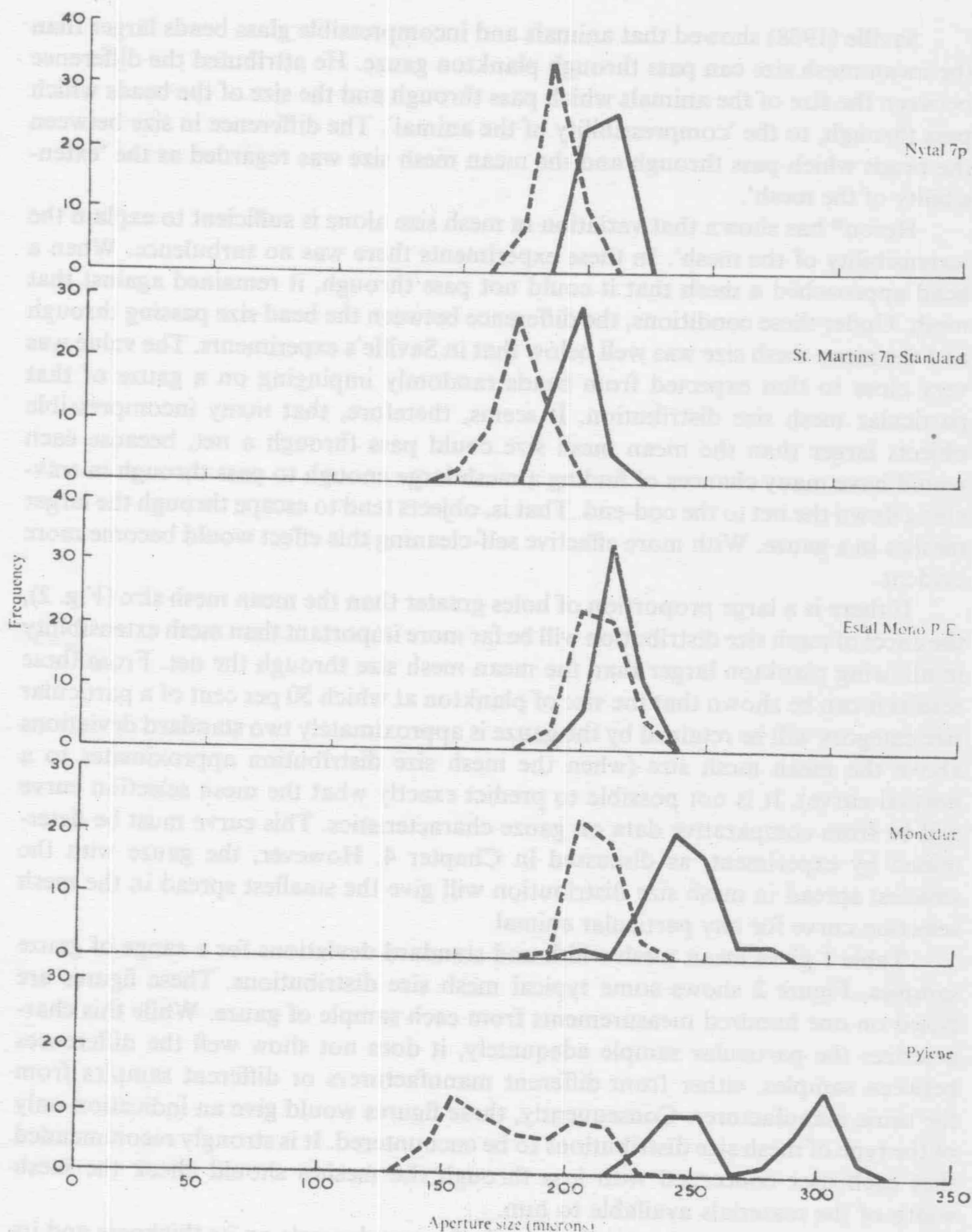5. Vereinigte Seidenwebereien A.G., 415 Krefeld, Federal Republic of Germany.

Figure 2
Mesh width measurements in some plankton gauzes
—————— warp to warp
- - - - - weft to weft

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Saville (1958) showed that animals and incompressible glass beads larger than the mean mesh size can pass through plankton gauze. He attributed the difference between the size of the animals which pass through and the size of the beads which pass through, to the 'compressibility of the animal'. The difference in size between the beads which pass through and the mean mesh size was regarded as the 'extensibility of the mesh'.

Heron* has shown that variation in mesh size alone is sufficient to explain the 'extensibility of the mesh'. In these experiments there was no turbulence. When a bead approached a mesh that it could not pass through, it remained against that mesh. Under these conditions, the difference between the bead size passing through and the mean mesh size was well below that in Saville's experiments. The value was very close to that expected from beads randomly impinging on a gauze of that particular mesh size distribution. It seems, therefore, that many incompressible objects larger than the mean mesh size could pass through a net, because each would have many chances of finding a mesh large enough to pass through in travelling down the net to the cod-end. That is, objects tend to escape through the larger meshes in a gauze. With more effective self-cleaning this effect would become more evident.

If there is a large proportion of holes greater than the mean mesh size (Fig. 2), the effect of mesh size distribution will be far more important than mesh extensibility in allowing plankton larger than the mean mesh size through the net. From these results it can be shown that the size of plankton at which 50 per cent of a particular size category will be retained by the gauze is approximately two standard deviations above the mean mesh size (when the mesh size distribution approximates to a normal curve). It is not possible to predict exactly what the mesh selection curve will be from comparative data on gauze characteristics. This curve must be determined by experiment, as discussed in Chapter 4. However, the gauze with the smallest spread in mesh size distribution will give the smallest spread in the mesh selection curve for any particular animal.

Table 1 gives mean mesh width and standard deviations for a range of gauze samples. Figure 2 shows some typical mesh size distributions. These figures are based on one hundred measurements from each sample of gauze. While this characterizes the particular sample adequately, it does not show well the differences between samples, either from different manufacturers or different samples from the same manufacturer. Consequently, these figures would give an indication only of the type of mesh size distributions to be encountered. It is strongly recommended that each user concerned with loss through the meshes should check the mesh width of the materials available to him.

The distortion resistance of a strand of gauze depends on its thickness and its chemical composition. A single *strand* of silk has a 50 per cent greater extension, at low loads, than a strand of nylon (Heron*). However, the linear extension of silk *gauze* at the same load is only 5-10 per cent greater than nylon gauze. This difference might occur because much of the extension of silk, at a given load, is due to the straightening of the crimps in the strand (a bending process). When the crimps cannot be straightened, as in woven gauze, the load is applied to the material of the strand itself (an elongation process). Monofilament 'plain weave' nylon shows

a 0-4 per cent linear expansion of mesh width at mesh velocities up to 1 knot (Heron*). Polyester, some polyamides, and nylon with thicker strands, are all stiffer than the nylon used in this experiment. It seems therefore that, except for silk, all the materials and strand thicknesses now in common use are stiff enough to resist serious distortion, providing they are woven suitably.

The distortion resistance of the mesh depends on the type of weave. 'Plain weave' locks strands from movement in both directions, while 'locking weave' monofilament locks strands from movement in only one direction. In 'plain weave' (Fig. 1a) as the weft passes alternately under and over the warp, it changes direction sharply. It engages the warp so tightly that depressions are formed in the surface of each strand. These depressions are superimposed on the normal crimps set in the strand. In 'simple locking weave—monofilament' (Fig. 1b), the weft strand passes under a single warp strand, between the next pair of warp strands, and then over the next single warp strand. The angle through which the weft strand changes direction is therefore less than in plain weave, and no depressions are formed at the points of contact. The warp, particularly the double strands, can therefore slide more easily along the weft than in 'plain weave'.

Hagmeier's* tests on abrasion resistance (Table 2) tend to support this conclusion. The warp strands of Nytal 7 and Nitex 202 (both simple locking weave, monofilament) were displaced considerably along the weft when abraded in the direction of the weft. The strands of the other materials tested (all plain weaves) were not displaced. Tests in the same series showed the largest diagonal distortion in Nitex 202 and Nytal 7 (both simple locking weave, monofilament nylon); less distortion in Nytal 7xxx, Nytal 7P (nylon plain weave), and Estal Mono P.E. (polyester plain weave); and no substantial distortion in Monodur (perlon plain weave).

Because the strands are very flexible in 'twist locking weave, multifilament' Fig. 1c), the weft is twisted sharply each time it passes through the double warp

TABLE 2. Abrasion and distortion tests on plankton gauze (Hagmeier*)

Treatment		Result
Abrasion		
10 min.	Strands displaced:	Nytal 7, Nitex 202
	Greatest loss of material:	Nytal 7, Nitex 202, Nytal 7xxx
	Least loss of material:	Monodur
60 min.	Strands broken:	Nytal 7
	Strands intact:	Estal Mono P.E.
Diagonal distortion		
1000 g load at 45° to strand axis	Deviation in angular diameter:	
	20 per cent	Nytal 7, Nitex 202
	14 per cent	Nytal 7P, Nytal 7xxx, Estal Mono P.E.
	3 per cent	Monodur

strands. While this locks the weave effectively at the points of cross-over, this same flexibility of the strands allows distortion between points.

The strands of some materials increase in size when they absorb water, resulting in a decrease in mesh size. Saville (1958) recorded a decrease in mesh width of 20 per cent for new silk and a decrease of 7 per cent for old silk. Heron* observed an increase of 11 per cent in strand diameter in new silk. No changes were observed in synthetics. Kofoid (1897b) observed a decrease of 50 per cent in the open area of bolting cloth on immersion. Wiborg (1948) observed decreases in mesh width of between 15 and 40 per cent in bolting silk. The Swiss Silk Bolting Cloth Manufacturing Co. Ltd. gave the following figures for moisture absorption at 20°C temperature, and 65 per cent relative humidity: 11 per cent for silk, 3-4 per cent for nylon, and 0.4 per cent for polyester. Saville (1958) recorded a permanent decrease in the mesh width of silk with age (Table 3).

Clogging is more likely to occur with multifilament strands, such as silk or stramin, than with monofilament strands. Clogging would be accelerated in the multifilament materials by broken filaments blocking the apertures.

TABLE 3. Decrease in mesh width of silk on immersion in water (Saville, 1958)

Material		Mean mesh width (mm)	Standard error
New silk	Dry	0.312	± 0.0034
	Wet	0.261	± 0.0029
Used silk	Dry	0.236	± 0.0040
	Wet	0.221	± 0.0073

Porosity

Porosities of plankton gauzes vary between about 30 and 60 per cent. Since the strand diameter can be varied independently of the mesh width, it is possible to obtain a range of porosities for any particular mesh width. The Swiss Silk Bolting Cloth Manufacturing Co. Ltd. (Hagmeier*) lists five different porosities in 0.200 mm monofilament plain weave, ranging from 34.5 to 55 per cent. Changes in porosity can result in changes in filtration efficiency and mesh velocity (Tranter and Heron, 1965).

Deterioration

Abrasion resistance is a property of the material of the strand. Hagmeier's* tests on abrasion resistance (Table 2) show a superiority of Monodur, Estal Mono P.E., and Nytal 7P over Nitex 202, Nytal 7, and Nytal 7xxx. The criterion for abrasion resistance in these tests did not distinguish between strand displacement and loss

of material, so that the superiority of Nytal 7P (plain weave) over Nytal 7 and Nitex 202 (locking weave, monofilament) might be due to the nature of the weave.

The chemical properties of some materials, obtained from Henry Simon Ltd. (Courtaulds) and the Swiss Silk Bolting Cloth Manufacturing Co. Ltd. are summarized in Table 4.

Henry Simon Ltd. recommend the following agents for cleaning nylon: (a) warm soap or detergent solution; (b) alkaline solutions up to 15 per cent strength; and (c) solvents such as benzene and acetone.

TABLE 4. Chemical resistance of some materials used : plankton gauze

Chemical	Nylon	Perlon	Polyester	Silk
Concentrated acids	Medium	Medium	Good	
Dilute acids	Good	Good	Good	Good
Alkalis	Good	Good	Medium	Poor
Alcohols	Good	Good		
Oxidizing agents	Medium	Medium	Good	
Bleaching agents	Medium	Medium	Good	
Sunlight	Medium	Medium	Good	Medium
Organic solvents	Good	Good	Good	Good
Soap	Good	Good	Good	Good
Petrol	Good	Good·		
Formic acid	Poor	Poor		
Phenol	Poor	Poor		

CONCLUSIONS

Variations in mesh size can have a significant effect on mesh selection. Because gauzes vary widely in the uniformity of their mesh width, measurements should be made to select the gauze with the least variation. The materials in most common use in the flour milling industry tend to have the least variation.

Monofilament nylon and polyester seem to have optimum strand stiffness. Multifilament nylon and silk are not stiff enough to resist some distortion under tow, while perlon might be too stiff for efficient self-cleaning.

Distortion resistance depends also on the nature of the weave. Of the monofilament weaves, 'plain weave' is superior to 'simple locking weave' as regards resistance to strands sliding over one another, and meshes distorting diagonally.

Taking into account all properties, monofilament nylon and polyester in 'plain weave' could be regarded as standards for flexible gauze.

Metal gauze appears to meet all requirements except flexibility. Because of its rigidity and weight it needs to be protected and supported. The toxicity of some metals may limit their use for live catches. As either metal or plastic perforated screens offer potential advantages in stability, porosity control, and resistance to clogging, they should be considered for future development.

3

Filtration performance

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SUMMARY

Towing a plankton net through the water disturbs both the water and the plankton it contains. The main disturbances are immediately upstream of the gauze, immediately upstream of the entrance, and in the wake of towing bridles and other obstructions. This interaction between net and water, which determines the volume of water filtered by the net and influences the composition and condition of the catch, constitutes what may be called filtration performance. Its main physical components are filtration efficiency, filtration pressure (pressure drop across the meshes), and perhaps mesh velocity. These change to some extent as the organisms filtered from the water accumulate upon the filtering surface, so adding to the complexity of the filtration process. The laws of fluid mechanics throw some light on this complexity.

The initial filtration efficiency of simple. unencased nets made from modern gauze is usually high (> 85 per cent). Towing velocity has little effect upon filtration efficiency above about 1 knot; more information is required about efficiency at lower speeds since, in the future, these may be adopted to minimize damage to the catch. The principal parameters of filtration efficiency in *unencased* nets are the porosity of the gauze and its surface area in relation to the mouth area of the net. Filtration efficiency increases with the area of gauze, reaching a comparative plateau when the open area of the gauze is more than three times the area of the net mouth.

Much less is known about *encased* samplers, because here the filtration efficiency is determined principally by the shape of the sampler rather than by the resistance of the net. Mouth-reducing cones (flares) lead to an increase, and net casings to a decrease, in filtration efficiency. It is possible and perhaps desirable to adjust the initial filtration efficiency to exactly 100 per cent; however, this value would decline with clogging.

Nets made from fine gauze are much more likely to clog than those made from coarse gauze. The volume which may be filtered efficiently before clogging reduces the usefulness of further sampling is increased approximately sixfold by doubling the area of gauze in the net. The rate of clogging can be further reduced by having a porous cylindrical collar in front of the filtering cone; the collar oscillates, probably in response to eddies shed by the ring, and so cleans itself of accumulated organisms. Clogging can be monitored by using two flowmeters, one inside and one outside

the net, both of which should be clear of local accelerations. A limit can be placed upon the extent of clogging by limiting the distance towed. Further investigations are needed to ease the clogging problem, particularly in encased samplers.

The flow through a plankton net approaches and leaves the gauze at a reduced velocity, accelerating momentarily in transit through the meshes. Damage to the organisms caught would appear to be caused by the pressure drop across the meshes which varies as the square of the approach velocity. Consequently the condition of the catch could probably be improved by lowering the speed of tow, by reducing the mouth area of the net, or by increasing the area of gauze. Mouth-reducing cones will not reduce flow through the net in proportion to the mouth reduction unless the gauze is separated from the faster flow around the net by a non-porous casing. More information is required concerning the effects of filtration pressure upon the plankton organisms in the net.

Acceleration fronts arising from the resistance of the net to the flow through the meshes could warn organisms of the net's approach. Such disturbances extend only a short distance ahead of the net mouth and are strongest at the periphery. Towing a net from the standard triple-leg bridle creates further disturbances ahead of the net; in such cases the flowmeter should not be located in the centre of the net mouth but between the centre and the rim. More attention could be given in design to alternative towing arrangements.

INTRODUCTION

Ever since Hensen initiated quantitative plankton sampling in the late 1800's there has been a gradual shift in emphasis from systematics, diversity, and zoogeography towards plankton ecology. In ecological work, an estimate of the volume of water filtered by the net is usually required, and the statistical treatment of the data obtained depends upon assumptions concerning the filtration performance of the net. It is the purpose of this chapter to review not only the physical basis of filtration in plankton nets but also the practical problems of filtration at sea, so that the design and use of plankton nets can conform to the requirements of a given investigation.

Hensen (1895) developed a method for calculating the volume of water filtered, by means of *filtrationkoefficienten* based on laboratory experiments; Birge (1895) compared catches taken by a net with those taken by a plankton trap from a known volume of water; and Reighard (1897) compared net catches of inanimate particles with their known concentration in the water. Hensen's technique is subject to error due to clogging of the gauze (Kofoid, 1897b; Kokubo and Tamura, 1931), particularly with fine nets; this led Reighard (1897) to recommend the use of a flowmeter to measure directly the volume of water filtered during the tow. Flowmeters are now widely adopted for quantitative sampling (Nansen, 1915; Clarke and Bumpus, 1950; Nakai, 1954), and methods for calibrating and using them are described (Harvey, 1934; Nishizawa and Anraku, 1956; Yentsch and Duxbury, 1956; Motoda, Anraku and Minoda, 1957; Ito and Nishimura, 1958; Nakai, 1954; Tranter, 1965; Jossi, 1966; Gehringer and Aron, this volume, Chapter 6).

Other research has attempted to evaluate the 'catching power' of a net. Hensen (1895) and Bridger (1958), for example, found that the use of mouth-reducing cones gave what appeared to be a better catch. Such results have usually proved to be equivocal. To eliminate interference from other sampling effects, recent evaluations of filtration in plankton nets have made use of hydrodynamic test channels (Enomoto, 1955; Sysoev, 1956; Nishizawa and Anraku, 1956; Miller, 1961; Currie, 1963; Higo, 1964; Tranter and Heron, 1965, 1967; Smith and Clutter, 1965; Mahnken and Jossi, 1967) and also wind-tunnels (Tranter and Heron, 1967). The data so derived have helped to evaluate the extent of net clogging at sea (Ito and Nishimura, 1958; Asaoka and Ohwada, 1960) and the rate at which it occurs (Smith, Counts, and Clutter*[1]; Fraser, 1966).

The technical problems of filtration performance are now more tractable than other major quantitative plankton sampling problems, such as patchiness, avoidance and mesh selection.

THEORETICAL BASIS

The planktologist has relied heavily in the past upon the empirical rather than the theoretical approach to filtration in plankton nets, and has met with some degree of success. However, as with most empirical approaches, the power to extrapolate has been severely limited, particularly in view of the diversity of samplers and sampling methods in common use.

The physical properties associated with filtration that are of greatest concern in plankton sampling are *filtration efficiency, filtration pressure, mesh velocity*, and *drag* (see Terminology). Filtration efficiency directly influences the volume of water filtered, and could also influence avoidance (see Chapter 4) and escapement (see Chapter 5). Filtration pressure influences the ultimate condition of the catch and might influence escapement also. Very little is known about the local acceleration of water through the meshes, but this could have an effect upon escapement distinct from that of filtration pressure. The drag on the net is an important consideration in the field (see Chapter 6) since it influences wire angle and can limit the speed and depth at which a net is towed.

Apart from Hensen's pioneering experiments, few investigations have been made, until recently, on the physical basis of filtration in plankton nets. Hensen (1895) tested the rate of flow of water through 12 silk gauzes at 75 increments of pressure. His experimental technique would appear to be at fault (Fig. 1) in that the flow discharged into still water, so giving an artificially high pressure head on the upstream side (Borda-Carnot effect). Sysoev (1956) measured the resstance of plankton nets in a laboratory flume. The significance of his results might not extend to field conditions because the entire flow through the flume was channelled into the net, and, as Tranter and Heron (1965, 1967) have shown, filtration is influenced in practice by the flow of water round a net.

Despite this, the work of Hensen and Sysoev has thrown a great deal of light upon the physical processes involved in filtration, and these may be further clarified

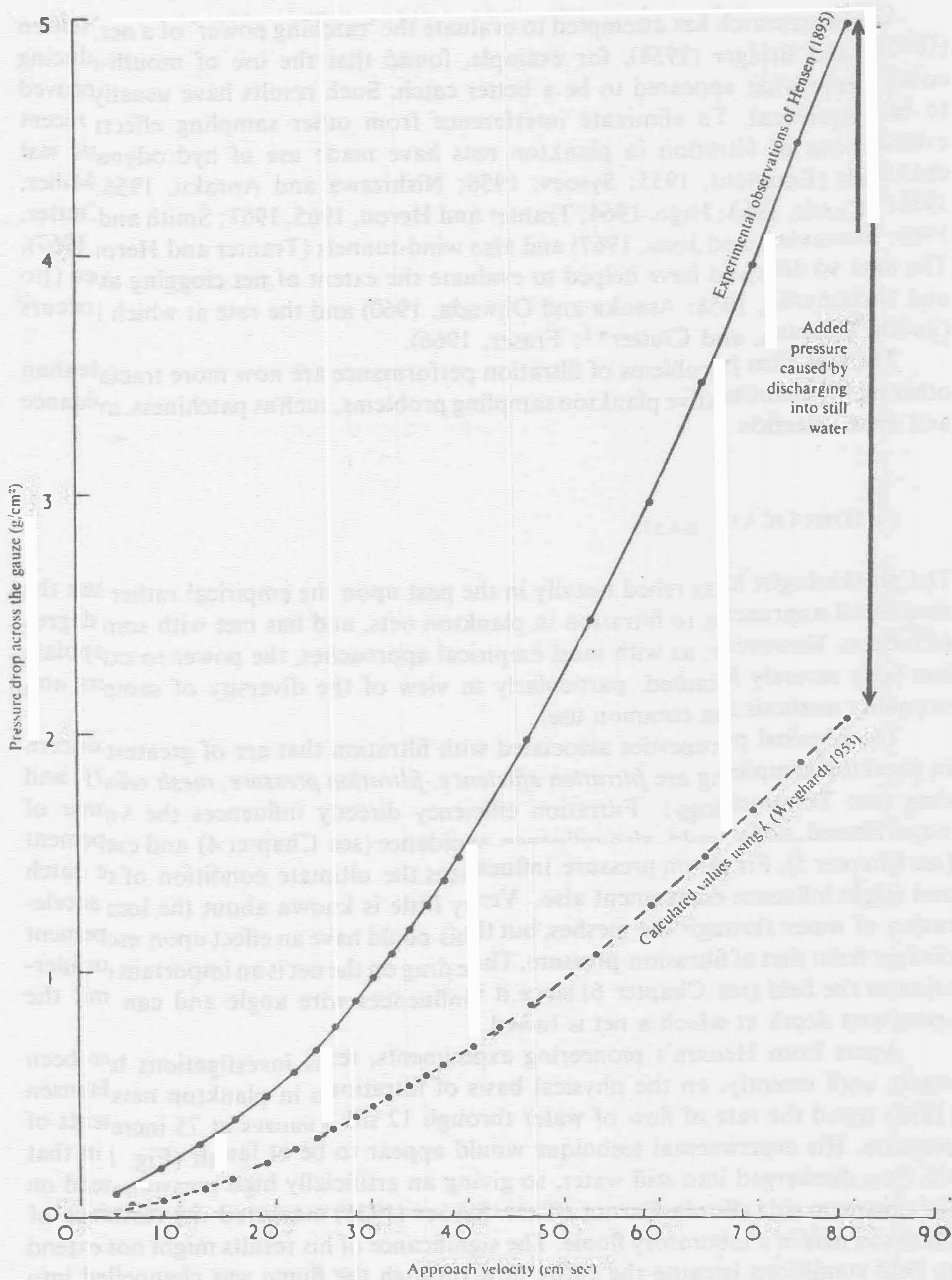1. Asterisked (*) references denote information presented at the Sydney Symposium.

Figure 1
Relation between the velocity of a stream of water normal
to a gauze and the pressure drop across it. The experimental
values of Hensen (1895) for a No. 3 gauze (porosity, 0.44;
strand diameter, 0.192 mm) are compared with values
calculated from the equation of Wieghardt (1953).

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by considering related investigations in fluid mechanics. Some work has been carried out on the flow associated with porous bodies, the investigations on the properties of the gauzes used in wind-tunnels being particularly relevant (Glauert *et al.,* 1932; Taylor and Davies, 1944; Simmons and Cowdrey, 1945; Schubauer *et al.,* 1950).

The relation between the flow through a gauze screen spanning a pipe or tunnel and the drop in pressure across the gauze is given by the equation

$$\Delta_P = K \cdot \tfrac{1}{2} \cdot \varrho \, V^2 \tag{1}$$

where Δ_P is the pressure drop, ϱ is the density of the fluid, V is the velocity of the flow, and K is the *resistance coefficient* (pressure-drop coefficient) of the gauze. Schubauer *et al.* (1950) showed that when the flow strikes the gauze at an angle θ *to the normal,* the pressure drop is determined by the normal component ($V \cos \theta$) of the approach velocity V. For angles of incidence up to 45°, it was observed that

$$\Delta_P \text{ (at angle } \theta) \approx K \cdot \tfrac{1}{2} \varrho \, (V \cos \theta)^2. \tag{2}$$

That is,

$$K_\theta \approx K \cdot \cos^2 \theta. \tag{3}$$

K_θ being the resistance coefficient at the angle of incidence θ.

Now Wieghardt (1953) has shown that the value of K at zero angle of incidence is determined by β, the porosity of the gauze (see Terminology), and by Reynolds' Number (Re), the relation being of the form

$$K \approx \frac{1-\beta}{\beta^2} \cdot 6 \, \text{Re}^{-1/3}. \tag{4}$$

Reynolds' Number is given by the equation

$$\text{Re} = \frac{V}{\beta} \cdot \frac{d}{v} \tag{5}$$

where d is the diameter of the strands in the gauze and v is the kinematic viscosity (dynamic viscosity/density) of the water ($v \approx 0.01$). The effective Reynolds' Number becomes Re $\cos \theta$ when the flow strikes the gauze at the angle θ to the normal.

The theory of the resistance of gauzes, as outlined above, would appear to be the basis on which a useful theory of filtration in plankton nets could be built. Schubauer's angle of incidence θ is equal to the side angle of a plankton net (see Fig. 2), and $\cos \theta$ is equal to the ratio of the mouth area of a conical net (A) to the area of porous surface (a). The question is, how well do equations 1 to 5 describe the filtration performance of plankton nets according to our empirical observations?
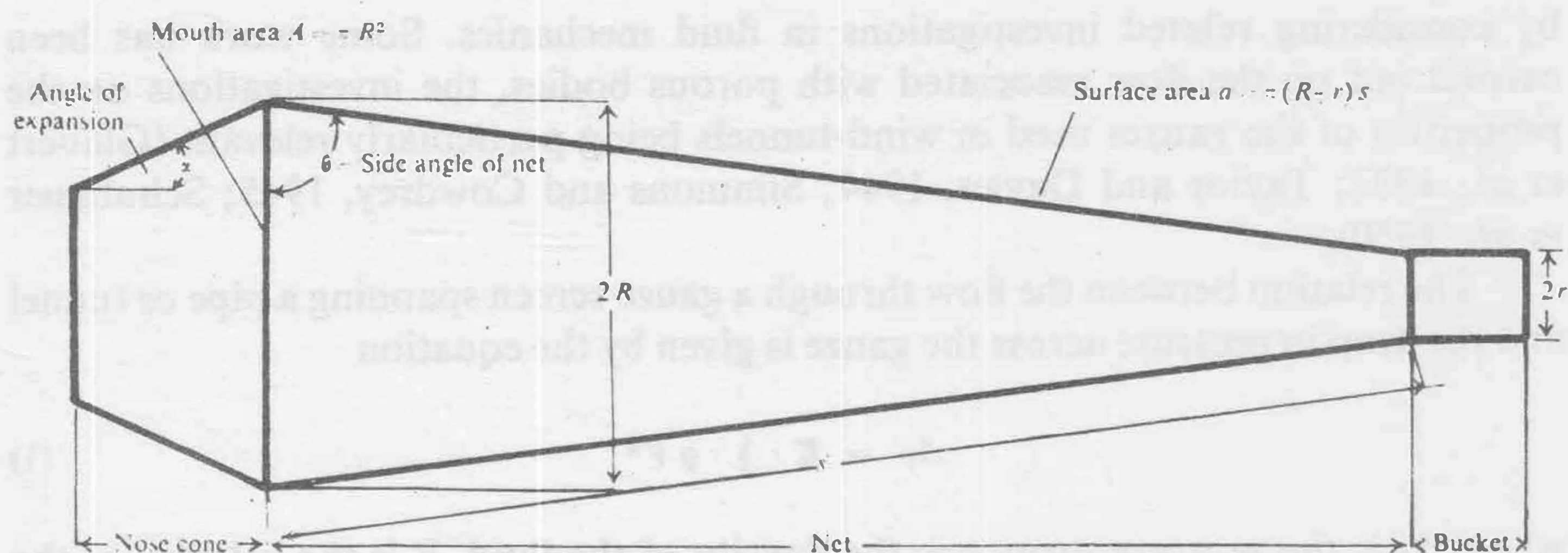
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Figure 2
Generalized geometry of a plankton net with a mouth-reducing cone (after Tranter and Heron, 1967).
For a conical net, $A/a = \dfrac{\pi R^2}{\pi RS} = \cos \theta$.

The filtration efficiency of plankton nets shows a sharp decrease, in conformity with equation 3, when the side angle falls below about 75° or the ratio A/a rises above approximately 0.2 (Tranter and Heron, 1965, 1967; Smith et al., 1964). However, at greater angles of incidence, this relation has only been shown to hold when all the water is channelled through the net (Sysoev, 1956); in plankton nets towed through the water, filtration efficiency shows little response to filtering area at these angles of incidence (Tranter and Heron, 1967). Tranter (1967) showed that filtration efficiency could be defined by the empirical equation

$$F \approx \frac{1}{1 + 0.01\,K} \tag{6}$$

K being a function of the gauze porosity and Reynolds' Number (equation 4).

The filtration pressure (Δ_p) is determined not primarily by the towing velocity (V), but by the velocity (v) at which the water approaches the gauze (approach velocity). That is,

$$\Delta_p = K \cdot \tfrac{1}{2}\, \varrho\, v^2. \tag{7}$$

The approach velocity v (see Terminology) is related to the towing velocity V by the equation

$$v = V \cdot F \cdot A/a. \tag{8}$$

The water approaching the gauze accelerates in transit through the meshes, the mesh velocity v' (see Terminology) being equal to v/β. It follows that

$$v' = V \cdot F \cdot A/a\beta. \tag{9}$$

The factor $a\beta/A$ has been combined into the factor R (Smith et al.*) which may be termed the open area ratio (see Terminology).

So far the discussion has been concerned with a 'simple' conical net. However, in most plankton nets there are other sources of resistance to flow through the net. Rings, bridles, flowmeters, mouth-reducing cones, casings, and so on produce what might be called *the resistance of the body of the sampler*. The effect of this resistance upon filtration efficiency must be determined empirically by towing the body of the sampler in a test tank and metering the flow.

The relation between the drag (D) of a plankton net and the velocity at which it is towed is given by the equation

$$D = C_D \cdot \tfrac{1}{2} \varrho \, V^2 A \qquad\qquad (10)$$

where C_D is the *drag coefficient* of the net. There is little information on the drag coefficients of plankton nets. Motoda (1962c) used a drag coefficient of 1.33 to calculate the expected drag on the Indian Ocean Standard net. Wind-tunnel tests show that the value for the WP-2 net is also of this order (Tranter and Heron, unpublished data). In simple nets, C_D would appear to be related to the resistance coefficient of the gauze (K) but the nature of the relation has yet to be determined. The drag coefficient of complex samplers would have to be determined empirically.

It is doubtful if the theory outlined above can be developed further at the present stage unless attention were given to filtration performance under conditions of diminishing gauze porosity. It is now necessary to examine the consequences of the theory in practical plankton sampling.

PRACTICAL CONSEQUENCES

Flow patterns

The interaction between a plankton net and the water through which it is towed produces a pattern of flow which reflects some features of the net's filtration performance. This interaction affects the sampling process, in relation to the volume of water filtered by the net and the accuracy with which it is measured, the distribution of pressures at the filtering surface, and the warning given to motile zooplankton of the approaching net. The form of the net determines the volume filtered and the distribution of filtration pressure; the velocity profile across the mouth determines the optimum site for a flowmeter to be placed; and the solid structures used to tow and support the net, together with its own resistance, create the disturbances which might cause plankton to take avoiding action.

All the water at rest in the path of a plankton net is accelerated. At the gauze, water is accelerated around the strands and through the meshes. At the mouth, water is accelerated and displaced around the net (Fig. 3) as a consequence of resistance to the flow through the meshes. Ahead of the mouth, water is accelerated around the towing members, the energy dissipating in turbulence in their wake.

At the gauze. In a net at rest, the pressures either side of the gauze are equal. In a moving net, the pressure inside is increased by the flow of water entering the mouth.
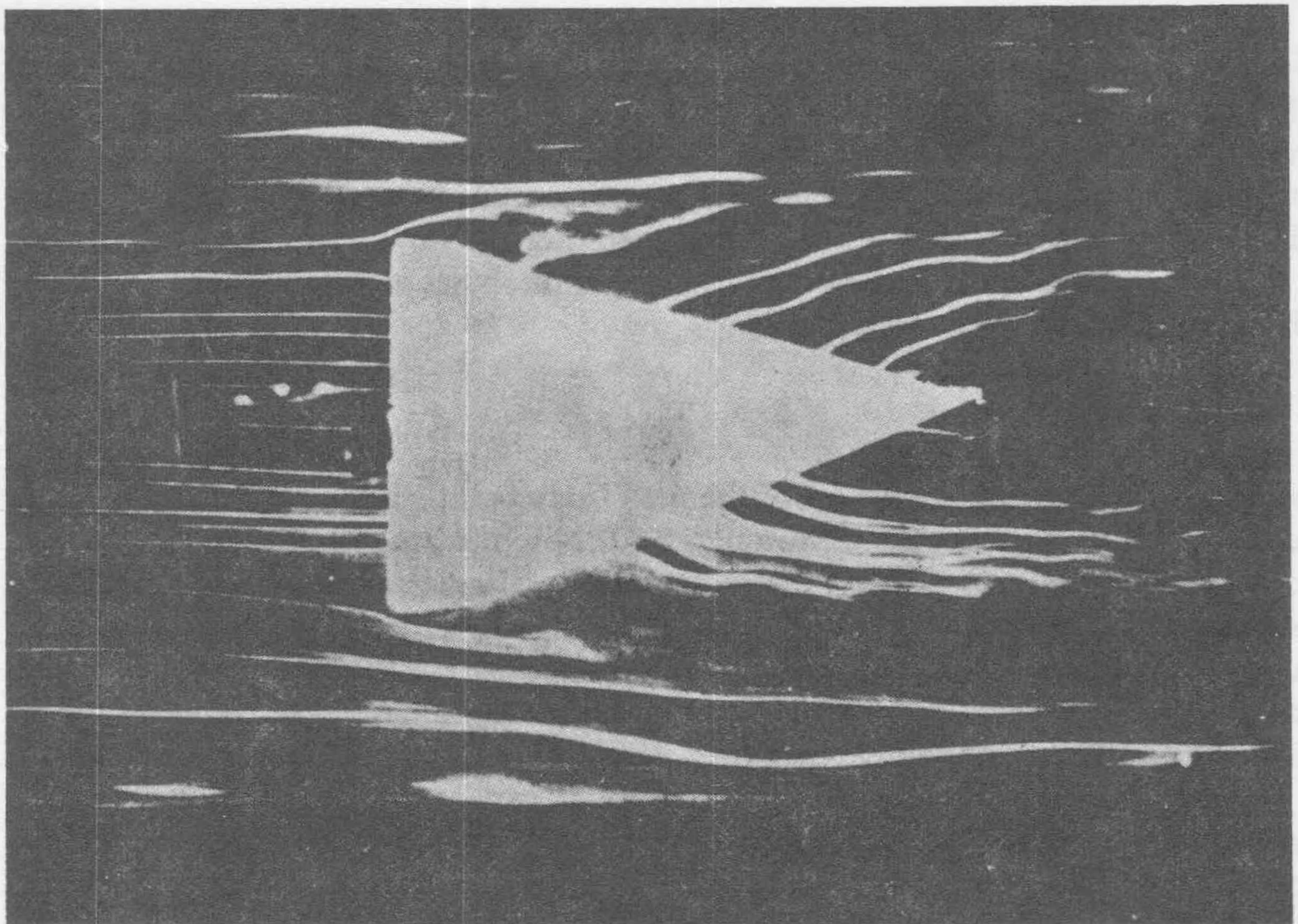
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Figure 3
Flow pattern through a model plankton net (porosity 0.47 and side angle 70º). The streamlines are traced out in trails of smoke, and show the distribution of angular accelerations (from Tranter and Heron, 1967).

The resultant pattern of flow through the meshes is determined by the distribution of pressures along the inner and outer surfaces of the net. In a conical net, these pressures are rather evenly distributed and as a result the flow rate through the gauze is fairly uniform. Velocity transects (Tranter and Heron, 1967) show a slight reduction in flow at the throat of the net, but it is not clear whether this is the result of slower approach velocities or of the turbulence associated with the ring.

If a porous cylindrical section is added ahead of the cone, some of the water rejected by the cone is filtered through the cylinder (Currie, 1963). The filtering rate decreases forward from the point adjacent to the cone. In the CalCOFI standard net, 60 per cent of the gauze is in the cone and 40 per cent in a forward cylinder, and of the total water filtered, 3 per cent was filtered in the forward half of the cylinder (20 per cent of the gauze), 7 per cent in the after half of the cylinder, and 90 per cent in the cone (Smith and Clutter, 1965).

This has two consequences in the field. Since flow is evenly distributed over the cone, the probability of clogging is similar over the whole surface, and the addition of a forward porous cylinder (of the same gauze as in the cone) provides a potential filtering area which operates at an increasing rate as the cone clogs up. The second consequence is that the surface of the gauze in the forward cylinder oscillates, probably in response to eddies which would be shed alternately from the

inner and outer peripheries of the net ring (Smith, Counts, and Clutter*; Halliday*). Smith and Clutter (1965) attribute the property of 'self-cleaning' to this oscillation.

The flow through the net approaches and leaves the gauze at a reduced velocity (Tranter and Heron, 1967) accelerating momentarily in transit through the meshes. Meanwhile the water deflected around the net is at near free-stream velocity. Tranter and Heron (1967) claim that this faster stream entrains the slower discharge. Enclosing a net within a non-porous cylindrical casing, for example, reduces the filtration efficiency of the net by approximately 40 per cent; part of this reduction could be due to the angular deformation of flow at the wall of the case.

At the mouth. Flow patterns at the mouth of a net are influenced both by the resistance of the net and by solid structures at, and forward of, the mouth. The mouth-reduction cone (such as on the Hensen Egg net, the Juday net, and most high-speed nets) increases filtration efficiency. As well as increasing the open area ratio, a reduction cone creates a low pressure area which draws a column of water wider than the reduced mouth through the sampler (Fig. 4c). Efficiencies higher than 130 per cent have been measured with the Hensen cone at 2.5 knots (Smith and Clutter, unpublished data). Tranter and Heron (1967) have used a flare behind the tube-mouth of the Clarke-Bumpus sampler to increase efficiency to 115 per cent.

Flow profiles across the entrance of large nets (Smith and Clutter, 1965; Jossi, 1966; Fraser, 1966; Mahnken and Jossi, 1967; Tranter and Heron, 1967) have shown the need to meter the flow at a site where the stream velocity is equal to the average through the entrance. In a net without forward bridles (Longhurst *et al.,* 1966) the centre position is probably representative. *Underestimates* would result if the flowmeter were placed behind solid structures such as the bridle apex or the closing apparatus (Jossi, 1966). Flowmeters outside the entrance of a net (Bé, 1962a; McGowan and Brown, 1966) would *overestimate* the flow through the entrance (Smith and Clutter, 1965) unless the net was fitted with a mouth-reducing cone. The magnitude of the error would depend on the filtration efficiency of the net and the degree of clogging. An overestimate would also be given in nets where the flowmeter is located at a coarse gauze section forward of the effective filtering surface, as in the Indian Ocean Standard net (Motoda, 1962b).

Ahead of the net. Flow patterns ahead of the net are represented here in two ways. In one method the trajectory of a parcel of water is represented by a line (streamline), and the rate at which adjacent lines diverge or converge is a measure of acceleration. By the other method, the magnitude and distribution of acceleration are represented directly.

Figure 4 illustrates the streamlines ahead of nets filtering at 75 per cent (Fig. 4a), 95 per cent (Fig. 4b), and 125 per cent (Fig. 4c) efficiency. Radial symmetry of flow is assumed, and each succeeding pair of lines from the centre adds another 10 per cent to the volume contained in a cylinder projected ahead of the entrance. The figures demonstrate that the consequences of filtration affect the water ahead of the net but not to great distances forward. The severity of angular deformation increases towards the rim, so influencing the capture of motile organisms (Fleminger and Clutter, 1965). Studies with mouth-reduction cones indicate that it may be possible
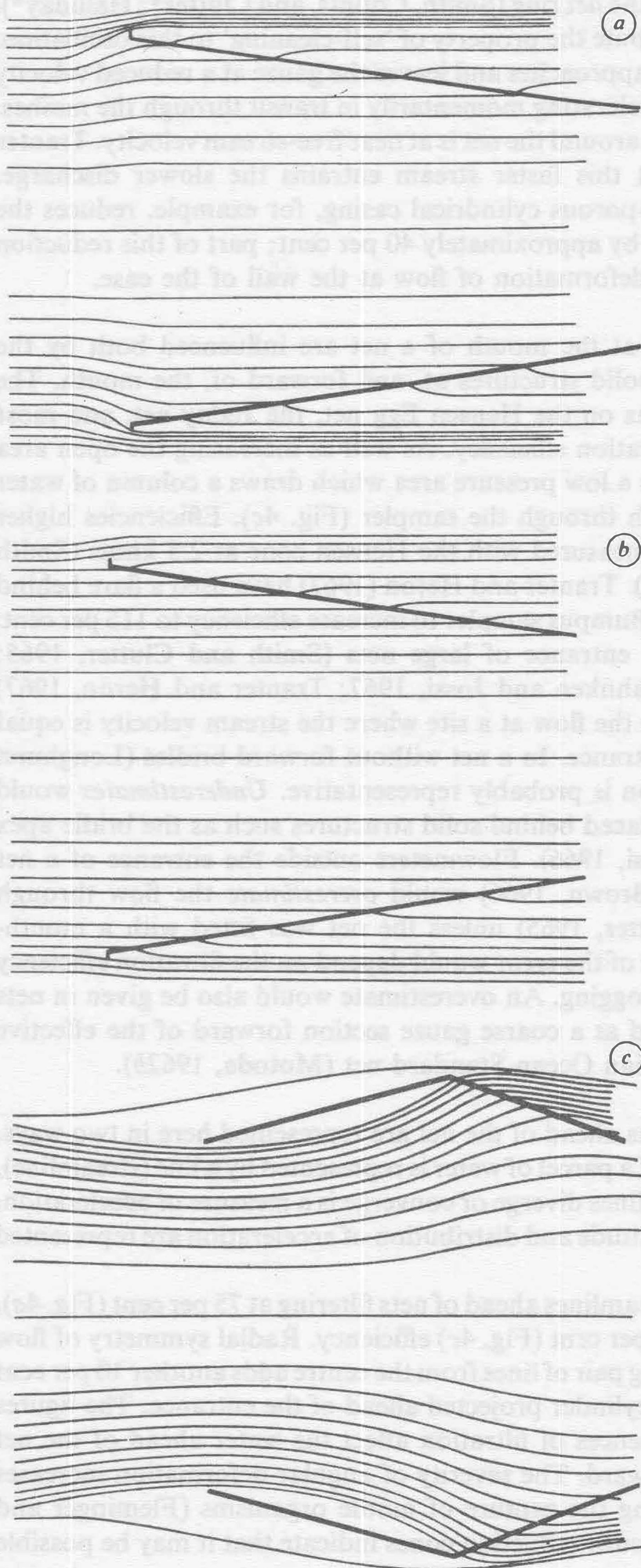
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Figure 4
Streamlines ahead of nets.
Each streamline encloses
10 per cent of the water
entering a circular net.
a A conical net which is
accepting 75 per cent of
the water presented to it.
b A conical net which
is accepting 95 per cent of
the water presented to it.
c A conical net, with a
mouth-reduction cone,
which is accepting 125 per
cent of the water presented
to it.

to eliminate the forward consequences of the net's approach by enclosing the diverging streamlines to the point where they are parallel (filtration efficiency = 100 per cent). The main problem in this approach is the design of a filtering surface that will maintain the same filtering efficiency throughout the course of the tow (Smith, Counts, and Clutter*).

Accelerations caused by the resistance of the net do not extend so far forward as disturbances from solid objects such as the bridle, lead-line, cable clamp, and towing warp. In Figure 5 the disturbances caused by a non-filtering cone (Fig. 5a), bridle, lead-line, and rim (Fig. 5b), and the combination of a net and towing apparatus (Fig. 5c) are shown. Possible consequences of these forward flow disturbances are discussed more fully in Chapter 4.

Flow patterns in basic sampling systems. The flow patterns associated with most contemporary samplers have not yet been observed. In particular, there is insufficient information concerning the flow patterns associated with encased plankton nets. The patterns shown in Figure 6 are those which might be expected with several basic forms of design. They are based more on our present level of understanding than on patterns actually observed.

Filtration efficiency

The effect of filtering area. When the open area of an unencased net is less than three times the area of its mouth, filtration efficiency undergoes a progressive decline (Smith and Clutter, 1965; Tranter and Heron, 1965, 1967). When this ratio (R) is greater than 3, filtration efficiency tends towards a plateau. Although the lower filtration efficiency of short nets follows from the theory of inclined gauzes (see equation 3 above), its relative constancy in longer nets is not immediately obvious. Tranter and Heron (1967) suggest that the two components of the equation counteract each other; the trend towards lower resistance at greater angles of incidence ($\cos^2 \theta$) may be countered by the trend towards higher values of K at lower Reynolds' Numbers (equation 4). However, it is the effect of filtering area upon *sustained filtration efficiency*, rather than upon initial filtration efficiency, that is of greater consequence in practice.

Smith, Counts, and Clutter* showed that in natural waters the area of gauze in a net influences the duration of efficient filtration. With nets of nylon gauze, of mesh width 0.33 mm, and open area ratios 3.2, 4.8, and 6.4, the volume filtered efficiently was increased sixfold by doubling the filtering area (Table 1). This

TABLE 1. The effect of open area ratio on sustained filtration efficiency (F) (from Smith, Counts, and Clutter*)

Open area ratio	Volume filtered (m³) at $F > 85$ per cent	
	'Green' water	'Blue' water
3.2	49	390
4.8	123	1 172
6.4	300	2 564

Figure 5
The accelerations (cm/sec) ahead of plankton nets.
a Linear accelerations ahead of a non-filtering cone
1 m in diameter without a bridle preceding the entrance.
The towing velocity is 77 cm/sec (1.5 knots).
b Linear accelerations ahead of a ring with bridle and
lead line. The towing velocity is 129 cm/sec (2.5 knots).
c Linear accelerations ahead of a plankton net ring,
bridle and lead line. The towing velocity is 129 cm/sec
(2.5 knots) (after Smith and Clutter*).

augmented gain was attributed to 'self-cleaning' during the tow, clogging being the inevitable result of filtering natural waters (Kofoid, 1897b; Yentsch and Duxbury, 1956; Ito and Nishimura, 1958; Asaoka and Ohwada, 1960).

The porosity of the gauze and consequently the open area ratio of the net may also change from tow to tow. For instance, the porosity of the silk gauze used during the Plankton Expedition changed from 14 to 7 per cent due to shrinkage

Figure 6
Probable flow pattern associated with some basic forms of plankton sampler.
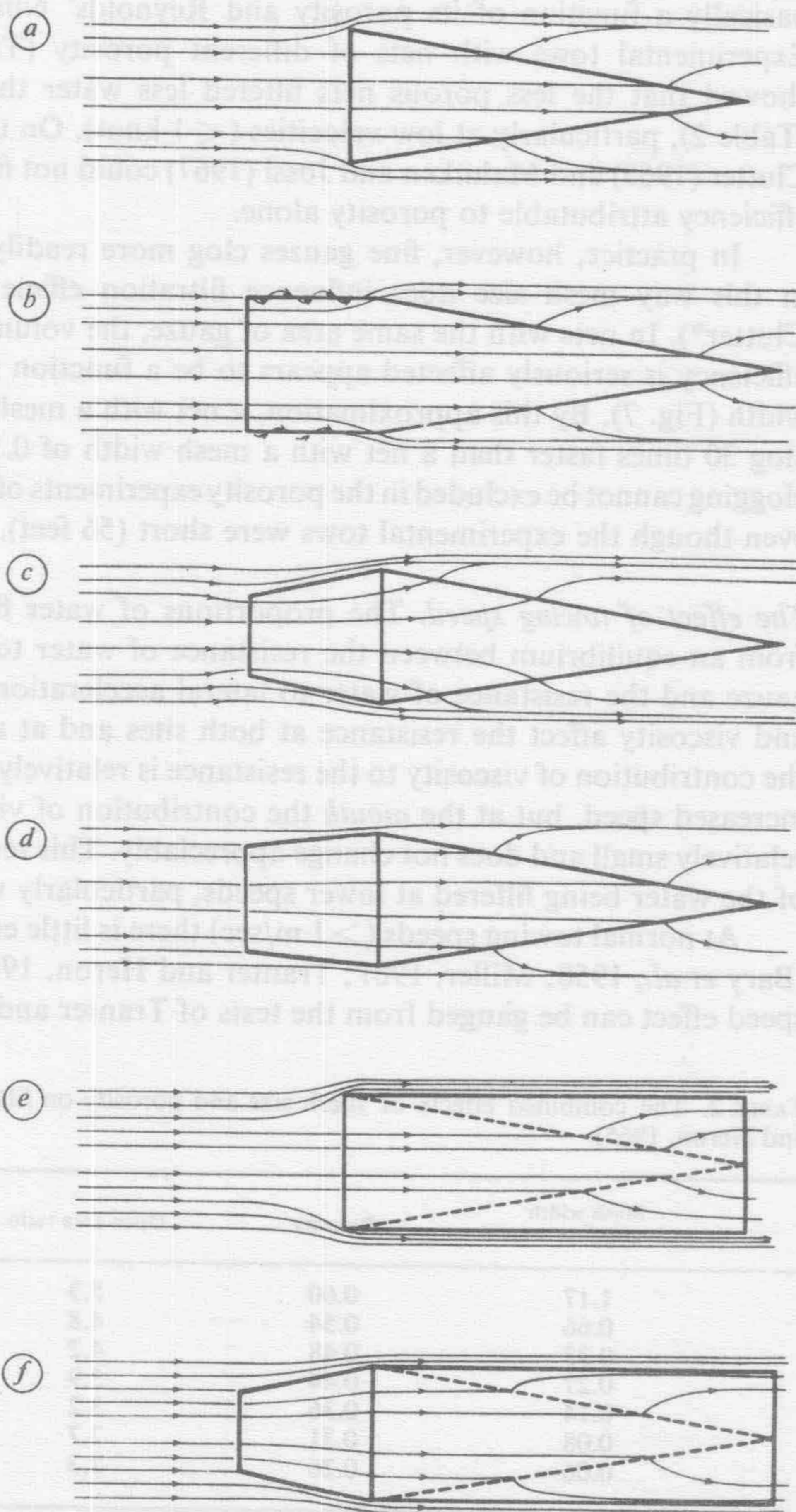a 'Simple' conical net ($F < 1$).
b Conical net with porous collar ($F \approx 1$).
c Conical net with non-porous mouth-reducing cone ($F > 1$).
d Conical net with non-porous mouth-reducing cone ($F = 1$).
e Conical net with non-porous casing ($F < 1$).
f Conical net with non-porous casing and non-porous mouth-reducing cone ($F = 1$).

and use (Hensen, 1895), and the open area ratio changed from 4:1 to 2:1. The effects of shrinkage on the mesh width and porosity of silk were described also by Ahlstrom (1948). Although monofilament nylon and metal gauzes do not shrink, they are more subject to the progressive accumulation of residual plankton (Ahlstrom, 1959), which dries more completely on monofilament than on multi-filament strands, and is difficult to remove by routine washing procedures.

The effect of mesh size. According to the theory, the resistance of a piece of gauze is basically a function of its porosity and Reynolds' Number (equation 4 above). Experimental tows with nets of different porosity (Tranter and Heron, 1965) showed that the less porous nets filtered less water than the more porous nets (Table 2), particularly at low velocities (< 1 knot). On the other hand, Smith and Clutter (1965) and Mahnken and Jossi (1967) could not find differences in filtration efficiency attributable to porosity alone.

In practice, however, fine gauzes clog more readily than coarse gauzes, and in this way mesh size does influence filtration efficiency (Smith, Counts, and Clutter*). In nets with the same area of gauze, the volume filtered before filtration efficiency is seriously affected appears to be a function of the square of the mesh width (Fig. 7). By this approximation, a net with a mesh width of 0.10 mm would clog 30 times faster than a net with a mesh width of 0.55 mm. The possibility of clogging cannot be excluded in the porosity experiments of Tranter and Heron (1965) even though the experimental tows were short (56 feet).

The effect of towing speed. The proportions of water filtered and rejected result from an equilibrium between the resistance of water to acceleration through the gauze and the resistance of water to lateral acceleration ahead of the net. Inertia and viscosity affect the resistance at both sites and at all velocities: at the *gauze* the contribution of viscosity to the resistance is relatively great and diminishes with increased speed, but at the *mouth* the contribution of viscosity to the resistance is relatively small and does not change appreciably. This results in a lower proportion of the water being filtered at lower speeds, particularly with fine gauzes.

At normal towing speeds (> 1 m/sec) there is little effect on filtration efficiency (Bary *et al.*, 1958; Miller, 1961; Tranter and Heron, 1967). The magnitude of the speed effect can be gauged from the tests of Tranter and Heron (1965). The differ-

TABLE 2. The combined effects of mesh size and porosity on filtration efficiency (from Tranter and Heron, 1965)

Mesh width (mm)	Porosity	Open area ratio	Reduction in efficiency (per cent)
1.17	0.60	5.3	0
0.66	0.54	4.8	0
0.33	0.48	4.2	0
0.27	0.44	3.9	3
0.14	0.36	3.2	4
0.08	0.31	2.7	8
0.06	0.26	2.3	12

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Figure 7
The effect of mesh width
on clogging rate in which
the area of the individual
aperture is the ordinate
and the volume filtered
before filtration efficiency
falls below 85 per cent is
the abscissa. The mesh
widths used are 0.10, 0.20,
0.33 and 0.55 mm, and the
individual aperture areas
are 0.01, 0.04, 0.11 and
0.30 mm². The coarsest
gauze had not clogged at
the end of the test (Smith,
Counts, and Clutter*).
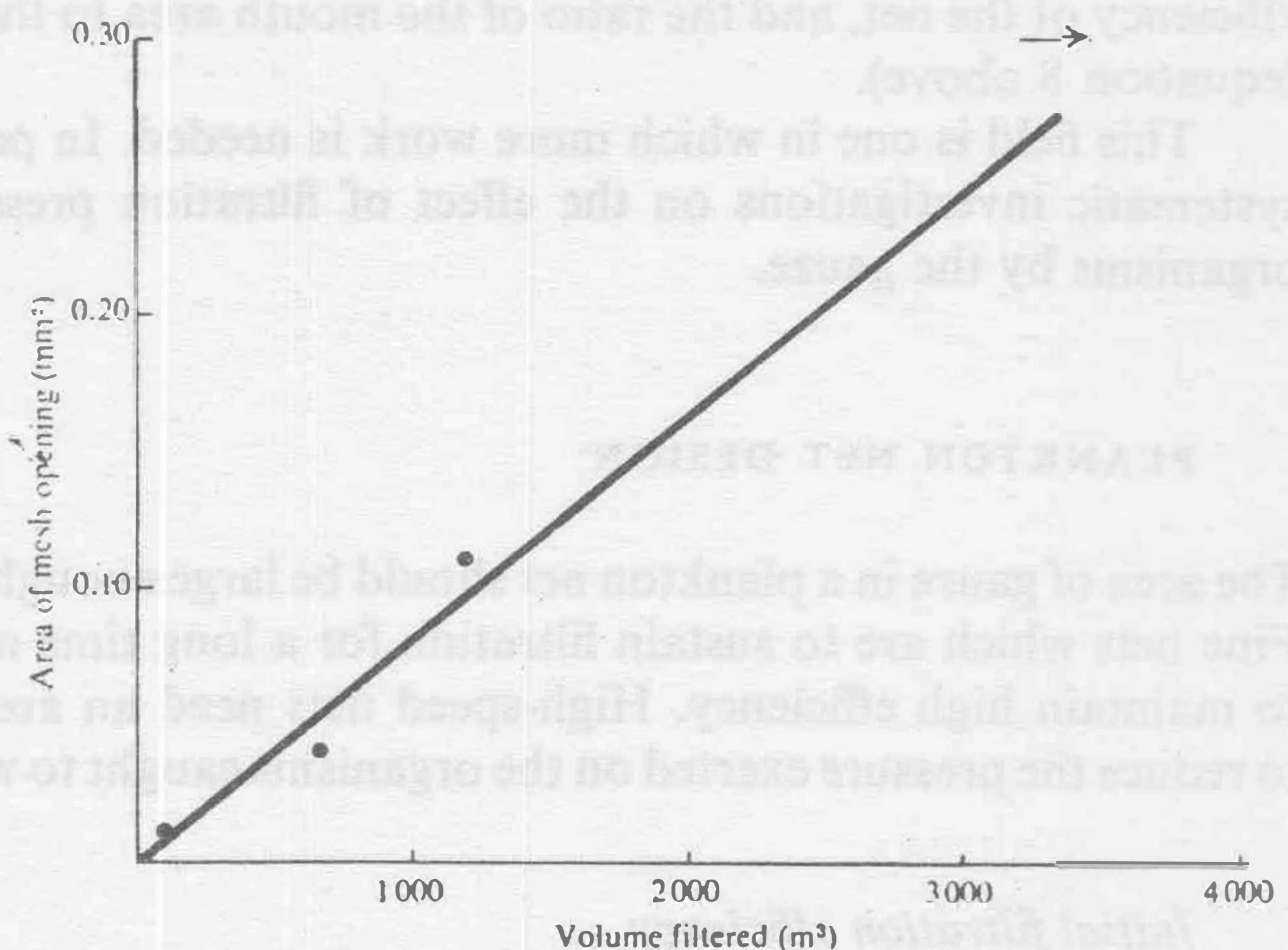
ences observed ranged from 3 to 4 per cent for gauzes ranging in mesh width from 0.27 to 1.17 mm and from 6 to 12 per cent for mesh widths of 0.06 to 0.14 mm, the greater part of the difference occurring below towing velocities of 0.6 m/sec (1.2 knots). Because low towing speeds might be adopted more commonly in future to improve the condition of the catch, these experiments should be repeated, preferably using a flowmeter with a low friction point.

Filtration pressure

It has often been observed that plankton organisms are taken in poorer condition at high towing velocities. For instance, Tranter, Kerr, and Heron* recorded progressive damage to Appendicularia between hauling speeds of 1.5 and 2.4 m/sec. Since velocity is unlikely to cause any direct damage, this is generally attributed to the associated pressure drop across the meshes. It is likely that this filtration pressure also influences the selectivity of organisms by the meshes (Vannucci: see Chapter 5 below); Hensen (1895), for example, found that a net with a high filtration pressure caught only two-thirds as many small copepods as a similar net with a low filtration pressure.

However, the pressure drop across the meshes of a plankton net has never been measured. It is therefore necessary to seek some understanding of the parameters of filtration pressure from the theory available. Hensen (1895) was the first to state the basic relationship

$$\Delta_P = K \cdot \tfrac{1}{2} \varrho \cdot v^2$$

between the velocity, v, at which a stream of water approaches a gauze, and Δ_P, the resultant pressure drop across it. Because this pressure varies, not as a linear function of the approach velocity, but *as the square of the approach velocity*, small changes in velocity will lead to relatively large changes in filtration pressure. The approach velocity is related to the velocity at which the net is towed, the filtration

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efficiency of the net, and the ratio of the mouth area to the area of gauze in the net (equation 8 above).

This field is one in which more work is needed. In particular, there should be systematic investigations on the effect of filtration pressure on the retention of organisms by the gauze.

PLANKTON NET DESIGN

The area of gauze in a plankton net should be large enough to filter water efficiently. Fine nets which are to sustain filtration for a long time need reserve filtering area to maintain high efficiency. High-speed nets need an area of gauze large enough to reduce the pressure exerted on the organisms caught to within an acceptable limit.

Initial filtration efficiency

In practice, the initial filtration efficiency of unencased nets is determined by their open area ratio (see 'Theoretical basis' above) regardless of mesh size and towing speed. The minimum open area ratio has not been generally determined for a range of mesh sizes, but it appears that any simple conical net made from a modern gauze would filter at more than 85 per cent efficiency provided the open area ratio were greater than 3; nets with an open area ratio greater than 5 could filter at up to 95 per cent efficiency. Ratios higher than this are unlikely to yield much higher efficiencies unless a mouth-reducing cone is used (Fig. 4c, 6c). Reducing cones are more efficient when their angle of expansion (see Fig. 2) is small (Tranter and Heron, 1967); for top efficiency the angle should be less than $3\frac{1}{2}°$ (Pankhurst and Holder, 1952).

The first step in plankton net design is to determine the grade of gauze necessary to retain the organisms desired (see Vannucci, Chapter 5 below). The porosity of the chosen gauze should then be determined. This specification is usually available from the distributors, but it can also be obtained by direct measurement (see Terminology) either with an eyepiece micrometer or by polar planimetry of photo-
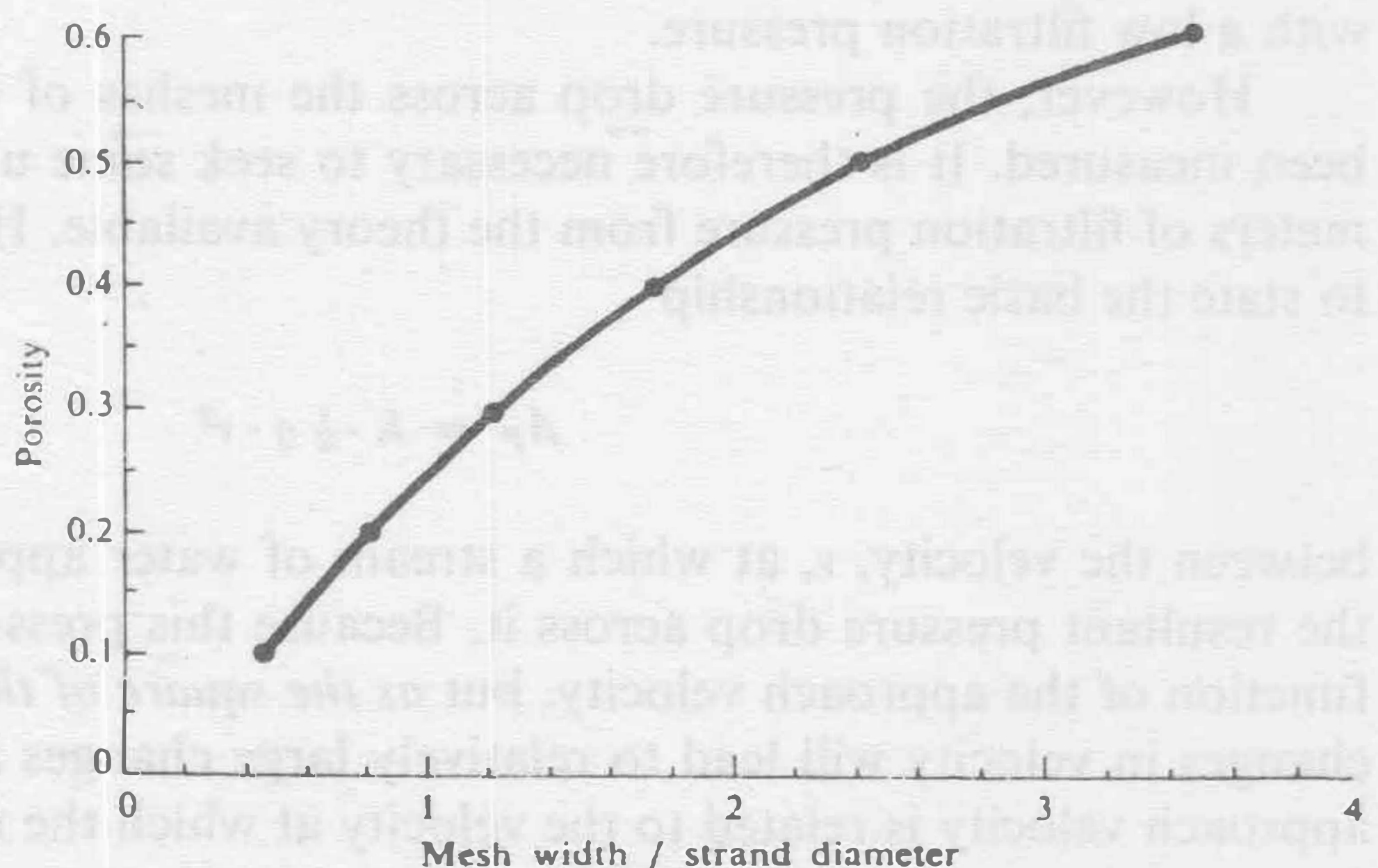
Figure 8
A graphic method of estimating porosity from the ratio of the mean mesh width to the mean strand diameter.
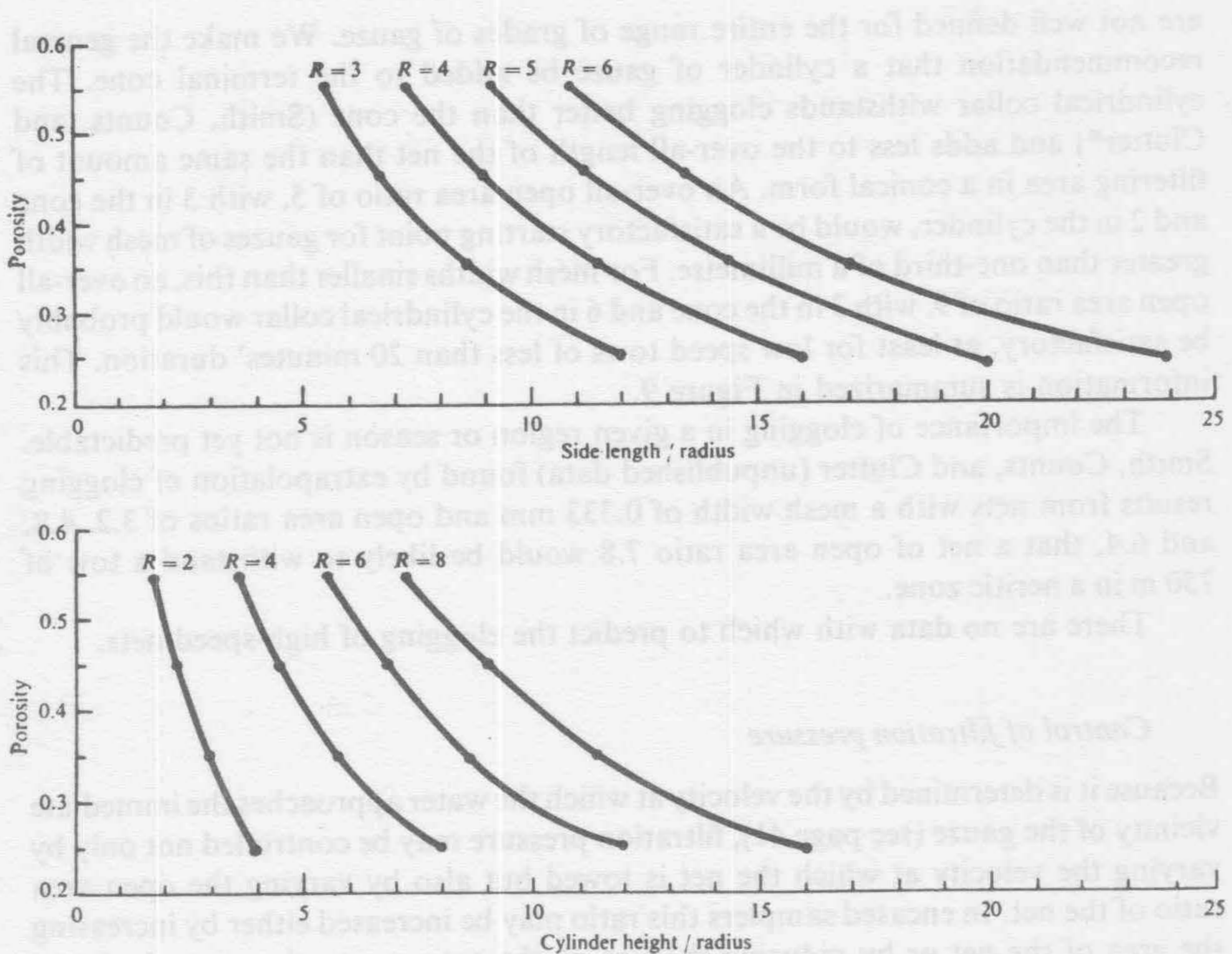
Figure 9
a A graphic method for estimating the cone side length
for nets with open area ratios of 3 to 6 where the gauze
porosity is between 0.25 and 0.55. The units on the abscissa
are to be multiplied by the radius to determine side length.
b A graphic method for estimating the cylinder height
of the reserve mesh to be added to a net for open area
ratios of 2 to 8. The units on the abscissa are to be
multiplied by the radius to determine cylinder height.

graphs or drawings. Figure 8 shows the approximate relation between porosity
and the ratio of mesh width to strand diameter. Given the porosity, the desired
open area ratio may then be selected using Figure 9. The radius of the mouth
entrance will be determined by other considerations, such as the volume to be
sampled (see Cassie, Chapter 7 below), the avoiding reactions of the organism
sought (see Clutter and Anraku, Chapter 4 below), or the limitations due to drag
(see Gehringer and Aron, Chapter 6 below).

Sustained filtration efficiency

Having established the requirements for a particular filtration performance, features
should then be included in the design to ensure that this performance will be sus-
tained throughout the haul or tow. The problems of sustaining filtration efficiency

are not well defined for the entire range of grades of gauze. We make the general recommendation that a cylinder of gauze be added to the terminal cone. The cylindrical collar withstands clogging better than the cone (Smith, Counts, and Clutter*) and adds less to the over-all length of the net than the same amount of filtering area in a conical form. An over-all open area ratio of 5, with 3 in the cone and 2 in the cylinder, would be a satisfactory starting point for gauzes of mesh width greater than one-third of a millimetre. For mesh widths smaller than this, an over-all open area ratio of 9, with 3 in the cone and 6 in the cylindrical collar would probably be satisfactory, at least for low speed tows of less than 20 minutes' duration. This information is summarized in Figure 9.

The importance of clogging in a given region or season is not yet predictable. Smith, Counts, and Clutter (unpublished data) found by extrapolation of clogging results from nets with a mesh width of 0.333 mm and open area ratios of 3.2, 4.8, and 6.4, that a net of open area ratio 7.8 would be likely to withstand a tow of 750 m in a neritic zone.

There are no data with which to predict the clogging of high-speed nets.

Control of filtration pressure

Because it is determined by the velocity at which the water approaches the immediate vicinity of the gauze (see page 41), filtration pressure may be controlled not only by varying the velocity at which the net is towed but also by varying the open area ratio of the net. In encased samplers this ratio may be increased either by increasing the area of the net or by reducing the size of the entrance to the case; the latter principle is basic to the design of high-speed samplers. In unencased samplers, on the other hand, the ratio can best be increased by increasing only the area of the net; mouth-reductions in unencased nets are to some extent self-defeating, their effect being to increase the effective area swept by the smaller mouth (Fig. 4c).

There is not enough information on the levels of filtration pressure, or upon their effects, to specify standards. These must ultimately be set by the practising planktologist.

Laboratory and field testing

Test tanks ('ship tanks') and wind-tunnels are standard equipment in hydrodynamics and aerodynamics laboratories and are well suited for testing plankton samplers. Flow patterns in air are directly comparable with those in water, provided allowance is made for the different kinematic viscosities of air and water (Alexseev, 1964; Miyazaki, 1964; Tranter, 1967).

The test tank is an open water channel through which instruments may be moved at predetermined velocities. Usually a pair of rails straddles the channel, and on these runs an electric trolley from which the sampler may be suspended by a vertical boom.

In many respects wind-tunnels are more convenient for testing plankton samplers. Air is drawn continuously through the tunnel by a fan, delivering an even stream of air through a working section with a viewing window. The sampler is

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Area (m²)

0.178
0.082
0.063
0.047
0.031
0.016
0.002
0.686
0.664
0.686
0.735
0.767
0.790
0.804

Velocity (m sec)
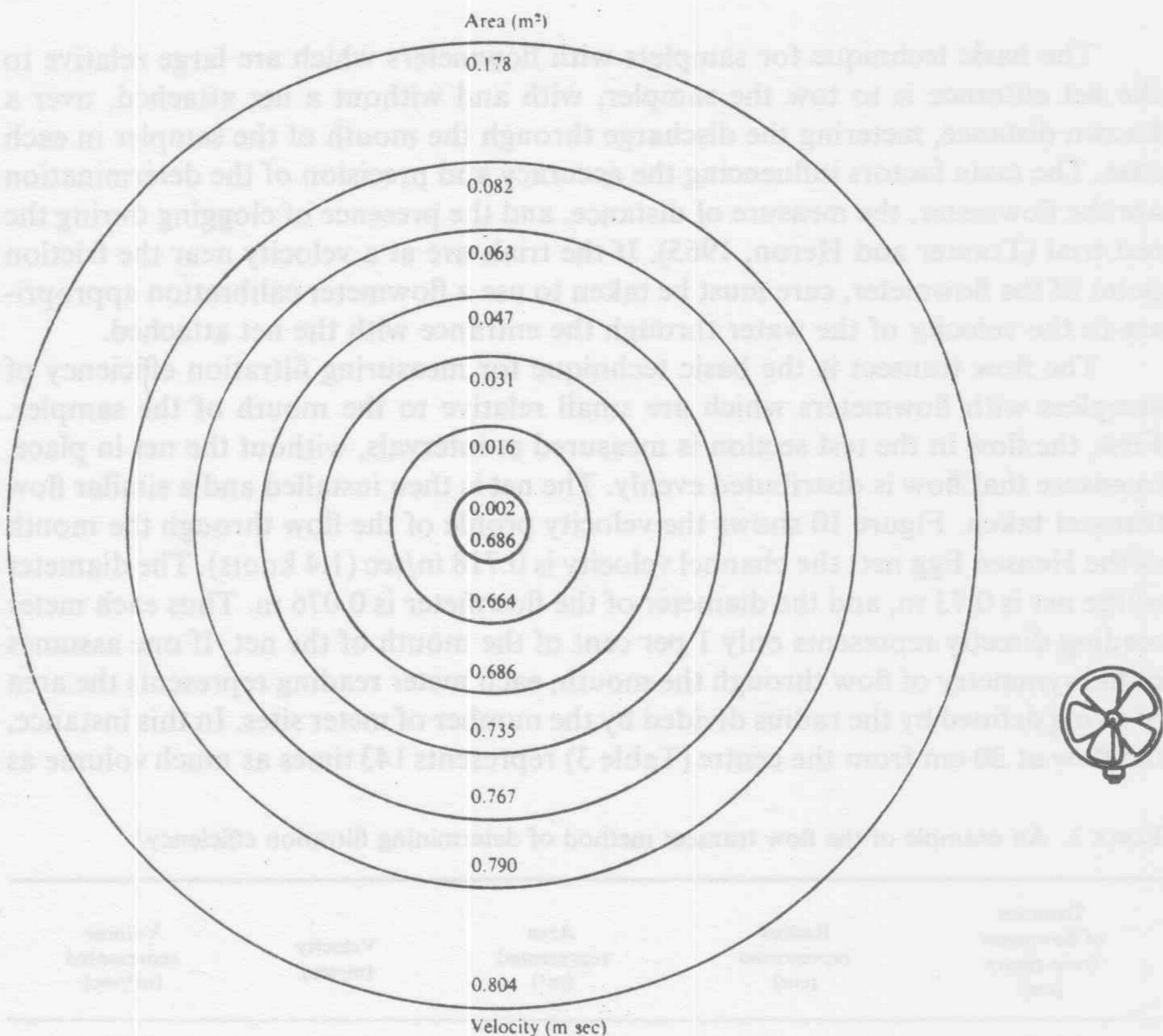
Figure 10
Diagram for computing the filtration efficiency of a net using the flow velocity transect method. The flowmeter is drawn to scale at the right. To convert from flow velocity to volume, the velocity is multiplied by the area it is intended to represent, assuming radial symmetry of flow (see Table 3).

suspended in the centre of the working section facing the airstream, and its properties are measured by probes inserted through the top or side of the tunnel: the pitot tube may be used to measure pressure; the hot-wire anemometer to measure velocity and turbulence; a mechanical balance to measure the drag of the net and its associated components; and the flow pattern may be observed by means of jets of smoke liberated upstream of the net (Fig. 3) or by tufts of thread attached at various points. The wind-tunnel may also be used to investigate the properties of towing warps (Alexseev, 1964) and depressors.

Filtration efficiency. The filtration efficiency of plankton samplers has been determined in irrigation canals (Smith and Clutter, 1965), in recirculating water channels (Mahnken and Jossi, 1967; Smith and Clutter*), in towing tanks (Tranter and Heron, 1965, 1967), in wind-tunnels (Tranter and Heron, 1967), and at sea (Currie and Foxton, 1957; Bary et al., 1958).

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The basic technique for samplers with flowmeters which are large relative to the net entrance is to tow the sampler, with and without a net attached, over a known distance, metering the discharge through the mouth of the sampler in each case. The main factors influencing the accuracy and precision of the determination are the flowmeter, the measure of distance, and the presence of clogging during the test trial (Tranter and Heron, 1965). If the trials are at a velocity near the friction point of the flowmeter, care must be taken to use a flowmeter calibration appropriate to the velocity of the water through the entrance with the net attached.

The flow transect is the basic technique for measuring filtration efficiency of samplers with flowmeters which are small relative to the mouth of the sampler. First, the flow in the test section is measured at intervals, without the net in place, to ensure that flow is distributed evenly. The net is then installed and a similar flow transect taken. Figure 10 shows the velocity profile of the flow through the mouth of the Hensen Egg net; the channel velocity is 0.718 m/sec (1.4 knots). The diameter of the net is 0.73 m, and the diameter of the flowmeter is 0.076 m. Thus each meter reading directly represents only 1 per cent of the mouth of the net. If one assumes radial symmetry of flow through the mouth, each meter reading represents the area of a ring defined by the radius divided by the number of meter sites. In this instance, the flow at 30 cm from the centre (Table 3) represents 143 times as much volume as

TABLE 3. An example of the flow transect method of determining filtration efficiency [1]

Distance of flowmeter from centre (cm)	Radius represented (cm)	Area represented (m²)	Velocity (m/sec)	Volume represented (m³/sec)
Centre	0—2.5	0.002	0.686	0.001
5	2.5—7.5	0.016	0.664	0.011
10	7.5—12.5	0.031	0.686	0.021
15	12.5—17.5	0.047	0.735	0.035
20	17.5—22.5	0.063	0.767	0.048
25	22.5—27.5	0.082	0.790	0.065
30	27.5—36.5	0.178	0.804	0.143
		0.419		0.324

1. Channel velocity = 0.718 m/sec; mean velocity through net entrance = 0.773 m/sec.

the flow at the centre; this proportion would vary with the number of metering sites chosen and with the mouth size. Table 3 shows that the mean velocity through the net mouth was approximately 0.773 m/sec, and that the flowmeter site which most closely represented this was 20 cm from the centre. The sum of the results of multiplying the velocity by the area represented by that site gives an estimate of the volume being filtered each second. At this velocity, the net is estimated to be 107 per cent efficient. By a similar process, filtration efficiency could be determined with several flowmeters installed in the mouth of the net at various distances from the centre.

Clogging. The effects of clogging may be studied either in the laboratory or in the field. In the field, clogging can be tested using ordinary flowmeters, one mounted

inside and another outside the rim. It should be borne in mind that the rate of the outer flowmeter could increase as the rate of the inner one decreases, due to acceleration of displaced water around the net. We suggest that the ratio of these readings be determined by several trials; at the normal duration of the tow, half the duration of tow, and twice the duration of tow. Preferably these trials should be conducted in areas known to yield high concentrations of plankton, and should be repeated after the nets have been in use for some time to detect differences due to shrinkage or to reduced porosity. The progress of clogging during a tow can be observed by telemetering the flow rate to the ship. It is also possible to record flow rate *in situ* for later examination (Currie and Foxton, 1957; Longhurst *et al.*, 1966).

Filtration pressure. The filtration pressures generated by a net are an essential consideration in the design of plankton samplers. Because Hensen's values are too high (see Fig. 1), it would be useful to repeat his work using modern silk gauzes, and those made from synthetic fibres and from metal. In particular, the equation of Wieghardt (1953), on which the present estimates of filtration pressure are based, needs to be confirmed for the gauzes usually used in plankton nets. However the greatest need of all is to determine in greater detail the effects of pressure on mesh selectivity and specimen condition.

Forward disturbances. Advance warning to motile zooplankton may well reduce the accuracy of plankton sampling (see Clutter and Anraku, Chapter 4 below). Some of the forward disturbances caused by the net and the towing apparatus can be measured in the laboratory. These may be divided into linear acceleration, angular acceleration, and turbulence. Linear accelerations may be estimated from flow transects forward of the mouth, but interpretation becomes more difficult in the presence of angular accelerations. These may be shown by classical techniques involving yarn tabs, dye trails, and smoke streams (see Fig. 3). Turbulence is likely to be important in stimulating small plankton organisms because the fluctuations of small-scale accelerations are greater than the onset of large-scale accelerations caused by the approach of the net. The hot-wire anemometer is a suitable instrument for measuring turbulence in air.

Net construction

Two forces interact to reduce oscillation of the filtering surface during the tow: the force of the water at right angles to the gauze, and the drag of the net which is parallel with the towing direction and acts on the longitudinal dimension of the net. The filtering pressure is kept low by design and is fairly evenly distributed over the gauze. However, the drag is additive from the posterior to the anterior part of the net. For this reason, longitudinal support webbing is required to relieve the tension on the gauze. Figure 11 shows the drag on the support ring of nets with mouth areas of 0.1 m² to 2.0 m², at towing velocities of 1 to 18 knots (0.5 to 9.5 m/sec). A minimum of four support webs, short enough to allow slack in the gauze, should be placed evenly on the circumference of the net to run its entire length. Nets with a mouth area of 1 m² or more should have eight such webs. Transverse webs should

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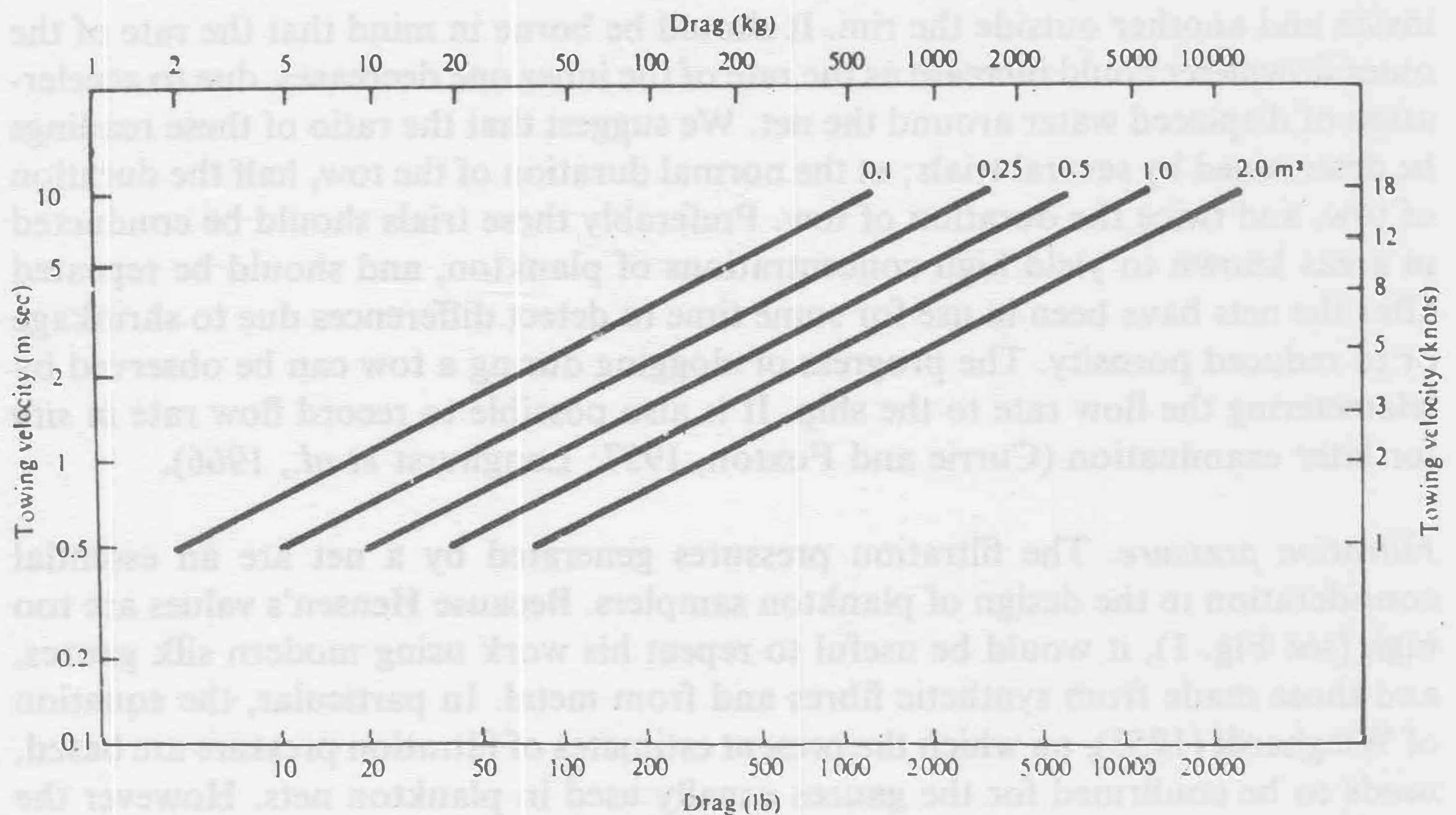
Figure 11

A graphical method for estimating the drag of nets with mouth areas of 0.1 to 2.0 m², towed at velocities of 0.5 m/sec (1 knot) to 9.50 m/sec (18 knots), assuming a drag coefficient of 1.33 (from Motoda, 1962).

not be used, as they stop the longitudinal oscillations of the filtering surface and are a site of plankton accumulation during the tow (Smith and Clutter, 1965).

CONTEMPORARY SAMPLERS

The diversity of nets in common use reflects the wide range of plankton species sought and the type of problems the nets are meant to solve. Most nets have not been tested thoroughly, either in the laboratory or in the field. We have attempted below to assess the probable filtration performance of a number of samplers whose specifications have been given in sufficient detail. In doing so, we would emphasize that assessments of this sort are an inadequate substitute for actual tests and should be checked against empirical observations whenever these can be obtained.

We have arbitrarily divided these samplers (Table 4) into high-speed (> 3 knots) and low-speed (< 3 knots) nets, with coarse (> 0.4 mm), medium (0.2-0.4 mm), and fine (< 0.2 mm) gauzes. Within each category, the nets are listed in decreasing order of open area ratio. An estimate of their initial filtration performance can be gauged from Tables 5 and 6.

Low-speed nets

These are taken to include those nets towed at less than 150 cm/sec, with the ship manoeuvred to maintain a vertical towing wire, adrift with a varying wire angle, or under way near its lower limit of speed to maintain a constant wire angle. In Table 5,

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values are given for the filtration efficiency, mesh velocity, approach velocity (and associated dynamic pressure), and filtration pressure, in some unenclosed nets with unreduced mouth openings and uniform mesh size. For the purposes of comparison, all the values are based on a towing velocity of 100 cm/sec (2 knots), but the towing velocities that would yield approach velocities of 5, 10, 15 and 20 cm/sec are also given.

The values in Table 5 are based on the resistance coefficient equation of Wieghardt (1953) and the filtration coefficient equation of Tranter (1967) (see 'Theoretical basis' above), assuming an even distribution of velocity and filtration pressure at all points on the filtering surface. Where nets have both cylindrical and conical sections, the values for the cylinder will be much lower, and the values for the cone much higher, than the average given here. If more accurate values of filtration efficiency are known from empirical observations, they should be substituted in the table to yield more accurate values of filtration pressure and mesh velocity.

The mesh velocities range from approximately 10-50 cm/sec and the filtration pressures from approximately 0.1-1 g/cm², the CalCOFI Anchovy Egg net and the Bongo net being at the lower end of the range, and the Marutoku nets at the higher. The table shows a parallel variation in the particular towing velocity which should be used to achieve a particular filtration performance. Some of the samplers could be towed at a much faster rate than 100 cm/sec while others should be towed more slowly. Because the cylinder-cone nets do not have an even pressure distribution at all points on the gauze, they are not suitable for an extension of the speed range without rearranging the proportions of gauze in the cone and cylinder.

It should be remembered that Table 5 indicates *initial* filtration performance only. The filtration performance at the end of a tow could be very different, depending on the fineness of the gauze, the open area ratio, the duration of the tow, and the plankton concentration in the water.

Coarse gauzes. The combination of large mesh size and high open area ratio (6.8) in the Bongo net would make clogging unlikely. The FAO larval tuna net (Matsumoto, 1967) was designed to filter 1,500 m³ of water at high efficiency, the mesh width being set at 0.5 mm (diagonal 0.7 mm); this net is not likely to clog because of the forward potential filtering section. Tests on the Interim net designed by WP-3 of the ICES-SCOR-Unesco Working Group on Zooplankton Sampling Methods (Smith, unpublished data) showed that it could filter 1,900 m³ of California Current water without clogging. The CalCOFI net (Ahlstrom, 1948) has a cylinder-cone shape, the mesh width (0.55 mm) being a compromise between the two sizes used in earlier nets (0.3 and 0.7 mm), to collect pelagic fish eggs and larvae; the probability of clogging is low in standard tows (15 minutes, oblique, from 140 m) but the net may not be able to withstand sustained towing in neritic surface waters.

Medium gauzes. The CalCOFI Anchovy Egg net was designed to filter 125 m³ of neritic water without change in filtration efficiency (Smith, Counts, and Clutter*); there has been no evidence of clogging in 2,000 15-minute tows in the California Current; the filtration pressure is low initially, but may rise considerably if clogging should reduce the open area ratio. The catch of the Australian Clarke-Bumpus

TABLE 4. Some contemporary nets

	Mouth area (m²)	Form	Mesh width (mm)	Porosity	Open area ratio	Reference
LOW-SPEED NETS (< 3 KNOTS)						
Coarse gauze (> 0.4 mm)						
Bongo net	0.38	Cone	0.51	0.51	6.8	McGowan and Brown, 1966
FAO-Larval tuna	0.79	Cyl-cone [1]	0.51	0.51	4.8	Matsumoto, 1966
WP-3 (Interim)	1.00	Cyl-cone	1.00	0.58	3.7	Fraser, 1966
CalCOFI Standard	0.79	Cyl-cone	0.55	0.36	3.2	Smith et al. *
Tropical Juday—large	1.00	Red-cone [2]	0.45	0.40	3.1	Bogorov, 1959
Medium gauze (0.2–0.4 mm)						
CalCOFI Anchovy Egg	0.20	Cyl-cone	0.33	0.46	7.8	Smith et al. *
Australian Clarke-Bumpus	0.012	Cone	0.27	0.44	5.3	Tranter, 1965
Indian Ocean Standard	1.00	Cyl-cone	0.33	0.46	4.3	Currie, 1963
NORPAC net	0.16	Cone	0.35	0.46	3.7	Motoda and Osawa, 1964
ICITA	0.79	Cone	0.28	0.42	3.1	Jossi, 1966
Marunaka	0.28	Cone	0.33	0.45	2.4	Nakai, 1962
Hensen Egg	0.42	Red-cone	0.30	0.44	2.1	Künné, 1933
Marutoku A	0.16	Cone	0.33	0.45	1.7	Nakai, 1962
Fine gauze (< 0.2 mm)						
WP-2	0.25	Cyl-cone	0.20	0.45	6.0	Fraser, 1966
Tropical Juday-Reg	0.50	Red-cone	0.17	0.32	4.2	Bogorov, 1959
Kitahara	0.05	Red-cone	0.11	0.32	4.2	Nakai, 1962
Flowmeter	0.38	Cyl-cone	0.17	0.32	3.2	Currie and Foxton, 1957
Bé net MPS	0.25	Pyramid	0.20	0.45	2.7	Bé, 1962a
Marutoku A	0.16	Cone	0.11	0.32	1.2	Nakai, 1962
Mixed gauzes			10.00			
International Standard	0.20	Cone	0.23	0.36		
			0.08	0.20	2.6	Ostenfeld and Jespersen, 1924
			10.00			
N 70	0.37	Cone	0.37	0.34	2.4	Foxton, 1956
			0.17	0.32		

Coarse gauze (> 0.4 mm)

Miller high speed I	0.0081	Red-cone[2]	0.95	0.57	28.0	Miller, 1961
Jet net	0.0110	Red-cone-Enc[3]	0.44	0.48	27.0	Clarke, 1964
Miller high speed II	0.0081	Red-cone	0.53	0.52	26.0	Miller, 1961

Medium gauze (0.2–0.4 mm)

Miller high speed II	0.0081	Red-cone	0.26	0.44	22.0	Miller, 1961
Gulf III modified	0.0320	Red-cone-Enc	0.38	0.44	13.1	Bridger, 1958
Hardy recorder	0.00016	Red-disc-Enc	0.22	0.37	11.8	Glover, 1953
Isaacs high speed	0.0005	Red-cyl-Enc	0.24	0.30	11.2	Ahlstrom et al., 1958
Catcher	0.0410	Red-cone-Enc	0.46	0.55	11.0	Bary et al., 1958
Hardy sampler	0.00029	Red-cone-Enc	0.22	0.37	8.1	Glover, 1953
Gulf III	0.1300	Red-cone-Enc	0.38	0.44	3.2	Gehringer, 1952
Small Hardy indicator	0.00013	Red-disc-Enc	0.22	0.37	2.3	Glover, 1953
Standard Hardy indicator	0.0011	Red-disc-Enc	0.22	0.37	1.4	Glover, 1953

Fine gauze (< 0.2 mm)

Jashnov high speed	0.25	Pyramid	0.17	0.32	1.9	Jashnov, 1961

1. Cylinder-cone.
2. Reduction cone-cone.
3. Encased gauze section.

TABLE 5. Initial filtration performance of some contemporary samplers, calculated from the equations of Wieghardt (1953) and Tranter (1967.)

Plankton sampler	Towing velocity: 100 cm/sec					Towing velocity which will give an approach velocity of:			
	Filtration efficiency (F)	Mesh velocity (v')	Approach velocity (v)	Dynamic pressure at v cm/sec (½ ρ v²)	Filtration pressure (K . ½ ρ v²)	$v = 5$	$v = 10$	$v = 15$	$v = 20$
		(cm/sec)	(cm/sec)	(g/cm²)	(g/cm²)		(cm/sec)		
Bongo	0.96	14	7	0.027	0.097	69	138	207	276
FAO Larval Tuna	0.97	20	10	0.054	0.176	49	97	146	194
WP-3 Interim	0.98	26	15	0.120	0.239	33	65	98	130
CalCOFI Standard	0.91	29	10	0.054	0.383	48	97	146	194
CalCOFI Anchovy Egg	0.95	12	6	0.016	0.089	90	179	269	358
Australian Clarke-Bumpus	0.88	17	7	0.027	0.158	52	104	156	208
Indian Ocean Standard	0.96	22	10	0.053	0.244	49	98	147	196
NORPAC	0.96	26	12	0.072	0.309	42	84	126	168
ICITA	0.95	31	13	0.084	0.456	39	78	117	156
Marunaka	0.88	37	16	0.138	0.553	30	61	91	121
Marutoku A (medium)	0.80	47	21	0.228	0.817	24	47	71	94
WP-2	0.94	16	7	0.025	0.161	71	142	213	284
Flowmeter	0.90	28	9	0.041	0.476	56	112	167	223
Bé Multiple	0.88	33	15	0.110	0.534	34	68	102	136
Marutoku A (fine)	0.59	49	16	0.125	1.237	32	64	96	128
Jashnov	0.78	41	13	0.089	0.871	38	76	113	151

(Tranter, 1965) compares favourably with that of the much larger Tropical Juday net and Indian Ocean Standard net (Barnes and Tranter, 1965); the filtration efficiency is only 4.6 per cent lower than in the sampler without a net (Tranter and Heron, 1965); clogging has been reported with other Clarke-Bumpus samplers (Yentsch and Duxbury, 1956; Regan, 1963) and in other mesh sizes; based on tests with nets of similar proportions, the sampler might begin to clog after filtering approximately 16 m³ of oceanic water and 4 m³ of neritic water.

The filtration efficiency of the Indian Ocean Standard net (Currie, 1963) has been measured at 70-90 per cent (Motoda *et al.*, 1963) but these figures are probably a little low; the net is not likely to clog when hauled vertically in central water masses, but may do so when the wire-angle is high or the water rich in plankton. The ICITA net (Jossi, 1966) was adopted as a general purpose net for oblique tows from 200 m in tropical waters; tests on analogous conical nets indicate a high probability of clogging in tows longer than 10 minutes, in all but the central water masses. The Marunaka and Marutoku nets (Nakai, 1962) are used in brief vertical tows; their initial filtration efficiency is low and would rapidly decrease with clogging. The Hensen Egg net (Table 6) was also designed for brief vertical tows; due to its reduction cone (see 'Practical consequences' above) the initial filtration efficiency is greater than 100 per cent but the low open area ratio (2.1) and the small mesh size make this net extremely sensitive to clogging; this would increase the filtration pressure and raise the mesh velocity through the remaining apertures.

Fine gauzes. The WP-2 net (Fraser, 1966) was designed to be hauled vertically from 200 m in the open ocean, and from near bottom to the surface on the continental shelf; tests on the prototype (Smith, unpublished data) showed that its initial filtration efficiency (94 per cent) dropped to 38 per cent after 5 minutes' towing at 2.3 knots (Fig. 12); as a result of the tests, the open area ratio was increased from 5 to 6 (Fraser, 1966) and it was recommended that two flowmeters be used to monitor clogging, one inside and one outside the entrance. The Tropical Juday net (Bogorov, 1959) and the Kitahara net (Nakai, 1962) have similar open area ratios (4.2); the initial filtration efficiency probably exceeds 100 per cent (due to the reduction cone) and the probability of clogging would be high in tows longer than 50 m in waters rich in plankton. The Flowmeter net (Currie and Foxton, 1957) is used for vertical tows, and has given no sign of a decrease in filtration efficiency attributable to clogging. The Bé multiple plankton sampler (Bé, 1962a) is usually used in a descending oblique tow, the entire net being changed within the entrance at preset depths; there would be an interaction between adjacent nets but the effect of this is difficult to predict; the filtration pressure would be relatively high and the particular net which samples the upper layer would be sensitive to clogging. The filtration efficiency of the Marutoku A net (Nakai, 1962) would be very low, and would rapidly decrease as the net clogs (Ito and Nishimura, 1958).

Mixed gauzes. The ICES Standard net would have an initial filtration efficiency of approximately 80 per cent; however, Gibbons and Fraser (1937b) found the net to be only 56 per cent efficient after filtering 3.5 m³ of neritic water containing *Ceratium*. The initial filtration efficiency of the Discovery N70 net (Foxton, 1956)
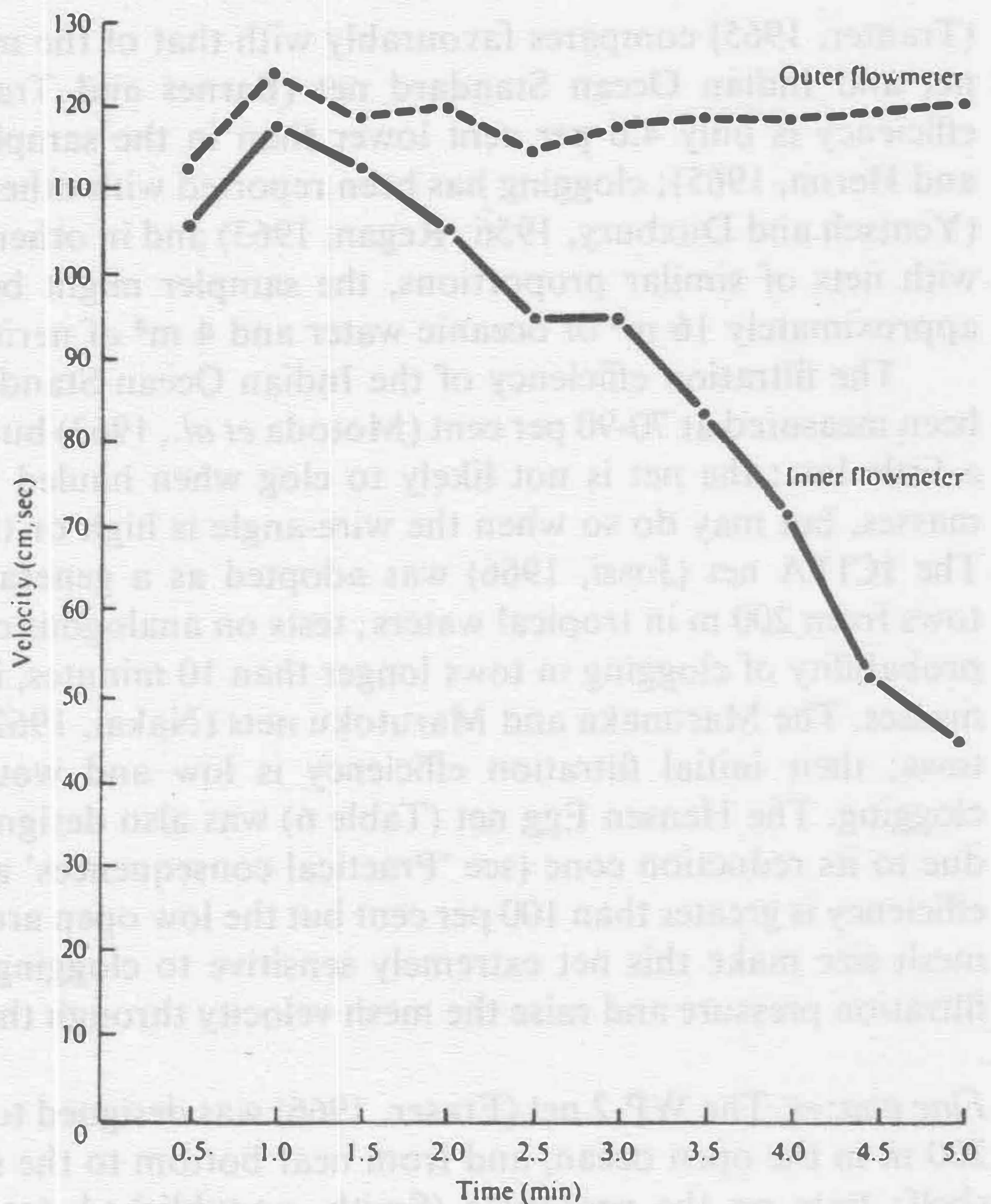
Figure 12
The clogging rate of an
early model of the WP-2
net (Fraser, 1966) being
towed at 120 cm/sec in
neritic water off San Diego,
California. Clogging is
indicated by the progressive
decrease in the velocity
of the water through
the mouth of the net.

is probably of the same order, and the posterior section of fine gauze (0.17 mm) is equally likely to clog.

The filtration performance of such nets is not well understood, particularly the effect of clogging in the finer part upon filtration in the coarser part. Presumably, as the fine gauze clogged the coarse part would progressively become the effective filtering surface, and the velocity of the water through the coarse meshes would increase. It is more difficult to nominate the consequent effect upon filtration pressure at various sites of filtration.

The usefulness of nets made from more than one gauze has yet to be clearly demonstrated. Sometimes a coarse gauze is used around the throat of the net to hasten its rate of descent, as in the Indian Ocean Standard net, but there could well be other equally satisfactory solutions to this logistic problem. Until much more is known about the complexity of their filtration performance, we would recommend that nets with mixed gauzes should be replaced by nets with a uniform gauze throughout.

High-speed nets

The filtration performance of contemporary high-speed nets is less well understood than that of low-speed nets. The presence of mouth-reduction cones, encasements,

TABLE 6. Formulae for the initial filtration performance of some contemporary plankton samplers with mouth-reducing cones (in terms of the filtration efficiency, F)

Plankton sampler	Filtration efficiency (F)	Towing velocity: 100 cm/sec				Towing velocity which will give an approach velocity of:			
		Mesh velocity (v')	Approach velocity (v)	Dynamic pressure at v cm/sec ($\frac{1}{2}\varrho v^2$)	Filtration pressure ($K . \frac{1}{2}\varrho v^2$)	$v = 5$	$v = 10$	$v = 15$	$v = 20$
		(cm/sec)	(cm/sec)	(g/cm²)	(g/cm²)	(cm/sec)			
Large Juday	—	32 F	13 F	0.085 F^2	—	39/F	77/F	116/F	155/F
Hensen Egg	—	48 F	21 F	0.224 F^2	—	24/F	48/F	72/F	95/F
Tropical Juday	—	24 F	7.6 F	0.030 F^2	—	66/F	131/F	197/F	263/F
Kitahara	—	24 F	7.6 F	0.030 F^2	—	66/F	131/F	197/F	263/F
Miller I	—	3.6 F	2.0 F	0.002 F^2	—	246/F	491/F	737/F	982/F
Jet	—	3.7 F	1.8 F	0.002 F^2	—	281/F	563/F	844/F	1125/F
Miller II (coarse)	—	3.8 F	2.0 F	0.002 F^2	—	250/F	500/F	750/F	1000/F
Miller II (medium)	—	4.5 F	2.0 F	0.002 F^2	—	250/F	500/F	750/F	1000/F
Gulf-III modified	—	7.6 F	3.4 F	0.006 F^2	—	149/F	298/F	447/F	595/F
Hardy recorder	—	8.5 F	3.1 F	0.005 F^2	—	159/F	319/F	478/F	638/F
Isaacs high speed	—	8.9 F	2.7 F	0.004 F^2	—	187/F	373/F	560/F	747/F
Bary catcher	—	9.1 F	5.0 F	0.013 F^2	—	100/F	200/F	300/F	400/F
Hardy sampler	—	12.3 F	4.6 F	0.011 F^2	—	109/F	219/F	328/F	438/F
Gulf III	—	31 F	14 F	0.096 F^2	—	36/F	73/F	109/F	145/F
Small Hardy indicator	—	43 F	16 F	0.132 F^2	—	31/F	62/F	93/F	124/F
Standard Hardy indicator	—	71 F	26 F	0.356 F^2	—	19/F	38/F	57/F	76/F

valves, constricted exhausts, or combinations of these, affects flow through these samplers more than does the filtering surface. For example, Bary *et al.* (1958) compared the flow through a 23 cm diameter cylindrical tube with the flow through the body of an encased sampler 23 cm in diameter at the entrance and exhaust and 30 cm in body diameter, the comparison being made both with nets and without. The filtration performance of the sampler, based on the volume of water contained in a 23 cm diameter cylinder projected ahead of the entrance, was 58 per cent for the sampler body without a net, 51 per cent for the sampler with a coarse net, and 46 per cent for the sampler with a fine net. The effective radius of collection corresponded to 11.4 cm for the open cylinder, 8.7 cm for the sampler with a coarse net, and 7.7 cm for the sampler with a fine net.

Because of this dependence upon their shape and their design, we have not attempted to estimate the filtration efficiency of such complex samplers. The comparison of filtration performance given in Table 6 is based upon an unknown filtration efficiency (F) which can be replaced with empirical values as they become available. It is probable, for instance, that the Miller nets, the Jet net, the Hardy recorder, and the modified Gulf III would be found to have relatively low filtration pressures at, say, 6-12 knots, while the Hardy indicators would be found to have relatively high filtration pressures. This conclusion must be weighed against the following observations: the Jet net has been launched and recovered at speeds as high as 18 knots (967 cm/sec) and living crustaceans have been taken from the sample (Clarke, personal communication); Miller high-speed nets are used routinely to 8 knots, but damage to fish larvae occurs at higher speeds (Le Brasseur, personal communication); Ahlstrom (personal communication) noted damage to fish larvae in the modified Gulf III at 9 knots, which was not evident at 6 knots; Glover (1953) found that catches with Hardy indicators 'suffer some squashing', whereas catches taken by the small Hardy sampler were 'quite undamaged'.

4

Avoidance of samplers

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SUMMARY

Despite contradictory results, the accumulated evidence that avoidance occurs among animals usually designated as 'plankton' is overwhelming. This is especially true for small fishes. Many kinds of zooplankton can respond to acceleration, cyclic and non-cyclic pressure variations, and light variations. Little is known about the details of these responses. Some of the more straightforward theoretical aspects of sampling geometry are considered. To specify, in detail, the design criteria for sampling devices requires knowing, in equal detail, the purpose and requirements of the intended sampling programme. Calibration of catching efficiency is only a partial solution to the avoidance problem; it must accompany the development of more effective samplers. Recommendations are made regarding the more obvious elements of the solution.

INTRODUCTION

There is no single instrument that can sample quantitatively the complete spectrum of pelagic organisms, nor even all components of the zooplankton (Anon., 1964a). In this review we are concerned only with the 'netable' plankton. Knowledge of this group is determined largely by the catching characteristics of the sampling devices. Very small animals may pass through net meshes (see Chapter 5). and larger, more responsive, and more motile animals may avoid capture.

Avoidance adversely affects estimates of total living matter, estimates of population parameters for individual species, indices of diversity (McGowan and Fraundorf, 1966; Lloyd and Ghelardi, 1964), and interpretation of vertical migration (Brinton. 1965; Pearcy and Laurs, 1966).

As pointed out by McGowan and Fraundorf (1966) and Fager and McGowan (1963), it is not sufficient to sample only the more abundant or more catchable kinds of animals. Most species encountered in a limited volume of water are represented by only a few individuals. But the sum of these uncommon species can be a numerically significant part of the community, and uncommon species can occupy key positions in food webs; carnivores are rarer than their prey. Further,

TABLE 1. Précis of some reports on avoidance of sampling devices

Reported by	Source of evidence	Kinds of animals	Conclusions
Mackintosh (1934).	Visual observation net at sea surface.	Euphausiids.	Avoidance observed.
Winsor et al. (1940).	12.7 cm diameter net compared 75 cm net.	Copepods.	Smaller net as reliable as net of more usual size.
Silliman (1943).	Day-night differences in 1 m diameter net.	Sardine.	Larger larvae under-sampled in daylight hours.
Bowers (1952).	Day-night differences in net catches.	Herring.	More larvae taken at night.
Ahlstrom (1954).	Day-night differences in 1 m diameter net.	Sardine.	Larger larvae markedly under-sampled during daylight hours.
Bridger (1956).	Day-night differences (including Helgoland and Petersen trawl).	Herring, pilchard.	More and larger post-larvae caught at night.
Bridger (1958).	Day-night comparison, 20 cm and 40 cm G-III nose cones.	Herring, *Sagitta*.	More per m³ 20 cm; more night than day 40 cm, night-day same 20 cm.
Ahlstrom et al. (1958).	2.5 cm diameter at 10 knots compared 1 m diameter at 1.5 knots.	Small fishes.	About 30 times as many taken in high-speed hauls.
Arnold (1958).	½ m G-III at 4–5 knots compared 1/2 m net at 1–2 knots.	Fish larvae.	Larger larvae and about 2 times as many in G-III samples.
	2.8 cm diameter sampler compared 1/2 m G-III at 4–5 knots.	Fish, plankton.	Higher volumes and 2.6–4.3 times more larvae per m³ in larger sampler.
Aron (1958).	½ m tow net compared 7.6 cm pump.	Copepods.	Pump samples contained more than tow net samples per m³.
Tibbo et al. (1958).	Day-night differences in 1 m diameter net.	Herring.	Greater numbers larvae at night, especially of larger sizes.
Ahlstrom (1959).	Day-night differences in 1 m diameter net.	Mackerel, anchovy.	Jack mackerel same day-night (1,000 samples). Anchovy 5 times more at night.
		12 other spp. larvae	12 other spp. night/day = 3.6 (range 1.7–14.4).
Hansen (1960).	High-speed (1.3 cm diameter) compared slow Hensen net.	Adult euphausiids	Many more taken per m³ in high-speed tows.
Colton et al. (1962).	Hardy recorder (2 cm) at 10 knots, compared 1 m net at 3 knots.	Herring.	More, larger larvae high speed; larger larvae avoid 1 m net day.
Henderson (1961).	Hardy recorder, high speed, compared conventional nets.	*Sebastes marinus*.	Sizes of larvae similar in samples.
Miller (1961).	Day-night differences 10 cm diameter sampler at 7 knots.	Haddock.	Catches of larvae same day and night.
Colton et al. (1962).	Hardy (2 cm) 10 knots compared 1 m net and C-B (13 cm) 3 knots.	Cod and haddock.	Larvae recorder samples larger (max. 40 mm) than 1 m net (29 mm) and C-B (11 mm).
			Recorder numbers same day-night (larvae larger night), C-B more at night than day.
Aron (1962b).	Isaacs-Kidd trawl compared conventional tow nets.	Mysids.	Consistent large catches mysids I-K trawl, infrequent conventional nets.

Reference	Method	Subject	Findings
Brinton (1962).	Isaacs-Kidd trawl compared Clarke-Bumpus sampler.	Adult euphausiids.	Euphausiids dominant in I-K trawl, rare in C-B samples.
Hansen (1962).[1]	1 m net compared 45 cm net.	15 spp. euphausiids.	No demonstrable differences between nets.
Hansen et al. (1962).	Gulf-III compared 2 m stramin net.	Whiting.	Stramin net large numbers larvae, G-III none.
	8 litre bottles compared Hensen and 1/2 m net.	Copepods.	More per m³ in bottle samples than in net samples.
Harry (1962).[2]	Gulf-III at 7 knots, 20 cm nose cone, compared 40 cm.	*Sagitta* spp.	More per m³ with 20 cm nose cone, both day and night.
Yentsch et al. (1962).	12 cm Clarke-Bumpus, 20 cm C-B and 75 cm net compared.	Plankton volume.	Similar volume per m³ for all three samplers.
Regan (1963).	12 cm Clarke-Bumpus at 2.3–3.6 knots compared 3.2–3.6 knots.	Euphausiids.	Somewhat more adults at higher speed.
Tranter (1963).	IOSN (113 cm), Juday (80 cm), C-B (12 cm) compared.	Plankton volume.	No demonstrable differences in volume per m³ among nets.
Barnes et al. (1965).	IOSN (113 cm), Juday (80 cm), C-B (12 cm) compared.	Weight and number of plankton.	No evidence larger zooplankton avoid small nets more than large.
Brinton (1965).	Day-night differences in 1 m diameter net.	Euphausiids.	Some vertical migrations, species same day-night; some fewer day. Non-migration upper layer, species fewer day.
Fleminger et al. (1965).	45, 32, 22 cm mouth nets in light and dark.	Mysids, 6 copepods.	Smaller nets fewer; fewer mysids caught in light.
Pearcy et al. (1966).	Day-night differences I-K trawl.	Mesopelagic fish.	Night-time increase 3 spp. near surface attributed to avoidance.
Clutter (unpublished).	Visual observations, 20 cm net under water.	5 spp. mysids.	Avoidance observed.
Le Brasseur et al. (1965).[3]	White and dark-coloured nets compared, day and night.	Cop., chaet., euph., amph.	Euphausiids: dark net 3 × white in day, 2 × white at night; night 2 × day for dark net, 4 × for white.
	Hauling speeds of 0.5–3 m/sec compared.	Cop., chaet., euph., amph.	Increased catch euphausiids at higher speed, other spp. variable.
	Nets 0.1, 0.25, 0.42 m² mouth areas compared.	Cop., chaet., euph., amph.	0.25 m² more than 0.1 m²; 0.42 m² not significantly more than 0.25 m².
Kinzer (1966).[3]	20 cm high speed compared 120 cm net and I-K trawl.	Mesopelagic fish.	Smaller mouth diameter high-speed sampler caught fewer fish.
Aron (1966).[4]	I-K trawl 2 knots and 4 knots, light measured.	Sergestide, fish.	Larger fish at higher speed, fewer fish in more light.
Aron (1966).[3]	I-K trawl 2 knots and 4 knots, light measured.	Sergestide, fish.	As above, except higher speed resulted in larger catch 1 sp. fish.
Clutter et al. (1966).[4]	45, 32, 22 cm nets; light and dark; 0.5, 1.5, 2.5 knots.	12 groups plankton.	No difference among nets of different size. More caught at higher speed.
Cushing (1966).[4]	Day-night differences, Gulf-III type sampler.	Plaice larvae.	More larvae of all stages by day than by night.

(Continued overleaf)

TABLE 1 (continued)

Reported by	Source of evidence	Kinds of animals	Conclusions
Gilfillan (1966).[3]	Nets 100 cm, 70 cm, Bary Catcher at 0.7, 2, 4 knots.	Euph., copepods.	Relative catch euphausiids, *Euchaeta* sp., *Calanus* spp.; more of all spp. at higher speeds.
McGowan *et al.* (1966).[4]	20, 40, 60, 80, 100, 140 cm nets, drogus station.	Molsc., euph., fish.	Smaller nets underestimated both number of species and abundance per m^3.
Neunes (1966).[4]	Sampler at 7 knots compared small ring nets.	Zooplankton.	More animals in samples taken at higher speed.
Pearcy (1966).[4]	Day-night differences in Isaacs-Kidd trawl.	Euphausiids, fish.	1.5–2.5 times as many fish at night; euphausiid avoidance uncertain.
Tranter (1966).[4]	$\frac{1}{2}$ m², $\frac{1}{4}$ m², $\frac{1}{20}$ m², mouth nets compared.	3 groups plankton.	No demonstrable differences among nets.
	Tow speeds 0.4–4.0 knots compared.	3 groups plankton.	More copepods and appendicularia, fewer euphausiids, at higher speeds.
Vannucci (1966).[1]	C-B samplers with, without nose cones, forward obstructions.	Zooplankton.	Effects obscured by other factors.

1. 'Discussion' in Gehringer (1962).
2. Reported by Gehringer (1962).
3. Unpublished personal communication.
4. Reported at the Symposium on the Hydrodynamics of Plankton Samplers. Sydney, February 1966.

determining the degree of spatial isolation between populations of given species of zooplankton is an important aspect of the study of speciation in the sea. The absence of certain animals from samples, whether by chance (see Chapter 7), or because they avoid capture, often must be construed as evidence that they do not occur at the place of sampling.

EVIDENCE OF AVOIDANCE

Nine papers giving evidence on avoidance were presented at the Symposium on Hydrodynamics of Plankton Samplers, Sydney, February 1966 (see latter part of Table 1). They dealt with net size, towing velocity, and light condition, or combinations of these, as they affected sampling for fishes and for invertebrates. Results of the experiments reported were inconsistent.

In two cases, large nets did not catch significantly more animals per unit volume filtered than small nets. Tranter[*][1] showed this for total euphausiids, total copepods, and total appendicularia. Clutter, Fleminger, and Smith* showed that net size was but one of the elements of capture for twelve groups of invertebrates. Conversely, McGowan and Fraundorf* reported that more species and greater numbers of pelagic molluscs, euphausiids, and fish larvae were taken with large nets. They indicated that avoidance did not become very apparent until nets with a fairly wide range of mouth sizes were compared.

In two cases, increased towing velocity did not result in significantly higher catches per unit volume. Aron's* data showed no demonstrable effect of towing speed on numbers of fishes and shrimps caught; however, fast tows caught more large fish and slow tows caught more small ones, suggesting that the larger fish avoided the net at low speed, and small ones were squeezed through the net at high speeds. In a later communication, Aron reported that, in subsequent trials, larger catches of one species of fish were taken at higher speeds. Tranter* reported that fewer euphausiids were caught at higher speeds. Conversely, Tranter* showed that more small copepods and appendicularia were taken at higher speeds; Neunes* found more animals in samples taken at higher towing speed; Clutter, Fleminger, and Smith* reported that, in general, more animals were taken at higher speeds; and Gilfillan* reported that catching efficiency increased with increased speed, especially for larger animals.

Vision-associated avoidance was demonstrated for mesopelagic fishes by Pearcy* and experimentally for mysids by Clutter et al.* Aron* reported that more fishes (Lampanyctus leucopsaris and Leuroglossus stilbius) were taken in lower light intensities: subsequent trials (personal communication) confirmed this. Cushing's data showed more plaice larvae taken by day than by night with a high-speed sampler.

Considering the inconsistent nature of other reported results on avoidance of sampling devices (Table 1), the inconsistencies noted above are not surprising. About three-fourths of the reports on fish larvae and about two-thirds of the reports on invertebrates indicated that avoidance occurred. Figures 1 and 2 are illustrative examples.

1. Asterisked (*) references denote information presented at the Sydney Symposium.
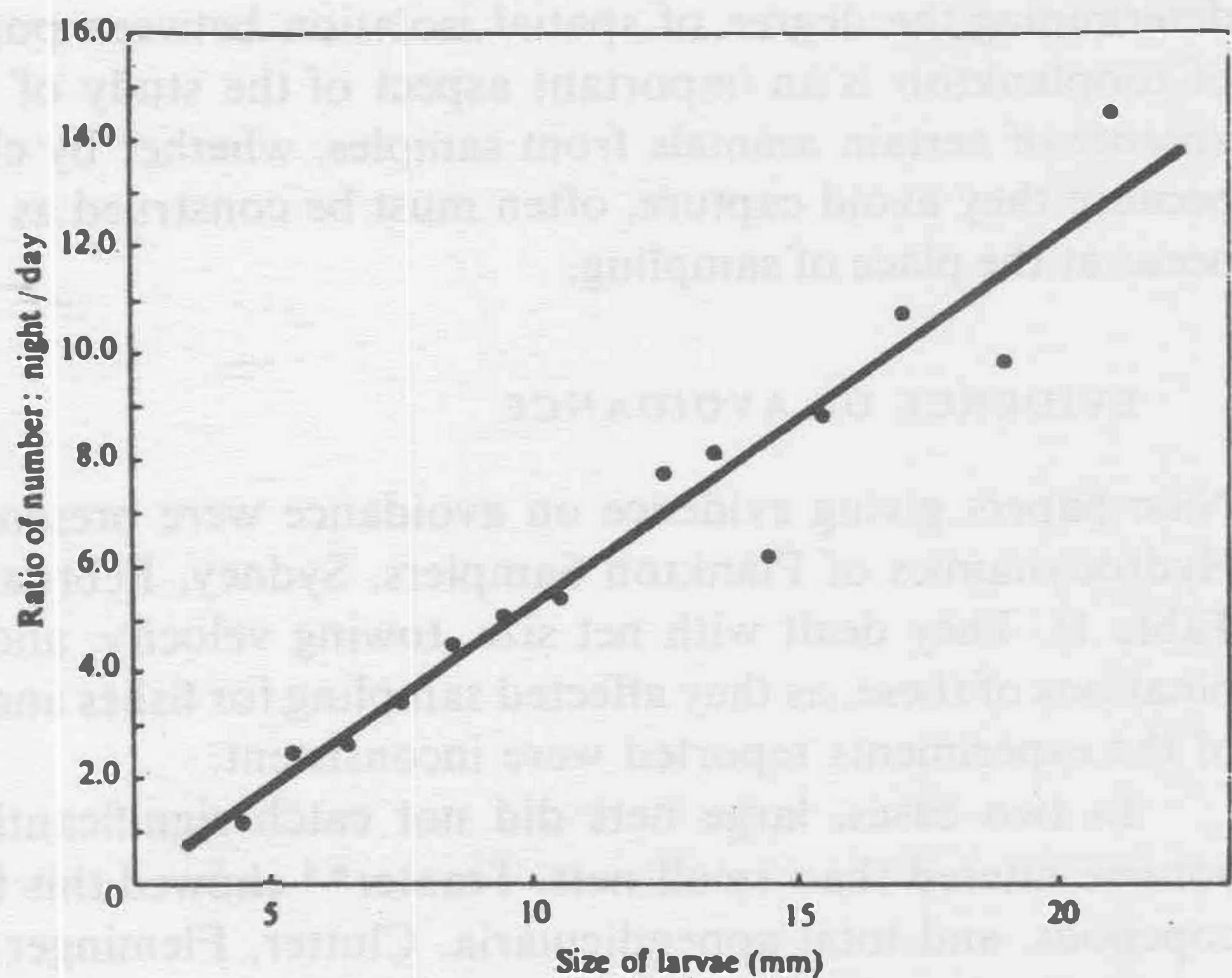
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Figure 1
Undersampling of sardine
larvae in daylight hauls
compared with night hauls,
as a function of size
(from Ahlstrom, 1954).

For several reasons, one must be cautious about making generalizations from the results of individual observations or experiments. Results of field sampling may include unmeasured differences in filtering rates of samplers (apparently, both Neunes'* and Vannucci's* results were so affected), and unmeasured effects caused by clogging of net meshes (see Chapter 3). For example, clogging might have caused the apparent lower number of copepods per cubic metre in nets compared with water-bottles, reported by Hansen and Andersen (1962). To determine avoidance in such cases, presumably non-motile organisms can be used as an index for comparing catches of motile animals between samplers, but the choice of index organisms is critical.

Escapement or extrusion through net meshes (see Chapter 5) sometimes may be confused with avoidance. For example, the data reported by Aron (1958b)—that more copepods per cubic metre were taken in 7.6 cm diameter pump samples than in simultaneous samples with a flow-metered half-metre tow net—may have resulted from extrusion through the meshes rather than from avoidance. This could have affected also the results of Hansen and Andersen (1962).

Evidence of avoidance can be obscured by the high sampling variability engendered by patchiness in plankton populations (see Chapter 7) and by vertical migrations. Perhaps the major shortcoming of field experiments on avoidance is that the variance between 'replicate' samples is so high (due to patchiness) that avoidance effects may be obscured. Also, samples to be compared sometimes are not taken in the same strata (e.g., Ahlstrom et al., 1958), or at the same time (e.g., Colton et al., 1962; Aron, 1962b; Arnold, 1958; Hansen, 1960). When comparing day-night catches of animals that undergo vertical migrations the entire water column in which they occur must be sampled (Ahlstrom, 1954; Pearcy and Laurs, 1966). The effect of patchiness can be reduced by sampling around drogues (McGowan and Fraundorf, 1966). One method of reducing some ·of the effects of vertical migration, large-scale patchiness, and variation caused by vessel speed and drift is to do experiments on captive populations (Fleminger and Clutter,
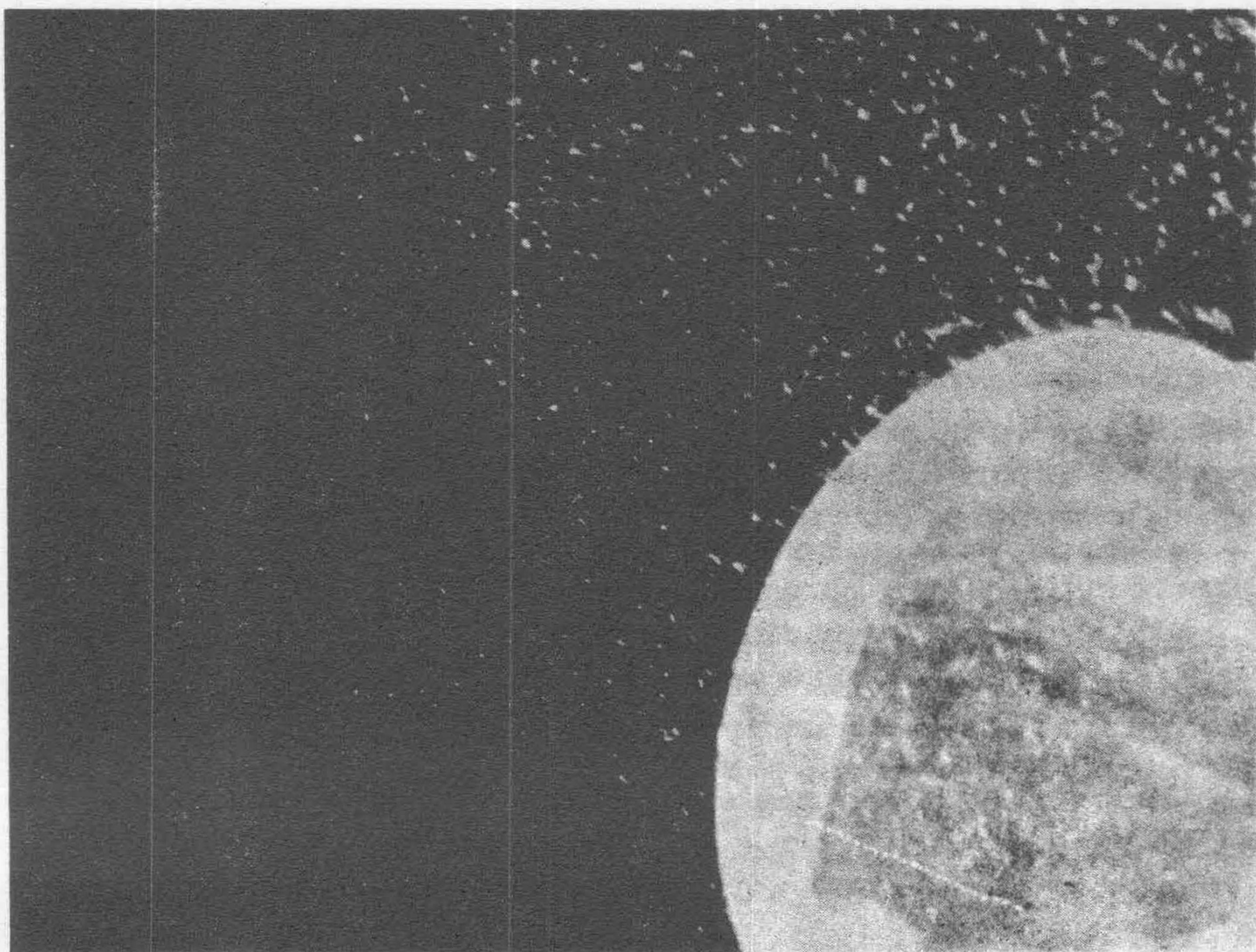
Figure 2
Reaction of schooling mysids to a sampling net. Animals
at the periphery of the swarm seem to sense the presence of
the net partly through the activity of those nearer to the source
of disturbance.

1965). But this limits the kinds of animals that can be studied and precludes studies
of natural diversity. Also, experimental conditions (e.g., light intensity) may not
duplicate natural conditions, and secondary problems such as reduced viability or
changes in behaviour can arise because of confinement of the animals (Clutter
et al.*).

Avoidance can result not only in a general underestimation of abundance but
also in selective sampling. The larvae or the juveniles of a species may exhibit
different behaviour, so that samples do not reflect true age distribution. Variations
in load or shape of the body associated with the carrying of eggs or young may
influence mobility. It is possible for physiologically weak animals, of any size or
stage of development, to be over-represented in samples, relative to robust animals.
Moulting and recently moulted Crustacea are not likely to be capable of much
avoidance, and Isaacs' (1965) statement: '. . . the day-caught (sardine) larvae
(compared with the night-caught larvae) are shown to be a measure of (natural)
mortality of the population', implies that only the weaker or less alert sardine
larvae are caught during the daytime.

Despite contradictory results, the accumulated evidence that avoidance occurs
among animals usually designated as plankton is overwhelming. Degree of avoidance

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is not necessarily a direct function of the size of the organism. Smaller species may show more avoidance than closely related larger species (Fleminger and Clutter, 1965; McGowan and Fraundorf, 1966). The evidence for avoidance is necessarily conservative, because all comparisons are made against non-absolute standards that may themselves include effects of avoidance.

PHYSICAL DISTURBANCES AND RESPONSE OF ZOOPLANKTON

Control of the swimming path or position can involve perception of any one or more of a variety of stimuli, including light, gravity, angular acceleration, linear acceleration, pressure variation, or direct contact with an object. Not very much is known concerning perception or response by plankton animals.

Towed plankton samplers are often preceded by solid objects such as bridles and tow lines. Halliday* pointed out that towed samplers cause water currents, acceleration, pressure variation in the form of low-frequency vibrations and sound waves, and variation in light intensity. The displacement of water by a towed object gives rise to a non-cyclic pressure variation that decays fairly rapidly with distance. The production of a frictional wake around a towed object leads to pressure variation comprised of both non-cyclic and cyclic components (low-frequency vibrations and sound) that decay less rapidly with distance. The disturbance caused by the towing cable is likely to contain very strong higher frequency components.

Acceleration

Smith* presented evidence that, even though they may be filtering water with high efficiency (95 per cent or more), 1 m diameter towed nets may be preceded by acceleration fronts that are detectable (with flowmeters) up to 1.5 m ahead of the net rims (Fig. 3). This acceleration increases as filtering efficiency decreases (see Chapter 3). Also, tow lines and bridles cause water acceleration and turbulence. Smith (personal communication) thinks that the observed acceleration fronts are adequate to elicit avoidance responses; the copepod *Labidocera* was found to respond to 0.1 ml of water moving at 7.5 cm/sec at 5 cm distance from the animal (see the discussion of swimming velocity, page 71).

Fishes can detect acceleration by means of the inner ear. Many pelagic invertebrate groups, including coelenterates, ctenophores, annelids, crustaceans, thecosomes, heteropods, squids, and octopus have statocysts by which angular accelerations may be detected. Some crustacea (*Homarus*) respond to angular accelerations of 6°-9°/sec. Information on detection of linear acceleration is meagre. Apparently one crustacean (*Astacus*) has been reported to be sensitive to linear acceleration and deceleration; there was no convincing evidence that the statocysts were involved (Cohen and Dijkgraaf, 1961). In animals without statocysts, reflex responses are still theoretically possible through 'proprioception' receptors that respond to the movements of internal organs or liquids, and through displacement of setae.

Acceleration fronts ahead of sampling devices are non-uniform. This is especially true for nets preceded by bridles and tow lines, and for devices that suck

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140 cm sec (2.8 knots)
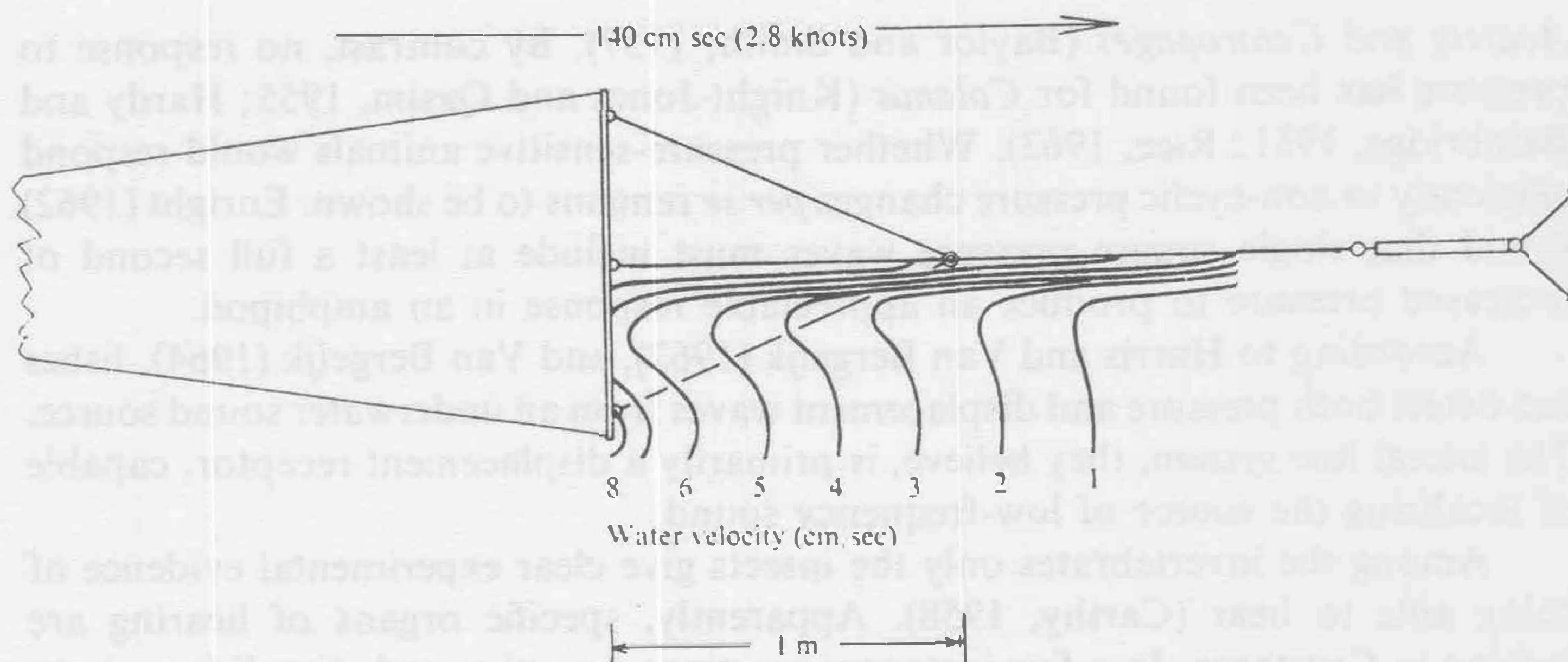
8 6 5 4 3 2 1

Water velocity (cm sec)

1 m

Figure 3
Velocity profile ahead of 1 m plankton net (from Smith
et al., unpublished tests on hydrodynamics of plankton
sampling devices done at the United States Navy David
Taylor Model Basin, Washington, D.C., May-June 1965).

water into their mouth openings (e.g., Hensen net). The shear forces associated
with uneven acceleration can be detected as pressures or tensions on the bodies,
and by tactile hairs or appendages used for steering. Through response of their
lateral line organs (Lowenstein, 1957), fishes can detect small currents created by
other fishes in their vicinity. Some mysids seem to be capable of responding to the
presence and orientation of their fellows by detecting respiratory and swimming
currents (Clutter, unpublished data).

Stone* pointed out some interesting aspects of the roles of particle size and
specific gravity in sampling bias associated with acceleration. The drag of a net
will cause some water to be pushed to the side; therefore, relative to the moving
net, the water particles will have a curved trajectory. Denser particles will tend
to take a straighter path than the water particles, and as a result will be over-
represented in the sample. The higher the specific gravity and the larger the particle
size, the stronger this effect will be. Conversely, the particles lighter than water
(e.g., some fish eggs) will be under-sampled. The reverse would hold for devices
that sucked water in at the mouth. In any case the effects would be insignificant if
the fall (or rise) velocity of the particle is less than about 0.5 cm/sec.

Pressure variation and cyclic displacement

The existence of acceleration implies the existence of pressure gradient. According
to Brooke and Woodward (1956) the reaction of copepods to rapid acceleration
is a function of changes in pressure field.

Non-cyclic changes in hydrostatic pressure are detected by fishes (Prosser and
Brown, 1961), amphipods (Enright, 1962), mysids (Rice, 1961), decapod larvae
(Hardy and Bainbridge, 1951), hydromedusae, ctenophores, larval worms, and
the copepod *Caligus rapax* (Knight-Jones and Qasim, 1955), and the copepods

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Acartia and *Centropages* (Baylor and Smith, 1957). By contrast, no response to pressure has been found for *Calanus* (Knight-Jones and Qasim, 1955; Hardy and Bainbridge, 1951; Rice, 1962). Whether pressure-sensitive animals would respond efficiently to non-cyclic pressure changes *per se* remains to be shown. Enright (1962) found that single square pressure waves must include at least a full second of increased pressure to produce an appreciable response in an amphipod.

According to Harris and Van Bergeijk (1962), and Van Bergeijk (1964), fishes can detect both pressure and displacement waves from an underwater sound source. The lateral line system, they believe, is primarily a displacement receptor, capable of localizing the source of low-frequency sound.

Among the invertebrates only the insects give clear experimental evidence of being able to hear (Carthy, 1958). Apparently, specific organs of hearing are lacking in Crustacea. In a few instances reactions to real sound stimuli have been observed, but the receptors involved were unidentified and might be unspecific (Cohen and Dijkgraaf, 1961). According to Prosser and Brown (1961), some shrimps and mysids (Hensen, 1863) are sensitive to sound waves and become less sensitive after removal of statocysts. On two occasions, Smith (unpublished data) observed several copepods of the genus *Labidocera* to show immediate locomotor activity in response to the operation of an underwater motion picture camera. Theoretically there is no reason why sound could not cause displacement of statocysts, hairs, or joints that have receptors sensitive to vibrations.

Even when sound is detected it might be difficult for plankton to locate the source. Sound shadows might play a part in localization, but they are not so well defined as light shadows. Many planktonic animals have about the same acoustical impedance as sea-water. For plankton to locate a sound source by comparing the time lag between pulses received at each of two paired receptors seems unlikely. For example, the maximum time lag between a sound pulse reaching the alternate tips of the antennules of a 3 mm copepod would be about 2×10^{-6} sec, and between the ears of a 5 mm anchovy larva about 2×10^{-7} sec. Nerve transmission is all-or-none, followed by a refractory period of inexcitability. The time constant range is 7×10^{-4} to 6×10^{-3} sec (Prosser and Brown, 1961). Therefore, the cycle of depolarization and repolarization of a reflex arc would take 350-30,000 times as long as the time lag between stimulus reception. If these values are correct, it would require that non-directional paired sensors be separated by a distance of something like 1 m to take a bearing on the direction of high-frequency vibrations. But if they have individual displacement sensors capable of indicating displacement direction, the animals should be able to localize the source.

Light variation

Man can detect broad-field light intensities of about 10^{-12} that of full noon sunlight. Epipelagic fishes may have similar capability. Partly because they have relatively the largest eyes of any vertebrates (Brett, 1957), bathypelagic fishes may be 10 to 100 times as sensitive to light as Man (Denton and Warren, 1957). Nicol (1959) determined the approximate minimum values for the attraction of Crustacea to be about 10^{-10} that of surface sunlight. This accords fairly well with the observation
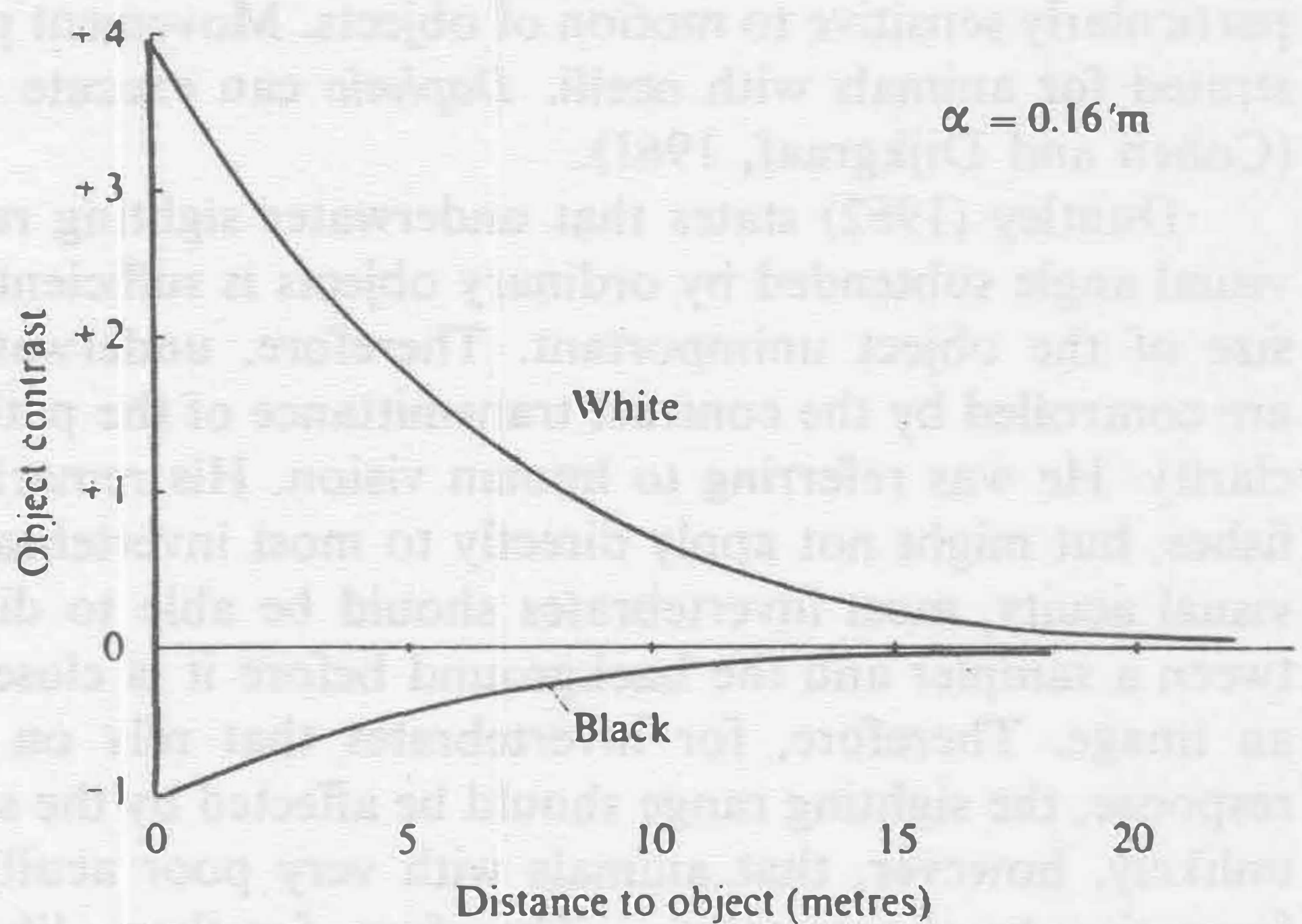
Figure 4
Change in contrast with
distance for two objects,
one with a high reflectance
white) and one with
a low reflectance (black)
(from Hester and Taylor,
1965).

that some bathypelagic carideans apparently respond to light by undertaking vertical migrations at depths of 800-1000 m (Waterman, 1961).

The minimum ratio of the just detectable difference in stimulus intensity to the prevailing light intensity (maximum intensity discrimination) for Man is about 0.6 per cent (Prosser and Brown, 1961). One might expect a value of about 1 per cent for fishes. For a crustacean with compound eyes, values were found to range from 1.2 to 4.2 per cent (Waterman, 1961). Values for Cladocera were 1-10 per cent (Baylor and Smith, 1957). Discrimination varies with prevailing intensity. For *Daphnia,* Heberdey and Kupka (1942) found the maximum discrimination to occur at 400 lux. Usually discrimination is less at lower ambient intensities.

Visual acuity (expressed as the reciprocal of the angle in minutes subtended at the eye by the minimum detectable detail) decreases with decreasing light intensities, even though contrast may remain constant. In fairly bright light Man has an acuity of about 2 (Prosser and Brown, 1961). Epipelagic tunas might have much less acuity (Nakamura, unpublished data). Fish larvae might not have true shape perception and good visual acuity until they are several days old. By anatomical studies, Schwassmann (1965) demonstrated that vision is not yet fully developed in sardine larvae 5 days old (about 6 mm). Cephalopod larvae are capable of form discrimination (Wells, 1958) immediately after emergence from the egg. Estimates of visual acuity for Crustacea range from about 0.4 to 0.001 (Waterman, 1961). Some polychaetes and heteropods, as well as fishes and cephalopods, are capable of accommodation (Carthy, 1958). Ocelli of plankton vary considerably in structure, ranging from simple layers of sensory cells mingled with pigment cells to cup-shaped structures such as are found in the pelagic Hydromedusae (e.g., *Sarsia*). Although commonly referred to as 'simple' eyes, some cases are known where such organs function in form discrimination (Waterman, 1961).

Fishes (Baylor and Shaw, 1962) and cephalopods perceive movement efficiently. According to Schwassmann (1965), the sardine at the beginning of the feeding stage should be capable of a very coarse type of movement perception even though acuity is limited. Because of overlapping ommatidial fields, arthropod eyes are

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particularly sensitive to motion of objects. Movement perception has been demonstrated for animals with ocelli. *Daphnia* can execute visual avoidance responses (Cohen and Dijkgraaf, 1961).

Duntley (1962) states that underwater sighting ranges are so short that the visual angle subtended by ordinary objects is sufficient to make the exact angular size of the object unimportant. Therefore, underwater sighting ranges usually are controlled by the contrast transmittance of the path of sight; that is, by water clarity. He was referring to human vision. His remarks doubtless apply to most fishes, but might not apply directly to most invertebrates. Because of their lower visual acuity, most invertebrates should be able to discriminate the contrast between a sampler and the background before it is close enough for them to form an image. Therefore, for invertebrates that rely on image formation to elicit response, the sighting range should be affected by the size of the sampler. It seems unlikely, however, that animals with very poor acuity would depend on image formation to elicit response. Therefore, for them, like fishes, the sighting range probably is controlled by contrast attenuation.

Localization of objects that contrast with the background is well known for fishes and cephalopods, and it is highly developed in mysids, and occurs in simpler animals such as post-trochophore larvae of marine annelids and tadpole larvae of ascidians (Prosser and Brown, 1961). Duntley (1962) shows that the apparent contrast (C_r) is a function of inherent contrast (C_o—the ratio of the difference between the brightness of the object and the brightness of the background), distance (r) of the observer from the object, beam transmittance coefficient (a) of the water, diffuse attenuation coefficient (k), and angle of inclination of the path of sight (θ):

$$C_r = C_o e^{(-a + k \cos\theta)r}.$$

For a horizontal line of sight ($\theta = 90°$):

$$C_r = C_o e^{-ar}.$$

Change in contrast with distance for two objects, one with high reflectance and one with low reflectance, is illustrated in Figure 4 (from Hester and Taylor, 1965). Hester and Taylor point out that at the distance where the black object's contrast is nearly zero, the white object's contrast still differs markedly from zero.

The inherent contrast, and consequently the apparent contrast, might be altered markedly by the position of the object relative to the position of the sun. Figure 5 (from Hester and Taylor, 1965) shows changes in horizontal sighting range for a dark fishing net, compared with a white surface, with changes in azimuth. The sighting range of the dark net remained about 13 m with changes in azimuth, while the range for the white surface changed from 0 to 21 m. Hester and Taylor emphasize that the inherent contrast of the white surface changes from slightly negative when seen between the observer and the sun to almost +14 when the sun is behind the observer, whereas the contrast of the dark net remains relatively unchanged at values near −1. This effect would be reduced as the strong directional component of sunlight at the surface becomes scattered with increase in depth.
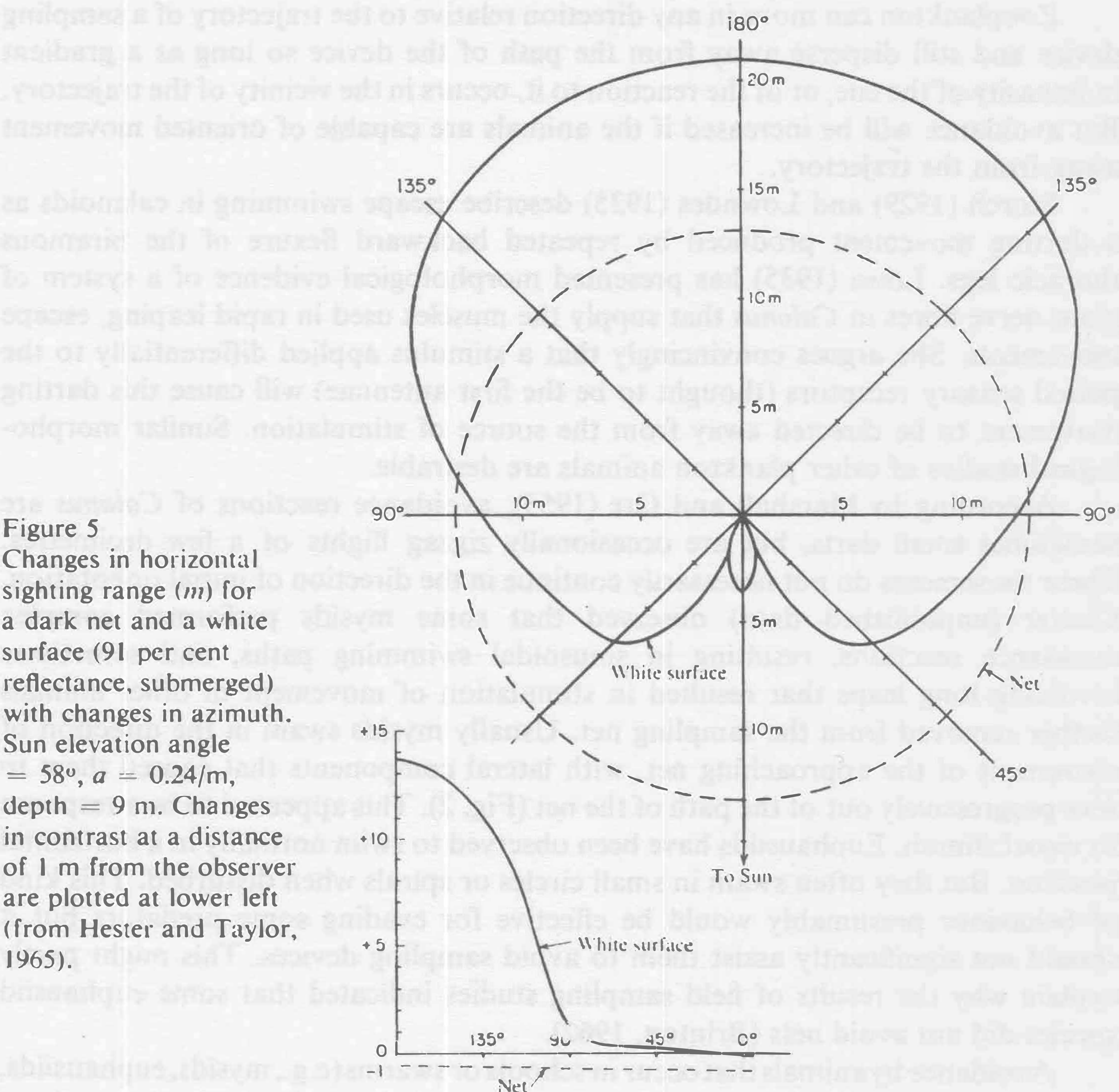
Figure 5
Changes in horizontal
sighting range (*m*) for
a dark net and a white
surface (91 per cent
reflectance, submerged)
with changes in azimuth.
Sun elevation angle
$= 58^{\circ}$, $a = 0.24/m$,
depth $= 9$ m. Changes
in contrast at a distance
of 1 m from the observer
are plotted at lower left
(from Hester and Taylor,
1965).

When sampling at depths where sunlight intensity is low, or when sampling at night, bioluminescence is likely to be important in making a sampling device visible. Possibly a light-coloured device would be more visible. Le Brasseur and McAllister (unpublished data) found that a dark-coloured net took more euphausiids than a light-coloured net, at night as well as during the day. Bioluminescence, providing continuous light or individual flashes of intensities above the threshold for animal perception, has been reported at all depths investigated to 3,750 m (Clarke and Hubbard, 1959). For a given intensity, small flashes of light are more detectable than broad fields, and, because flashes are intermittent, invertebrates need not have good resolving power to detect them.

Mobility and orientation of zooplankton

Once an animal has received a stimulus that causes motor response, the probability of effective avoidance will depend on the direction, the rate, and the persistence of movement relative to the sampling device.

Zooplankton can move in any direction relative to the trajectory of a sampling device and still disperse away from the path of the device so long as a gradient in intensity of the cue, or of the reaction to it, occurs in the vicinity of the trajectory. But avoidance will be increased if the animals are capable of oriented movement away from the trajectory.

Storch (1929) and Lowndes (1935) describe escape swimming in calanoids as a darting movement produced by repeated backward flexure of the biramous thoracic legs. Lowe (1935) has presented morphological evidence of a system of giant nerve fibres in *Calanus* that supply the muscles used in rapid leaping, escape movements. She argues convincingly that a stimulus applied differentially to the paired sensory receptors (thought to be the first antennae) will cause this darting movement to be directed away from the source of stimulation. Similar morphological studies of other plankton animals are desirable.

According to Marshall and Orr (1955), avoidance reactions of *Calanus* are sometimes small darts, but are occasionally zigzag flights of a few decimetres. These movements do not necessarily continue in the direction of initial orientation. Clutter (unpublished data) observed that some mysids performed complex avoidance reactions, resulting in sinusoidal swimming paths, and sometimes involving long leaps that resulted in stimulation of movement in other animals farther removed from the sampling net. Usually mysids swam in the direction of movement of the approaching net, with lateral components that caused them to veer progressively out of the path of the net (Fig. 2). This appeared to be a response to visual stimuli. Euphausiids have been observed to swim normally in a horizontal position. But they often swam in small circles or spirals when disturbed. This kind of behaviour presumably would be effective for evading some predators but it should not significantly assist them to avoid sampling devices. This might partly explain why the results of field sampling studies indicated that some euphausiid species did not avoid nets (Brinton, 1962).

Avoidance by animals that occur in schools or swarms (e.g., mysids, euphausiids, and some decapods) might be more pronounced than that exhibited by solitary animals of the same kinds. An avoiding animal might stimulate and orient other school members that are not stimulated by the sampler directly.

Initial direction of movement depends largely on how the animal is usually suspended in the water. Some animals (e.g., chaetognaths, and the copepods *Eucalanus* and *Paracalanus*) appear to assume a wide variety of positions in the water. More often certain positions are favoured. Since *Calanus* usually hangs in a vertical position (Hardy and Bainbridge, 1954) any movement of its swimming feet must start it travelling upward. Conversely, the dorsoventrally flattened copepod *Sapphirina* swims upward only about 3 per cent of the time and spends 97 per cent of the time sinking in a horizontal position (Smith, unpublished data). Initial movements of the swimming feet of mysids and euphausiids would cause them to move forward horizontally. But strong flexure of the abdomen might take them upward and backward as well as forward. The copepods *Calanus* and *Diaptomus*, isopods, shrimps, portunid crabs, galatheid crabs, lobsters, and many decapod larvae can swim backward (Lochhead, 1961). Cephalopod young as well as adults follow moving objects with their eyes, at the same time turning their bodies so that

the siphon is pointed in the direction of the object (Carthy, 1958). This allows them to expel water and dart backward away from the object when sufficiently stimulated.

The expected direction of movement of animals in response to water currents caused by movements of a sampler, or its bridle and tow line, is not easy to predict on theoretical grounds. Many animals exhibit positive rheotaxis. This might be useful in avoiding fishes that suck in water to catch their prey. But, in invertebrates as well as fishes, position maintenance in the absence of tactile cues seems to depend on optical fixation (Fraenkel and Gunn, 1961). Therefore, unless the animals were to orient against the direction of acceleration, those that have the visual competence might be more likely to move in the same direction as the moving sampler than to head into the current created by the sampler.

Some animals might respond to disturbances by moving in a fixed direction, regardless of their initial orientation or the direction of the stimulus. Greenwood* stated that a Russian worker showed that ctenophores have a downward directional response to high-frequency vibration. Hempel* cited fish larvae as responding with a downward movement no matter what the stimulus. Smith (unpublished data) observed that, in the laboratory, the mesopelagic copepods *Gaussia princeps* and *Euchirella galeata* invariably moved downward when suddenly exposed to light, touched with a solid object, or when the side of the aquarium was struck. McGowan* stated that, when disturbed, pteropods retract their wings and sink.

Locomotion of zooplankton varies widely in efficiency and form. When the development of a species includes a series of larval stages, striking changes in methods of locomotion can occur between one instar and the next. Other changes in rate of locomotion can result from changes in water temperature, partly because of changes in metabolic rate and partly because of changing viscosity of the water. Variations in the load carried, or in the shape and size of the body, might be expected to influence rate of locomotion. For example, in *Daphnia magna* a higher number of eggs in the brood pouch causes a posterior displacement of the centre of gravity (Lochhead, 1961).

Maximum speeds for herring larvae range from about 3 cm/sec for 8 mm larvae, to 30 cm/sec for 20 mm larvae, with a rather sudden increase in swimming ability, when the caudal fin is formed at about 15 mm (Blaxter, 1962). We have no quantitative information on swimming speeds of cephalopod larvae. In very many tows made with a 0.5 m plankton net at 2 knots, directly over dense beds of squid eggs from which larvae were known to be emerging continuously, very few larvae were caught (McGowan, 1954).

The swimming velocities of marine copepods have been estimated to be between 0.7 cm/sec and 12 cm/sec by Welsh (1933), Hardy and Bainbridge (1954), and Nishizawa, Fukuda, and Inoue (1954). These observations included cruising velocities and therefore are not applicable directly to avoidance behaviour. Lukjanova (1940) reported more directly applicable velocities of up to 15 cm/sec for *Anomalocera,* and Lowndes (1933) observed a rate of 20 cm/sec for *Diaptomus gracilis.* By applying the data of Storch (1929) on thoracic leg movements, Lochhead (1961) calculated that speeds in excess of 20 cm/sec should certainly be possible. Recent analyses of films (Clampitt, unpublished data) showed that *Calanus helgolandicus* juveniles (stage V) swam at rates up to 67 cm (220 body lengths) per

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second over distances up to 7 cm. *Rhincalanus nasutus* adults achieved speeds of 24 cm (60 body lengths) per second for distances up to 5 cm. *Labidocera trispinosa* was recorded at 70 cm/sec, and *Labidocera acutifrons* at 80 cm (230 body lengths) per second over distances of at least 15 cm (Smith, unpublished data). The mesopelagic copepod *Euchirella galeata* is capable of long spurts (1.5 m) of swimming at 100 cm/sec (Smith, unpublished data).

Clampitt (unpublished data) found that euphausiids *(Euphausia pacifica)* could cruise at up to 17 cm/sec, and mysids *(Metamysidopsis elongata)* at up to 7 cm/sec. Clutter (unpublished data) found similar cruising velocities for 4-6 mm *Metamysidopsis elongata,* and 6-9 mm *Acanthomysis* sp. Often *Acanthomysis* sp. was observed in nature to leap forward several centimetres, apparently spontaneously, at rates up to 36 cm/sec. In aquaria, *Metamysidopsis* males (5 mm) maintained swimming velocities of 12 cm/sec for several seconds prior to copulation. MacKay (1943) reported that the megalops larvae of *Cancer magister* maintained position against a current of about 18 cm/sec.

Effective avoidance of sampling devices probably occurs, for the most part, before the animals pass into the mouths of samplers that are filtering water efficiently. It seems unlikely that most plankton animals are capable of the sustained and highly directed movement at velocities of 100 cm/sec (2 knots) or more, necessary for them to escape out the mouth of samplers propelled at constant speed. But this might not be true for nets that are not straining water efficiently, or when the vessel rises and falls during vertical hauls, or when wave action (especially in a following sea) causes cyclic slowing during horizontal hauls near the surface.

SOME CONSIDERATIONS OF GEOMETRY

Determining the theoretical effectiveness of towed net samplers is a rather complex problem in analytical geometry. Except for particular cases, the formulation of deterministic models seems unlikely to lead to a complete solution, because not all animals have unvarying behavioural responses. Frequency of response, direction of movement, and rate of movement can be expected to have probability distributions rather than fixed values. In part at least, the problem seems to have features that are analogous to those encountered in the study of turbulent diffusion. Nevertheless, consideration of some of the more straightforward aspects of sampling geometry can be very useful.

Barkley (1964) calculated optimum values for sampler sizes based on an assumed relationship between towing speed and the radius of the sampler. He concluded that the minimum velocities at which animals must move to avoid capture decrease rapidly as the sampler radius is decreased below the optimum values. Therefore, assuming that forewarning distance does not decrease in proportion to sampler size, it is inefficient to reduce the net opening to low values, because the gain in speed of tow is more than offset by the ease with which the smaller net may be avoided.

Barkley shows (his Fig. 4) that for animals with perfect orientation (i.e., taking the path most likely to result in avoidance), responding when the sampler is 1 m

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away, and capable of swimming at 1 m/sec, about one-half would succeed in avoiding a 150 cm diameter net. We have seen that some copepods can swim 1 m/sec and that the acceleration fronts that might elicit response can extend 1 m ahead of nets only 1 m in diameter, even when they are filtering at 95 per cent efficiency.

Perhaps it is unrealistic to assume perfect avoidance orientation. But, as we have seen, it might not be unrealistic to expect some animals to move in only one direction when disturbed by an approaching sampler. In the simplest case, where only the animals directly in the path of the net are disturbed (uniformly), the catching efficiency (see Terminology) can be calculated from the relation:

$$C = 1 - \frac{1}{\pi R^2} \left[a \left(R^2 - \frac{a^2}{4} \right)^{1/2} + 2R^2 \sin^{-1} \frac{a}{2R} \right]$$

where

C = catching efficiency;

R = net radius;

a = distance animals move between the time of response and the time the net reaches their plane.

Fleminger and Clutter (1965) calculated 'apparent minimal peripheral escape zone (ΔR)' for six species of copepods in each of two populations by comparing the catches of two smaller nets with those of a larger net. This was done by assuming that the effective sampling areas of the smaller nets were proportional to their catches. The range for 24 values was 0.3-8.5 cm. More recent work (Clutter, Fleminger, and Smith*) has suggested that the long towing line used in the first experiments may have been an important cause of avoidance. This view is supported by the evidence that the mean of the ratios of ΔR for larger net (32 cm) to ΔR for smaller net (22 cm) was less than 1 (0.85). If only the tow line was responsible for the avoidance, one might expect that it caused a void at the centre of the sampling path. Assuming that the spacing between individuals outside that void did not change, the radius of the void ($\Delta R'$) was calculated. The range for 24 values was 3.2-14.1 cm. The mean of the ratios of $\Delta R'$, larger net, to $\Delta R'$, smaller net, was found to be greater than 1 (1.28). This result might be evidence that both central and peripheral factors were responsible for the observed avoidance. Alternatively, it might be evidence that there was a gradient of density, decreasing nearer the tow line.

Gilfillan* presented a theoretical model for assessing avoidance as a function of towing speed. In this model the difference (ΔR) between the true net radius (R) and the apparent 'effective' net radius (R') is assumed to be a linear function of towing speed:

$$\Delta R \qquad R - R' = \frac{K}{S}$$

where

K = the product of the mean escape speed (the mean of all components of animal velocities perpendicular to the trajectory of the sampler) and the distance ahead of the sampler at which the animals detect and respond to the sampler;

S = towing speed.

The value K, assumed to be constant regardless of towing speed, is determined empirically from the relation:

$$\frac{C_1}{C_2} = \left[\frac{R - \dfrac{K}{S_1}}{R - \dfrac{K}{S_2}} \right] \quad \text{or} \quad K = \frac{R \left[\left(\dfrac{C_1}{C_2} \right)^{1/2} - 1 \right]}{\dfrac{1}{S_2} \left(\dfrac{C_1}{C_2} \right)^{1/2} - \dfrac{1}{S_1}}$$

where C_1 and C_2 are numbers of animals caught at towing speeds S_1 and S_2.

After K is evaluated, the relative catch (catching efficiency) is calculated for each towing speed (S_i) as:

$$\frac{C_i}{N} = \left[\frac{R - \dfrac{K}{S_i}}{R} \right]^2$$

where

C_i = actual catch at speed S_i;

N = number of animals in path of sampler.

According to Gilfillan* the results of field trials with a 1 m net, a 70 cm net (canvas collar removed), and the Bary catcher, indicated that the assumptions involved were valid. That is, the parameter K (detection distance × escape speed) was nearly constant regardless of towing speed. Catches of *Calanus* spp., *Euchaeta japonica*, and euphausiids, from tows made at 0.7, 2 and 4 knots were analysed. He concluded that the larger animals tended to be the most capable of avoiding the samplers. Catching efficiency was reduced at lower towing speeds, especially at speeds less than 2 knots.

SOME POSSIBLE SOLUTIONS

It would be reckless to specify in detail the design criteria for sampling devices without knowing in equal detail the purpose and requirements of the intended sampling programme. Criteria would depend on the volume of water to be strained, the depths of strata to be sampled, the kinds of animals to be sampled, and whether integrated samples (surveys) or samples from a particular parcel of water (community studies) were desired.

Some elements of the solution to the avoidance problem are obvious, and not novel. Where adequate handling facilities are available, it is desirable to use very large samplers. This is desirable from other considerations as well as avoidance. The optimum size of towed nets depends on the drag characteristics of the nets, and the power of the vessel and hauling winch (Barkley, 1964). Very large ring nets have been used in the past, and then abandoned in favour of smaller nets (Richard, 1910) because they were difficult to handle. That large nets may be cumbersome seems to be insufficient reason not to use them. Compared with the great cost of operating oceanographic vessels, the cost of installing efficient handling equipment is not very high. Recently, three types of large samplers capable of taking fairly small zooplankton as well as large have been deployed successfully.

The first of these is a 3.6 m (12 ft) Isaacs-Kidd trawl modified by using plankton gauze (0.55 mm) throughout the straining surface (Murphy, unpublished data). The second type is a surround-net of plankton gauze (0.33 mm) constructed on the principle of the purse-seine, designed to encircle a surface area of 72 m² and enclose a volume of about 500 m³, extending from the surface to a depth of 7 m (Murphy and Clutter, unpublished data). Neither of these devices has yet been fully evaluated. The third kind of large sampler is the encased high-speed type represented by the formidable (1 ton, 50 cm mouth diameter) device employed by Kinzer (unpublished data), and the similar large (35 cm mouth) high-speed samplers developed at Lowestoft.

There is much evidence that higher towing speeds result in larger catches, especially of fishes. This is attributable to the reduction of the evasion time. The advantage of high-speed samplers is offset in varying degrees by the reduction in the distance that animals need to displace themselves to avoid capture, high-speed samplers usually having smaller mouths than conventional nets. Also higher speeds may cause damage to organisms unless provision is made to preclude this (Clarke, 1964).

Some of the advantage sometimes attributed to higher towing speed may be due to reduced disturbance, associated with the absence of tow lines and bridles, and better streamlining of the samplers. Halliday* remarked that noise produced by the tube of a sampler would be an order of magnitude less than that produced by such things as bars, shutters, or towing wires in front of a sampler. Clutter, Fleminger, and Smith* suggested that long tow lines may be especially undesirable. Most high-speed samplers (Gehringer, 1962; Clarke, 1964), and some conical low-speed nets (McGowan and Brown, 1966) have been designed to eliminate forward obstructions. The reports of Bridger (1958) and Gehringer (1962) indicated that 'bow-waves' associated with devices that are not filtering at high efficiency can cause reduced catches. Clarke (1964) has reduced the bow-wave by streamlining the body of his high-speed sampler and has extended the sampler mouth ahead of the body.

It is always desirable to make the sampler itself as unobtrusive as possible. But some (as yet unevaluated) experiments have been done on the premise that, by harshly and uniformly disturbing the animals just ahead of a net in a field much larger than a net, they will not recover enough to respond to the relatively mild disturbance caused by the sampler when it reaches them (Isaacs and Murphy, unpublished data).

The results of tests of a dark-coloured net compared with a light-coloured net (Le Brasseur and McAllister, unpublished data) seem to confirm the thesis of Hester and Taylor (1965) that, for most circumstances, contrast between sampler and background is important, and generally can be reduced by using dark-coloured samplers. Halliday* stressed that shiny surfaces should be eliminated, especially on moving parts that would cause cyclic reflections, such as the rotor blades of flowmeters.

Some towing directions might be more desirable than others. For example, if the animals sought had a tendency to move downward regardless of the direction of stimulus, it would be most efficient to make vertical hauls. But any advantage

gained by this could be offset by having a long tow line preceding the sampler, if it were hauled upward. For light-coloured samplers, towing in a direction away from the sun would make the sampler less conspicuous.

Calibration of caching efficiency is only a partial solution to the avoidance problem, especially for conventional devices. Test results show high variability even in general conclusions, indicating that it may be difficult to specify avoidance effects, in any universal sense, within useful numerical limits. Some of the variability in the results of avoidance tests was caused by differences in techniques and conditions during sampling, and reflected differences among plankton species. Therefore, the results of past sampling experience do not deny the possibility of evaluating avoidance for particular groups or complexes of animals under particular conditions. Calibration must accompany the development of more effective samplers. Perhaps there will never be a 'no-avoidance' net, but it seems entirely feasible to design practicable sampling systems for particular animals.

In brief, we recommend that samplers be:

1. Made as large as possible, consonant with vessel and winch capability, up to the size where drag would slow the vessel below the optimum balance between size and speed.
2. Propelled as fast as possible consonant with vessel capability, sampler drag, and complete retention of animals after capture.
3. Propelled at constant speed.
4. Fitted with enough filtering surface to remain 85 per cent efficient throughout the tow.
5. Free of forward obstructions such as tow lines and bridles, and streamlined as much a possible (including towing wire near the sampler).
6. Dark-coloured unless propelled near the surface in a direction away from the sun, and have no shiny surfaces.
7. Evaluated in the context of the environmental conditions and the purposes for which they are used.

5

Loss of organisms through the meshes

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INTRODUCTION

When sampling plankton at sea, a certain fraction of the organisms present in the water filtered is lost through the meshes of the net. It is desirable to obtain some measure of the capacity of different nets for retaining different types and sizes of organisms.

Various terms have been used to describe this effect depending on whether one is more concerned with the organisms retained or with those that are lost through the meshes. To avoid confusion, the term *mesh selection,* already in current use by fishery biologists, will be used in this review and it is commended for general adoption. 'Mesh selection' is defined as the capacity of the net to select individual organisms from the population in the water that has passed through the mouth of the net. It embraces the concepts of *escapement* through the meshes and *retention* by the meshes.

Kofoid (1897b) was one of the first to become concerned about the leakage of plankton through silk gauze, and he compared catches taken with the Hensen net with those obtained by filtering or centrifuging water samples taken under various conditions and at various seasons. He reached the conclusion that the net retained 45 to 50 per cent of the solid content, but the amount escaping through the silk had no constant relation to the amount retained. He emphasized that when choosing a sampler, a mesh size, and a sampling procedure, one must bear in mind the biological content of the environment. Kofoid also recommended that the Hensen method should be supplemented to give a better picture of the species association present. He noticed the difference between active and passive escapement and that the presence of silt or other particles would alter quantitative measurements.

Wiborg (1948) considered the effect of shrinkage of the net on mesh selection. He provided tables for the commonest species and their developmental stages in the coastal waters of Norway to show what was retained and what was lost. Wiborg also compared catches obtained by pump with those obtained with a Clarke-Bumpus sampler.

King (1950) centrifuged water samples, from the coastal waters of Florida, and examined the solids to determine the loss of minute plankton organisms,

particularly dinoflagellates and copepods, through the meshes of nets. King and other authors estimated that 2 to 50 per cent of the nanoplankton would be lost by using a net with 173 meshes/inch. Such values, however, would be different in other bodies of water.

Banse and Semon (1963) compared catches obtained by Bary's plankton catcher with those by the Isaacs-Kidd midwater trawl, to estimate the effective cross-section of the 6 foot trawl. They found that a possible funnelling effect of the front section of the trawl was compensated for by the loss of animals through the lining (1.27 cm) of the second section of the trawl.

Wickstead (1963a), working off the Zanzibar coast, compared the catching efficiency of the International Council Standard net (58 meshes/inch) with the Currie-Foxton net (74 meshes/inch) and found that the coarser net caught the most animals, so ruling out the effect of mesh selection.

Adams*[1] covered the monel gauze net (0.23 mm mesh width) of a Gulf III sampler with nylon gauze of smaller mesh size (0.069 mm) in order to measure escapement. One of the most striking results was a large variation from month to month in the percentage of the population of each species which was retained by the monel gauze of the Gulf III.

Cushing* investigated the mesh selection factor for plaice larvae taken by the Tin Tow net covered with gauze of 60 meshes/inch, and was able to evaluate this factor for five different larval stages.

For fisheries management purposes it is necessary to allow a certain portion of the population to escape in order to grow in the sea to a larger individual size. The main aim of fisheries research is to establish a basis on which to advise on how much fish can be taken from the sea and still keep the yield as high as possible, year after year. Fishing intensity and mesh size may be varied to achieve this purpose (Beverton and Holt, 1957). Fisheries scientists have paid much attention to the problem and have conducted extensive experiments on mesh selection, especially on bag-type nets and gill-nets. Although plankton research can benefit from the results achieved by investigators in fisheries research, one must be aware of the fact that in plankton sampling at sea the problem is exactly the reverse. The fisheries manager tries to select certain size classes and/or species against others, while the planktologist tries to obtain as representative a sample as possible of the mixed association living in the sea. Another important difference is that clogging of a fishing net is not a major problem while it is frequently a serious source of error in plankton sampling in fertile areas of the sea. Also plankton samplers have different hydrodynamical properties to fishing nets.

Fisheries research on mesh selection has followed three main approaches: by covering the net; by taking replicate samples; and by using the 'trouser trawl', i.e., a trawl with two cod-ends side by side. According to Saville* and other authors, the covered cod-end method is the most reliable method, because of the high inter-haul variance in replicate sampling. The replicate sampling method is probably even less satisfactory for studying mesh selection in plankton nets, because plankton occurs in patches, both vertically and horizontally. There is a high degree of variance between replicates even when identical nets are hauled simultaneously

1. Asterisked (*) references denote information presented at the Sydney Symposium.

on either side of the ship. The trouser trawl presents operational difficulties. As in fisheries research, covering the net with a finer outer net seems to offer the greatest promise.

FACTORS AFFECTING MESH SELECTION

The main factors which govern the selectivity of a net are escapement, nature and weave of the material, clogging, and the age of the net.

Escapement

The escape of organisms through the meshes of a net may be either an active or a passive process. Escapement is a function of the size, shape and behaviour of the organism in relation to the mesh size. *Passive escapement* is the process by which organisms or inert particles are passed through the meshes without actively aiding the process. Suspended particles, whether organisms (either living or dead), or particulate matter (either organic or silt) will pass through the meshes if the size of the particles is small enough and if their shape will permit. The pressure drop across the net may actually squeeze organisms through the meshes and in such case increased speed of towing would lead to a greater number of organisms being squeezed through. *Active escapement* is the process by which animals caught in the net may squeeze out through the meshes. This involves behavioural patterns that vary with the species and with the developmental stage. The properties of this parameter cannot be generalized. Observations relating to a given species or stage under certain environmental conditions may not be valid for other species and for other environmental conditions.

All individuals of a species should be retained when its maximum girth is larger than the mesh perimeter. However, active escapement and plasticity (Saville, 1958) cause organisms and inert particles to be lost even when the mesh size is slightly smaller than the organism. Heron* has shown that mesh aperture size is quite variable in some materials, and this may add to the variability in the size of the organisms near the 50 per cent retention point (see Chapter 2).

Smith (personal communication) towed paired nets similar in all respects except mesh size. He found that, in the field, small copepods 0.35 mm wide were caught by the 0.20 mm net and missed by the 0.33 mm net, but in the laboratory they were retained by a 0.40 mm sieve. He believed that when the organisms were alive their appendages were flexible, allowing the small body to pass through the 0.33 mm meshes but not the 0.20 mm meshes. After the animals had been fixed in formalin, the appendages were rigid and extended causing them to be retained, in the laboratory, on 0.40 mm meshes. Also anchovy eggs were absent in the catch of the 0.57 mm net, but were retained in the laboratory by the 0.57 mm sieve, having become slightly smaller but more rigid after being fixed in formalin. In addition to this, the filtration pressure through the apertures might have been higher in the field than in the laboratory.

Size. It is obvious that particles much larger than the meshes will be retained by the net, and conversely that particles much smaller will be filtered through.

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Consequently, down to certain size limits, the retention of an organism by a net, or inversely, its escape through the meshes, will depend on the relative size of mesh and organism. However, at the level where the order of magnitude is approximately the same for both, irregularities usually occur. Organisms smaller than the orifices may be retained while larger ones may escape (Saville, 1958). Retention of relatively small particles is usually due to progressive clogging of the net while the exit of particles larger than the mesh aperture is fundamentally due to the shape and behaviour of the particles and to the elasticity of the meshes. Saville performed experiments with glass beads. He produced tables giving 100 per cent and 50 per cent release points and 100 per cent retention points of the commonest North Sea organisms, and found that the percentage escape of any single species was proportional to size. However, he noticed that animals, larvae, eggs, and even glass beads may escape at a mean mesh width less than their own diameter.

Barnes and Tranter (1965) hauled the Tropical Juday net (TJN), the Indian Ocean Standard net (IOSN), and the Clarke-Bumpus sampler (CBS) at the same station and found that, because of different mesh sizes, the size distribution of the organisms caught in the three nets was different. Smaller zooplankton organisms evidently escaped more readily through the IOSN due to its coarser meshes (0.33 mm) which rarely retained copepods smaller than 1 mm. The CBS (mesh width 0.27 mm) retained copepods as small as 0.8 mm, and the TJN (mesh width 0.17) retained those as small as 0.6 mm.

Jensen (1949) has shown that there is a relationship between the mean length at which fish are retained and the size of the cod-end meshes, thus $L_p' = b$ (mesh aperture size) where b is a constant varying with the species, and L_p' is the threshold length above which the fish is always retained (knife-edge selection).

Omori et al. (1965) estimated mesh selection by towing nets, identical in all respects but mesh size, for approximately 50 minutes. The nets were ORI-200, ORI-33, and ORI-C, respectively with meshes of 1.97 mm, 0.33 mm, and a combination of the two (the finer meshes in the cod-end portion of the net). They showed that increase in towing speed increased the catch of agile organisms (Sergestes lucens) and that, if clogging did not occur and the filtering efficiency of the net was the same, the fine net took the largest catch and sampled the widest range of sizes. The catch of the nets differed in composition however, and the ORI-33 and the ORI-C caught a much greater percentage of animals (93.2 and 83.8 per cent respectively). The ORI-200 (large meshes) caught the greatest percentage of large organisms (up to 59.1 per cent). The difference in catch between fine and coarse nets was greater for numbers of organisms than for weight. The mean width of the large euphausiids retained by the ORI-200 was 2.02 mm which is very close to the 1.97 mm mesh width of this net. The percentage composition of the catch of euphausiids taken by the three nets (Fig. 1) indicated that the ORI-200 selected against small animals, while the ORI-33 caught the small animals but apparently did not select against the larger ones. The ORI-C caught all sizes. It is interesting to note that the number of euphausiids (whether longer or shorter than 10 mm) increased with decreasing mesh size (it was intermediate with the ORI-C net), whereas the wet weight of the catch remained approximately the same with a slight increase in favour of more numerous smaller organisms. On the other hand, the

catch of copepods (whether longer or shorter than 5 mm) showed a different pattern. The larger the mesh size the fewer the number of copepods, and the smaller the wet weight of the animals. Further, the number of organisms increased with decreasing mesh size at a much greater rate than did the weight of copepods. The explanation for these differences may be that there were animals larger than the meshes, in the euphausiid population, and that they have an active behaviour more like fish, so favouring active escapement. Omori *et al.* (1965) showed also that the maximum width of all the copepods caught was less than 2.10 mm, very few being above the 100 per cent retention size. Thus there was no mesh selection of very small copepods with these mesh sizes. These must represent a large percentage of the copepod population. Their data suggest also that chaetognaths behave like euphausiids and fishes; whereas with ORI-200 most specimens escaped and those that were caught had a very large mean weight, with ORI-33 large numbers were retained with a very small mean weight.

Graham (1956) has shown that the relation between mesh size and fish catch, expressed both by numbers and by weight, is similar to what Omori *et al.* have found for euphausiids, and unlike what they found for copepods.

Shape. Escapement is hindered or facilitated by the shape and behaviour of the organisms. Streamlined, smooth, or slimy organisms will be released more readily than spiny, squarish, or irregularly shaped organisms, particularly those covered with bristles or provided with long appendices, or those with a coarse, rough, or sticky surface. According to the observations made by Saville (1958) the 50 per cent retention point of *Oithona* is at a much smaller size than for other copepods of approximately the same dimensions. In *Oithona*, 90 per cent of the specimens had their antennae extended away from the body.

Fish of commercial interest have a length-girth relationship and a regular shape that make it possible to establish a length-selection curve (Saville*) on the basis of which optimum mesh size may be established. This is a logistic curve with the following form:

$$p = \frac{1}{1 + e^{-(a + bl)}}$$

where $p \times 100$ is the percentage of escaping fish at length l, and a and b are parameters to be estimated from the data; in this case the 50 per cent retention length is equal to a/b..

Another expression of this (see Cassie, 1955) is the Buchanan-Wollaston equation:

$$p = 100/(\sqrt{2\pi}) \int_{-\infty}^{t} \exp(-t^2/2)\, dt$$

where

$t = (l-\bar{l})/s_l$;

l = fish length (or other linear measure such as girth);

$\bar{l}$ = length for 50 per cent escapement;
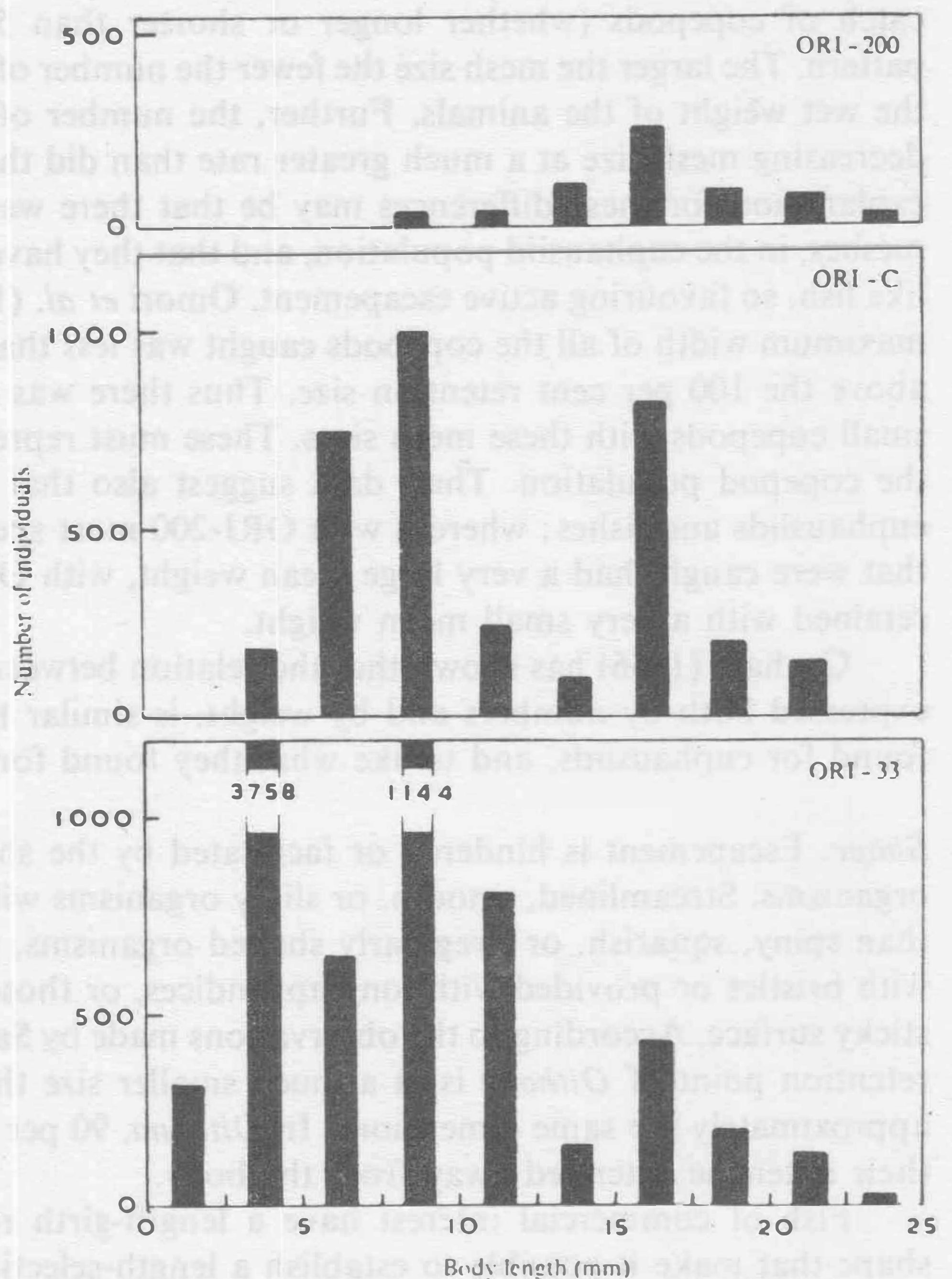
s_l = standard deviation.

Figure 1
Variation in size of
euphausiids caught by the
three ORI nets (after Omori
et al., 1965).

In the case of perfect selection, the curve would be a vertical straight line; any departure from this will be measured by the standard deviation in the latter formula or indicated by a and b in the former.

Plasticity. Experiments performed by Saville (1958) suggested that organisms are far more compressible than was supposed earlier (Figs. 2-4). For example, the mean escapement of fish eggs of 1.403 mm diameter is at a mesh width of 1.188 ± 0.010 mm. However, Saville also showed that beads may also pass through smaller meshes. For instance, he found the 50 per cent release point of glass balls of diameter 0.261 mm to be at a mesh width of 0.222 · 0.003 mm. Some factor other than compressibility is operative in this case. Similar observations were recorded with fish larvae and copepods. The curves obtained for glass beads are lower than for organisms. This indicates that the escape of organisms larger than the meshes is aided by the compressibility of the organisms and the flexibility of the meshes, the latter accounting for the escape of glass beads larger than the meshes.

Heron (see Chapter 2 above) suggests that organisms are passed from mesh to mesh until they encounter one large enough to slip through, and that the
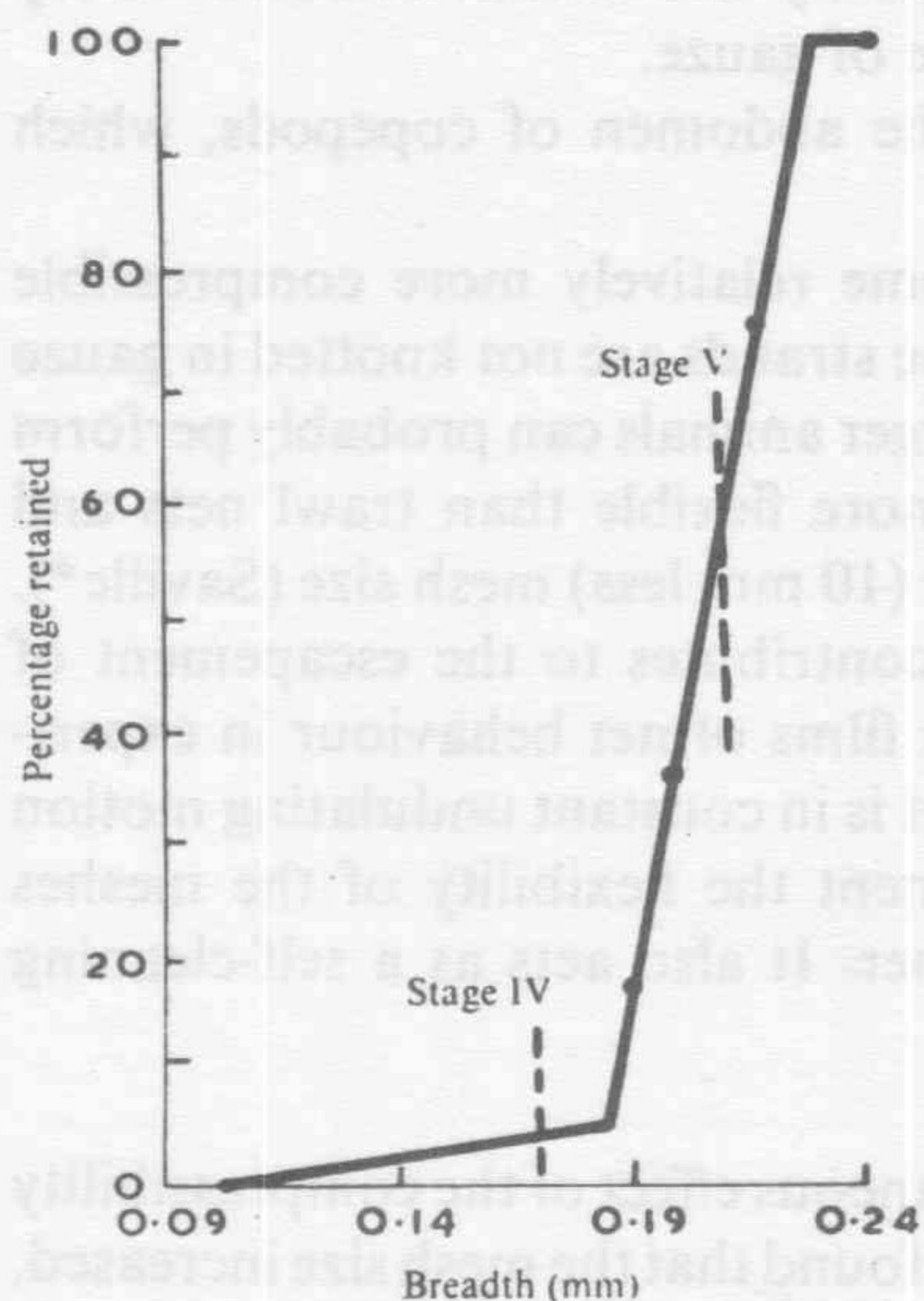
Figure 2
Selection curve of 60-mesh silk for *Oithona*.
Maximum breadth of organism was used
and the dashed lines indicate mean sizes of
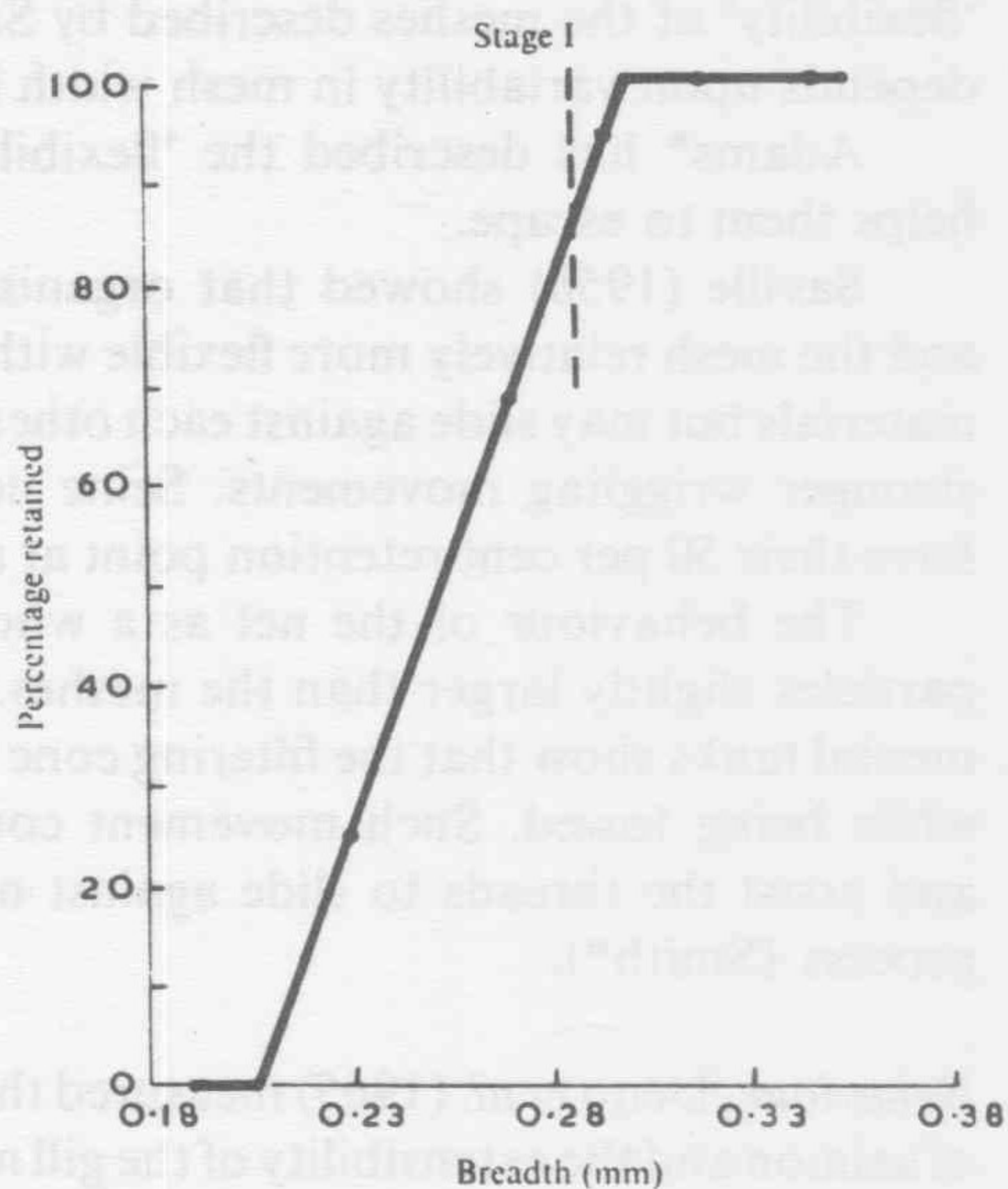copepodid stages (after Saville, 1958.)

Figure 3
Selection curve of 60-mesh silk for *Calanus*
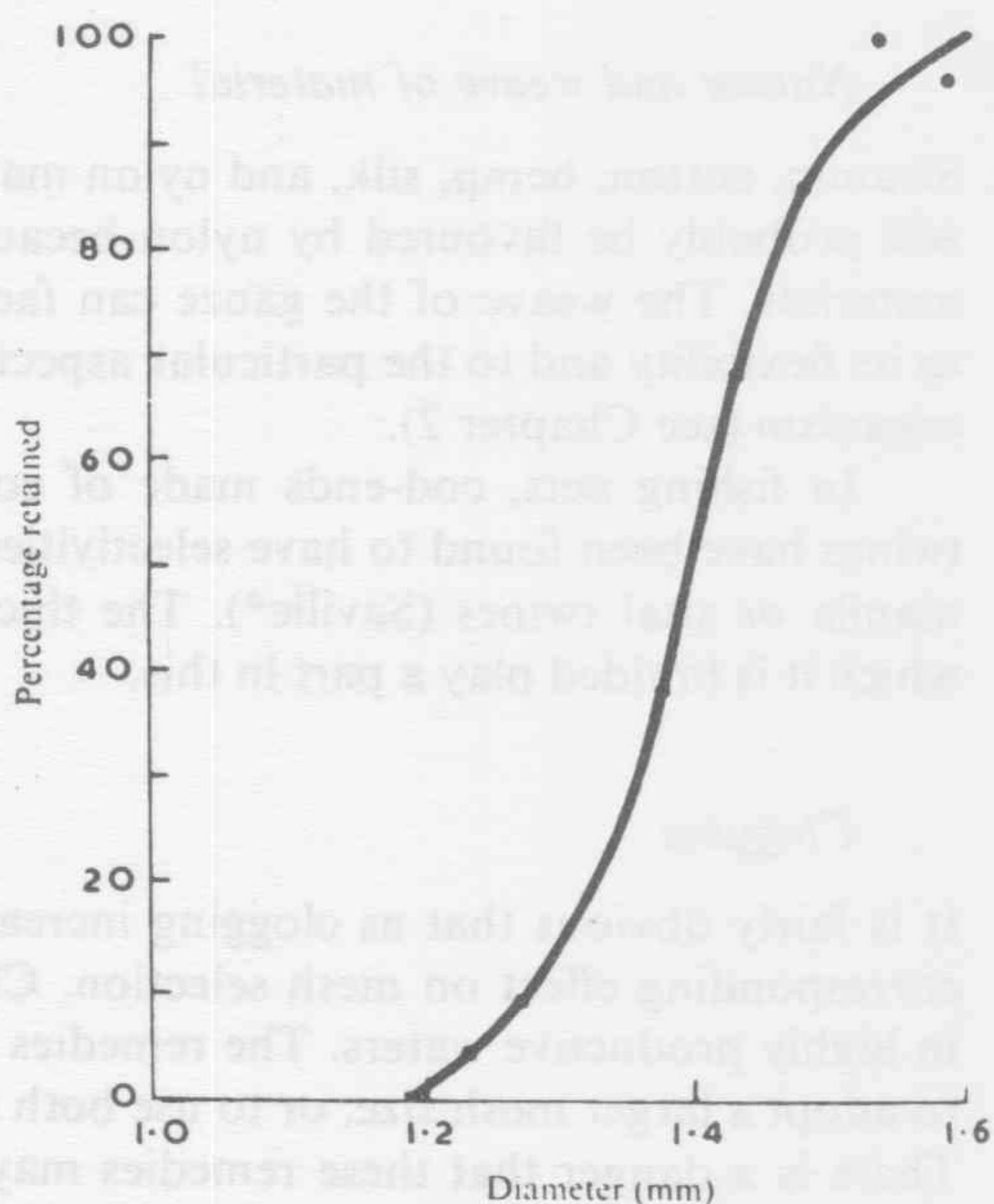(see Fig. 2).

Figure 4
Selection curve of 16-mesh silk for fish eggs
(see Fig. 2).

'flexibility' of the meshes described by Saville is partly due to this. Heron's theory depends upon variability in mesh width in a piece of gauze.

Adams* has described the 'flexibility' of the abdomen of copepods, which helps them to escape.

Saville (1958) showed that organisms become relatively more compressible and the mesh relatively more flexible with size. The strands are not knotted in gauze materials but may slide against each other, and larger animals can probably perform stronger wriggling movements. Seine nets are more flexible than trawl nets and have their 50 per cent retention point at a smaller (10 mm less) mesh size (Saville*).

The behaviour of the net as a whole also contributes to the escapement of particles slightly larger than the meshes. Cinema films of net behaviour in experimental tanks show that the filtering cone of the net is in constant undulating motion while being towed. Such movement could augment the flexibility of the meshes and assist the threads to slide against one another. It also acts as a self-cleaning process (Smith*).

Behaviour. Ueno *et al*. (1965) measured the simultaneous effect of the compressibility of salmon and the extensibility of the gill net. They found that the mesh size increased, by up to 3 per cent of its original size, and that the compressibility of the fish varied with the species. Reactions of organisms (especially fishes) to encounters with the meshes and the water flowing through could well lead to them actively escaping (Saville*). Films have been made of fish escaping through the cod-end of trawls in this way.

Nature and weave of material

Stramin, cotton, hemp, silk, and nylon materials vary in smoothness. Escapement will probably be favoured by nylon because it offers less friction than the other materials. The weave of the gauze can facilitate or hinder escapement according to its flexibility and to the particular aspect in which the pores are presented to the organism (see Chapter 2).

In fishing nets, cod-ends made of cotton, hemp, polyamide, and polyester twines have been found to have selectivities 10 to 15 per cent higher than those of manila or sisal twines (Saville*). The thickness of the twine and the manner in which it is braided play a part in this.

Clogging

It is fairly obvious that as clogging increases the mesh size will decrease, with a corresponding effect on mesh selection. Clogging is greater with fine meshes and in highly productive waters. The remedies for this problem are to filter less water, to adopt a larger mesh size, or to use both fine and coarse nets at the same station. There is a danger that these remedies may defeat the object of the sampling and generally a compromise has to be sought. Kofoid (1897b) was among the first to show clogging to be a source of error in quantitative sampling. Anraku (1956) observed no significant difference between the catches from 10 to 20 minute tows

with a stramin net (a fairly coarse net). If clogging had occurred then one might have expected to see a change in the composition of the catch. Barnes and Tranter (1965), when comparing the catching efficiency of the TJN, the IOSN, and the CBS, showed that the TJN gave the greatest variability. Such variability they ascribed to the smaller meshes.

Some experiments with fish trawls showed reduction in mesh selection when the catch was large, while others did not (Saville*).

Theoretically, if uniform clogging of the net occurs, then the mesh size will be effectively reduced. If clogging occurs mostly at the rear end of the net, the net length is effectively reduced and the mesh velocity is increased in the forward part of the net. This may lead to an increase in passive escapement in that area (Anraku*). The remedies for this problem are to filter less water by reducing the mouth aperture or speed of tow, to use a larger mesh size, or to increase the filtering area.

Age of net

The age of the net influences mesh selection in two ways: firstly a silk net shrinks after the first few tows and mesh apertures are reduced; secondly a certain amount of debris and organic matter sticks to all kinds of fabrics and is not normally removed entirely by the usual washing of the net between stations. This factor will vary with the fabrics and may well be at a minimum with nylon monofilament. Smith* emphasized this problem and recommended that nets be laundered frequently.

Swelling and fraying of the filaments of cotton, hemp and silk strands, with use, also decrease the mesh aperture. Kofoid (1897b) showed that after use the total area of the openings of bolting cloth may decrease by 50 per cent. Not all meshes are reduced in the same proportions.

MEASURE OF MESH SELECTION

Clearly a measure of *mesh selection* cannot be precise for technical reasons, and can only be estimated. The best evaluation can probably be made by enclosing the net in a covering bag made of finer gauze, and examining the *size distribution* and *shape* of the organisms selected by the two nets (e.g., Saville, 1958). An alternative evaluation may be made by comparing the catches of identical nets fitted with different mesh sizes (e.g., Wiborg, 1948). More frequently, however, comparisons of the *abundance* of organisms have been made (e.g., Omori *et al.*, 1965), but this approach is subject to the error introduced by the varying abundance of organisms of different sizes in the populations being sampled. In still other instances completely different nets have been used (e.g., Kurashige, 1932; Künné, 1933, Barnes and Tranter, 1965), making an assessment of mesh selection even more difficult.

The size distribution of the organisms of a plankton population being sampled at sea is an important factor in determining the percentage of organisms lost through the meshes. The catch taken by a net will differ in different ways according to the original composition of the population present in the water filtered by the

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net. For instance, the catch taken by a net filtering water containing large plankton anorgisms, as in temperate or cold oceans, will have less escapement than the same net filtering water containing small and sparse organisms, as in tropical waters. Furthermore, the mesh selection of a net may not be very constant since it will be influenced by such factors as clogging, age, and whether it is clean or not.

While no absolute values can be put on mesh selection it would be possible to estimate its importance for the particular organisms being studied. The most satisfactory means of doing this at present would seem to be to measure their 50 per cent release point, the maximum size of complete escape, and the minimum size of complete retention for the particular net in use. This can probably be done best by taking a net with an outer fine gauze cover, and comparing the size frequency distribution of the organisms in the net and in the cover. Selection curves similar to those by Saville (1958) would be obtained.

Some error will be present. Davis (1934) has shown that fitting a cover over the cod-end of a trawl caused a retention of relatively smaller fish. The same may happen when covering a plankton net because the outer bag will reduce mesh velocity in the main net. This in turn may reduce both active and passive escapement.

CONCLUSIONS

The net selected for a particular task should be chosen with a clear idea of the problem which is to be tackled and the limitations which mesh selection will impose upon it. The net should provide an adequate estimate of the population being studied.

It is desirable to avoid filtering more water than is absolutely necessary, particularly if clogging is expected to occur. In the worst conditions a net with a reduced mouth area can be used.

It is probable that the lower the mesh velocity, the lower will be the escapement and this emphasizes the desirability of keeping the mesh velocity low and towing the net, so far as possible, at a constant speed.

It is clear from the various factors affecting mesh selection that some simple precautions can help to limit its variability. For example, the use of some types of gauze and some mesh sizes is preferable to others. Nets should be laundered thoroughly and as frequently as possible (Smith*). Bary* has suggested that washing nylon nets in potassium hydroxide might help to reduce progressive accumulation of organic debris. However, it should be remembered that potassium hydroxide will destroy silk nets (see Chapter 2).

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Field techniques[1]

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SUMMARY

Variation in kinds, size, mobility, abundance, and distribution of marine zoo-plankton precludes use of the same sampler and methodology for all purposes. This discussion covers samplers and towing procedures in common use today; associated gear; methods required to place samplers at the desired depth, to determine depth and path of tow, and to estimate the quantity of water filtered; and care of sampling equipment. Particular stress is placed on standardization of technique to reduce variability imposed by sampling procedure.

INTRODUCTION

The term 'field techniques' is defined here as methods and procedures for operating plankton samplers. In the introductory chapter, Fraser traces the history of the development of plankton samplers and sampling methods; these were described in more detail in recent reviews by Aron (1962b), Currie (1962), Yentsch et al. (1962), Omaly (1966), and Linger (unpublished manuscript, 1960).

Most of the samplers were designed by biologists for specific objectives, and have met with varying degrees of success and acceptance. Unfortunately, not much is known about gear efficiency, and general use of a device is usually based on convenience and the premise that 'it appears to do a better job than others'. Limited studies on selected characteristics of a few samplers have been conducted ashore and at sea, but until much more definitive data on their field performance are available, a rating for them cannot be given.

Our discussion covers the samplers and towing procedures in common use today; associated gear; and methods required to place the samplers at the desired depth, to determine depth and path of tow, and to estimate the quantity of water filtered. We also comment on care of sampling equipment.

LOW-SPEED SAMPLING

Simple net tow

The simplest arrangement for sampling zooplankton is a near-surface tow with a cone-shaped net affixed to a rigid ring, which is attached by bridles to a towing warp. This net is essentially the one Fraser describes in Chapter 1 as first used in the mid-1800 s. Towing speed is generally less than 3 knots, and a weight attached to the end of the towing cable keeps the net below the surface. The net may be visible from the towing vessel and its depth known; sampling time and speed can be closely controlled. This net may also be used for vertical and oblique tows. In a vertical tow, the vessel is stopped, the weight is attached below the cod-end, the net is lowered to desired depth, cod-end first, and then is retrieved—the net fishes only on the way up. In an oblique tow, the vessel runs at low speed, sufficient cable is paid out to allow the net to sink to desired depth and the net is then slowly retrieved. Care must be taken to prevent the cable from paying out so rapidly that it slackens and kinks or entangles the net.

Modifications for subsurface towing

Modification of the simple net and weight arrangement described above is required to obtain samples from subsurface waters without contamination by material from the upper layers. The approaches used range from messenger-operated throttling devices, for taking one sample, to more complex equipment, triggered either hydrostatically or electrically, for taking multiple collections from several depths during a single tow.

Single net, mouth closure. Of the single net closing systems, that of throttling the net is the most widely used. The Nansen system, in wide use today, was first described by Gran (1905). Variations of the original design were described by Murray and Hjort (1912), Nansen (1915), Ostenfeld and Jespersen (1924), Kemp and Hardy (1929), Hentschel (1932), and Künné (1933). Basically, the Nansen net is a conical silk net with a canvas sleeve below the net ring and a noose line strung through a series of rings encircling the lower portion of the sleeve. When a messenger-operated hook releases the towing line, the strain is transferred to the noose line, throttling the net just below the mouth. Variations of the design include replacement of the canvas sleeve with open mesh netting to reduce water resistance; modification of the messenger-activated, single-action closing mechanism to permit opening and closing actions (Murray and Hjort, 1912; Kemp and Hardy, 1929; Leavitt, 1938; Motoda, 1959; Niskin and Jones, 1963); internal throttling of the net (Kemp and Hardy, 1929; Marr, 1940); and changes in location of the throttling point on the net. Throttling should be accomplished (especially in vertical tows) without permitting the net to fall backward through the water, to prevent backflow and loss of material from the mouth.

Opening and closing operations in the Nansen system were initiated by messengers or weights sliding down the towing cable to the tripping mechanism at the net,

or by tripping ropes leading from the vessel to the net. The cables for a throttling system create a hazard to successful operation of the opening and closing actions, and care must be taken during launching to prevent tangling the gear. Tripping is not always reliable, and other systems have been devised for closing and opening operations. A solenoid-activated release, powered through a two-conductor rubber-covered cable, was described by Van Cleve (1937). The mechanism is cocked with the net in the collapsed position; at first release the net is opened, and at second release the net is closed by the noose rope. Opening-closing actions which are pressure operated at preset depths were described by Yentsch et al. (1962).

The Clarke-Bumpus sampler (Clarke and Bumpus, 1950) has a messenger-activated, spring-loaded, disc-closing mechanism. It can be attached to the wire at any point, and a series of samplers can be tripped on a single cable. This sampler has been widely used in studying vertical distribution of organisms. Improvements in its design and increase in size have been described by Paquette and Frolander (1957), Paquette, Scott, and Sund (1961), and Tranter (1965). Yentsch et al. (1962) described a pressure-operated opening-closing mechanism.

Single net, cod-end closure. Cod-end closure of a single net has been a recent development. Barham (1958) described a cod-end device consisting of an open-end box, equipped with butterfly valves activated in sequence by a propeller mechanism. Yentsch et al. (1962) described an electrically fired, explosive squib-controlled unit for meter nets. Foxton's device for large plankton nets and midwater trawls is an inverted Y-tube with spring-loaded flap at the crotch which divides the catch into two parts (Foxton, 1963). Aron et al. (1964) described several cod-end opening and closing devices. The most recently developed model is a tube with four chambers and four sets of doors, the doors being closed in order from rear to front by an electrical impulse through a single-conductor cable (which serves also as a towing cable), separating the catch into four discrete samples. Pearcy and Hubbard (1964) adapted the multiple net sampler described by Bé (1962) to serve as a multiple cod-end sampler for the Isaacs-Kidd midwater trawl (Isaacs and Kidd, 1953).

Recently, Longhurst et al. (1966) described a filtering mechanism similar to that employed in the Hardy continuous plankton recorder (Hardy, 1936a) to be used as a cod-end device on a half-metre net. Discrete samples are obtained as the filtering gauze is advanced in steps rather than continuously as in the Hardy sampler. Electrical drives are powered through a self-contained power supply. This device does not crush organisms as badly as does the Hardy recorder, and it can be used with a net which filters a much larger volume of water.

Multiple net sampler. Probably the most widely used multiple net system is that described by Bé et al. (1959) for vertical tows. In the initial design messenger-activated pivoting rods presented three previously folded nets in sequence to the flow. The first net is folded out of the way and closed as the second net is unfolded to the flow, and so on. This sampler was subsequently modified for horizontal towing, so that it can be opened and closed by a pressure-activated piston-type release mechanism (Bé, 1962).
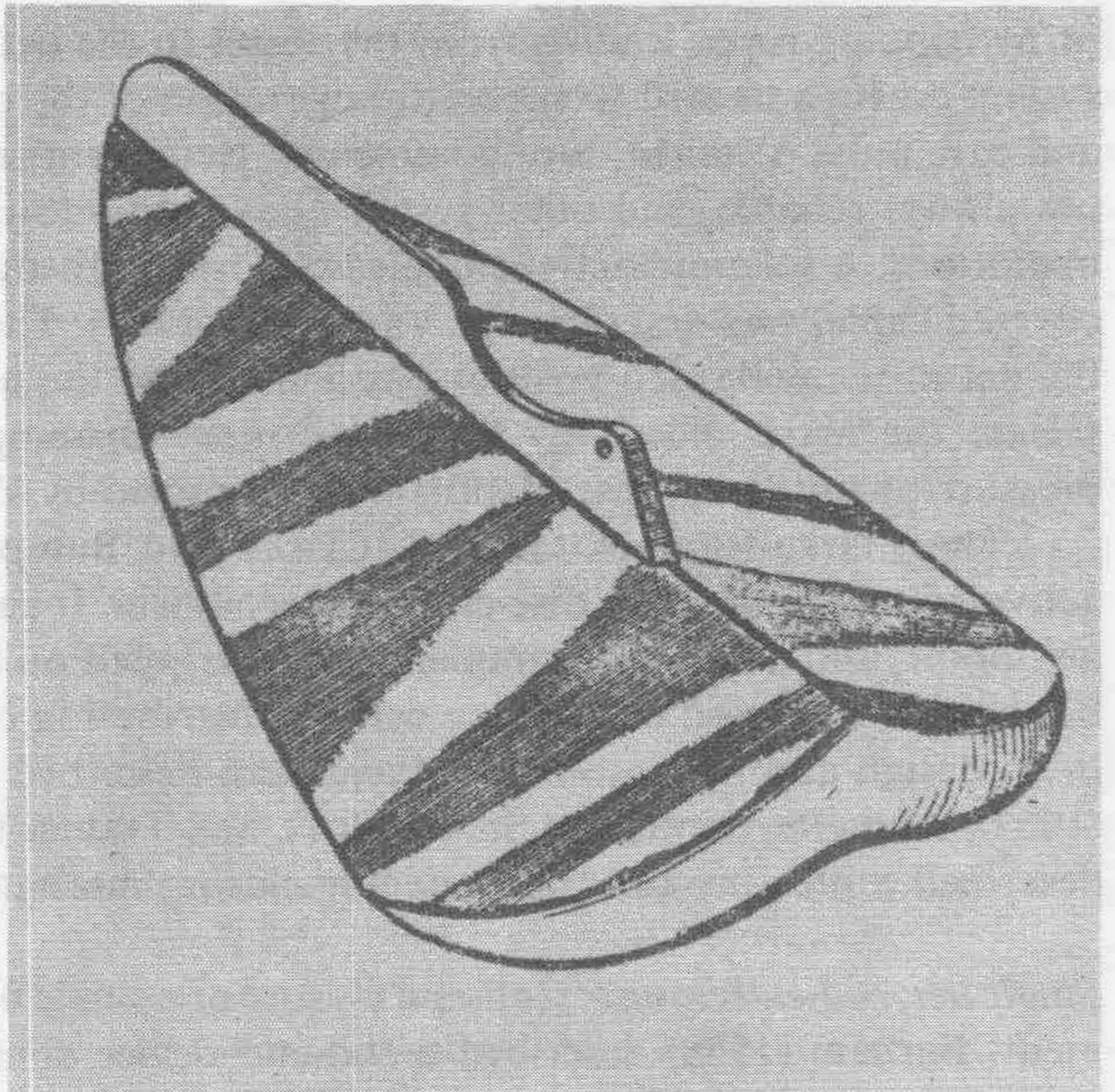
Figure 1
Scripps cable depressor
(from Isaacs, 1953).

HIGH-SPEED SAMPLING

High-speed samplers have been developed mainly because of the assumptions that tows at high speed take more representative catches of mobile organisms, and that costs are reduced by sampling at or near the ship's cruising speed. Comparative data on catch of high- and low-speed samplers are meagre and the validity of the assumption of better catching power of high-speed samplers is questionable. Of considerable merit, however, is the second aspect. Reduction in time necessary to cover a sampling grid can represent a significant saving of money and man-hours.

High-speed samplers

High-speed plankton samplers can be divided into three groups; those without, and those with opening-closing devices, and those which separate portions of the sample.

Samplers without closing devices include: a group with small mouth aperture (12 to 50 mm diameter) represented by several versions of the Hardy indicator (Arnold, 1952; Glover, 1953; 1961; Ahlstrom *et al.*, 1958; Miller, 1961); two with medium-sized mouth apertures (90 to 115 mm diameter), the Icelandic high-speed sampler (Jakob Jakobsson, personal communication), and the Jet net (Clarke, 1964); and several designs with large mouth diameters (200 to 485 mm diameter), based on the Gulf III (Gehringer, 1952; Bridger, 1958; Beverton and Tungate, manuscript). The Jet net and the Gulf III may be fitted with flowmeters.

High-speed samplers with closing devices are: the Bary catcher (Bary *et al.*, 1958) and two samplers based on the Gulf III. Bary (personal communication)
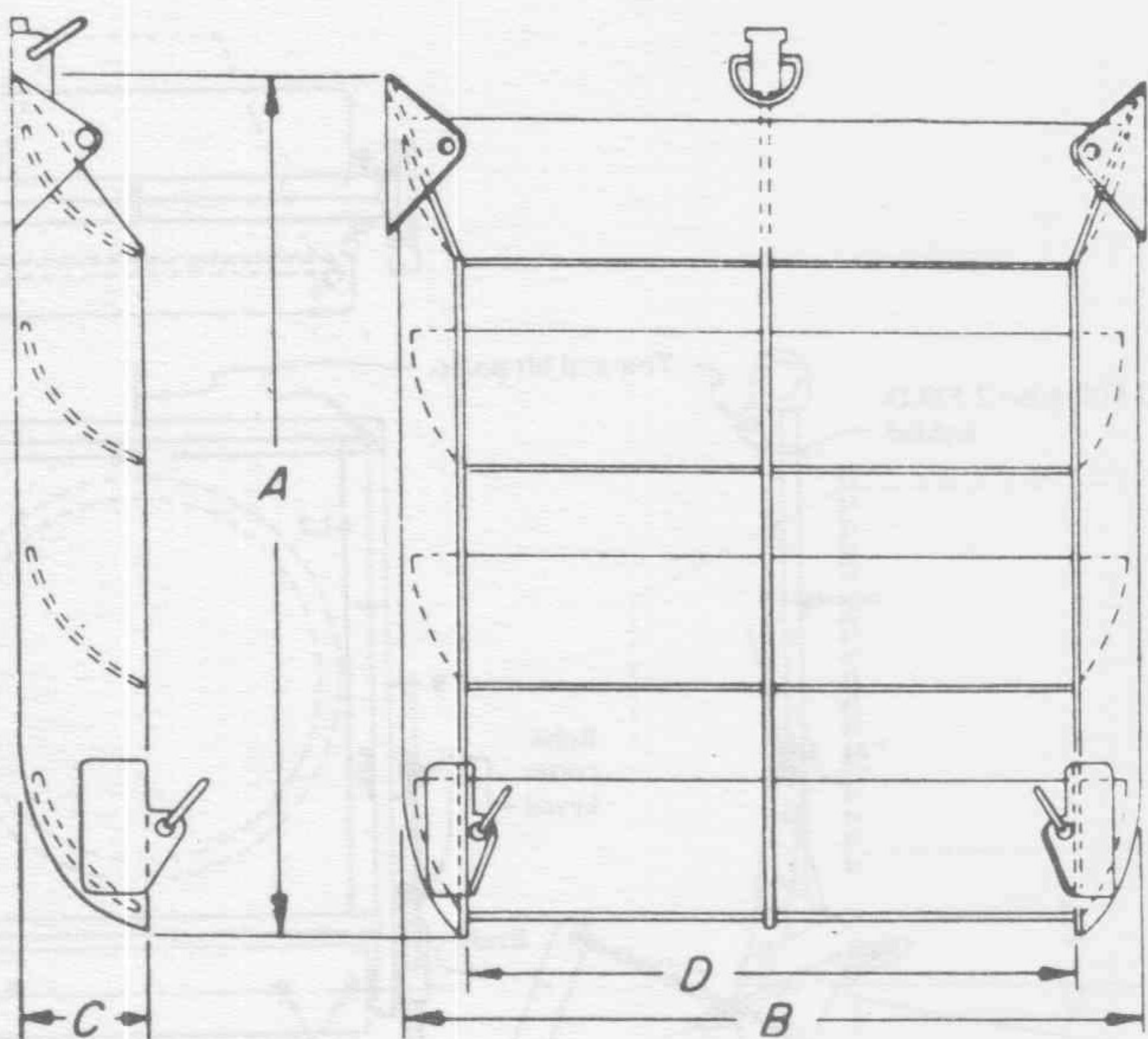
Figure 2
Multiplane kite-otter
depressor
(from Colton, 1959).

U.S. Navy No.	Weight	Approximate tow load			Dimensions			
		5k	7k	10k	A	B	C	D
	(lb.)	(lb.)	(lb.)	(lb.)				
1	500	3 800		14 000	5'5¾"	5'2½"	9"	4'3½"
4	180	2 600		6 000	3'10½"	3'8"	6⁷/₈"	3'0¼"
5	60	800	1 800	3 000	3'0¾"	2'10¼"	5"	2'4"

replaced the sleeve valve in the original version of the Bary catcher with a closing disc as in the Clarke-Bumpus sampler. A limitation is that water pressure interferes with closure of the disc at high speeds in samplers with large mouth apertures. A German version of the Gulf III, the 'Hai', has a messenger-triggered, spring-loaded lid closure that covers the nose aperture (Kinzer, 1962 and 1966); and a recent development by the Fisheries Laboratory, Lowestoft, England, uses Bé's technique of changing filtering nets (Derek Harding, personal communication). Bary's catcher and some versions of the Gulf III are fitted with flowmeters.

The third group of high-speed samplers includes those which take a series of discrete samples or a continuous sample. Neither of the samplers for taking multiple samples (Motoda, 1959; Williamson, 1963) has been widely used, but the Hardy continuous plankton recorder (Hardy, 1936a) has been routinely operated from merchant ships in the course of their normal business. The Hardy recorder takes a continuous sample as a propeller drive winds a band of gauze across the flow of water on to a storage spool in a preservation chamber. A closing device is not needed. A measure of water volume filtered is provided. Recently, Glover (1967) presented a proposal for the design and development of a general oceanographic vehicle, based on the Hardy recorder, which would undulate vertically in the upper
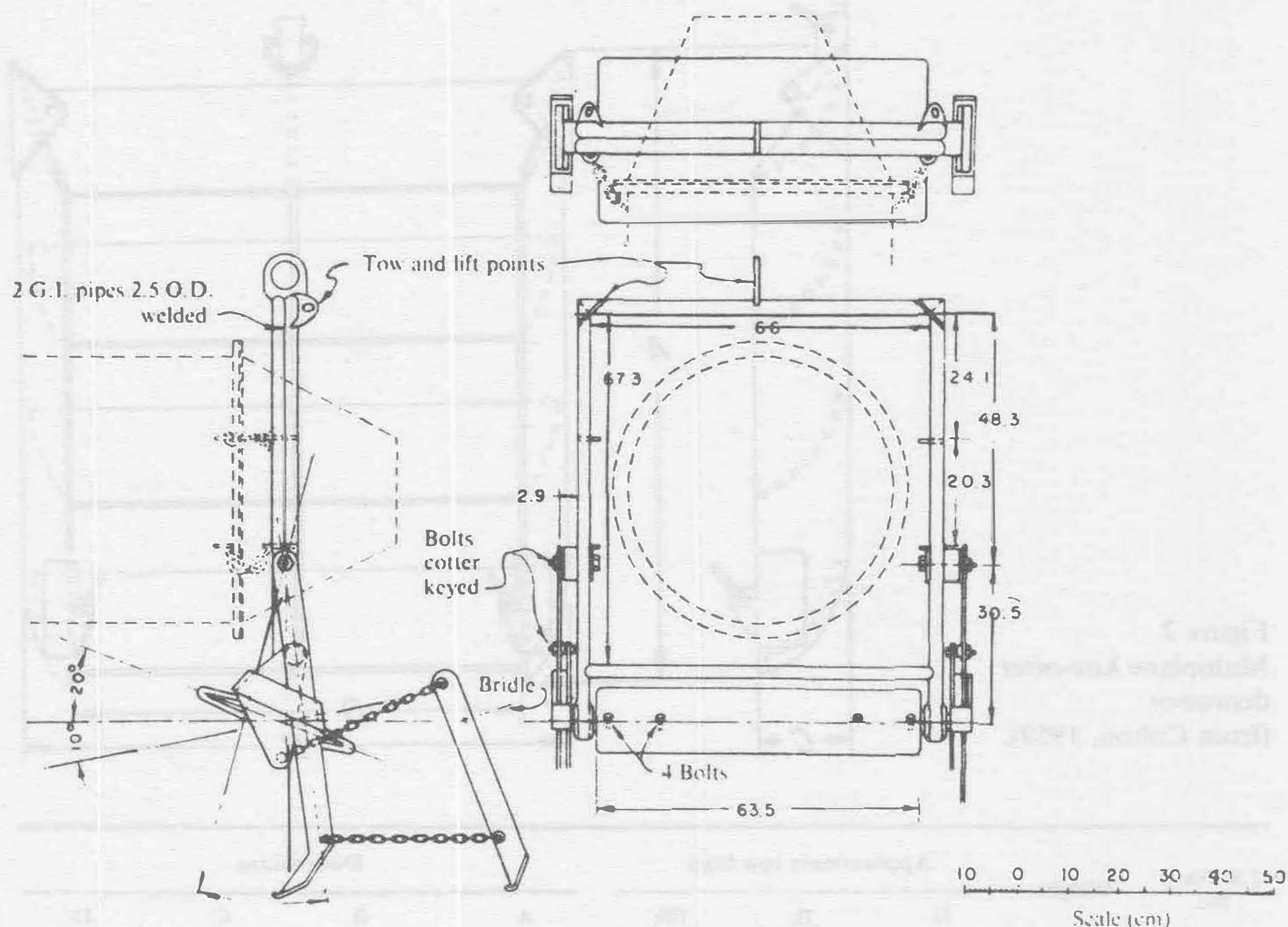
Figure 3
Boothbay depressor No. 3 (from Graham and Vaughan, 1966).

100 metres as it is towed at normal cruising speeds, and would record physical variables as well as sample the plankton.

Special problems of high-speed sampling

Increased drag of samplers and towing cable in high-speed towing introduces special problems. Dead weights, streamlined or not, are the only suitable means of taking a net to depth in vertical hauls and other tows at speeds below about 3 knots. They have the advantages of simplicity, ruggedness, and low cost. The weight required to attain depth at higher speeds, however, is large enough to cause serious handling problems, and to become hazardous during rough weather.

Depressors. The problem of attaining high depressing force without great weight has been partially solved through the evolution of hydrodynamic depressors which have high lift/drag ratio. One of the earliest depressors was a square iron plate hinged at an angle to the lower edge of the frame of the Heligoland young fish trawl (Ehrenbaum and Strodtmann, 1904). Since then hydrodynamic depressors of many kinds have been developed either as integral parts of the sampling device, as in the young fish trawl, or as separate units that can be used with a variety of towed objects.

The Scripps homogeneous depressor (Isaacs, 1953) shown in Figure 1, probably

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Figure 4

Isaacs-Kidd midwater trawl (from Isaacs and Kidd, 1953).
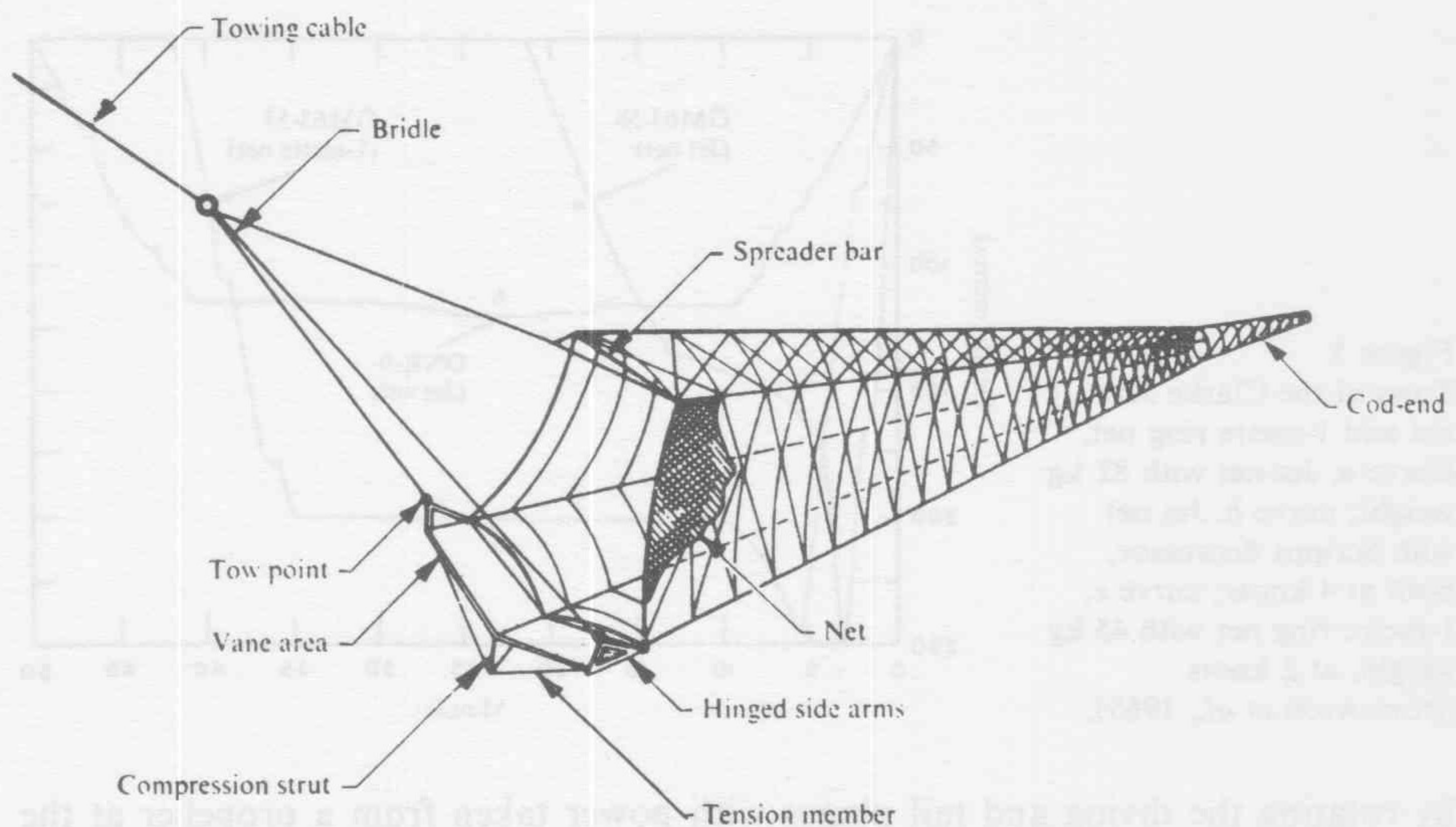
the most widely used device of this kind, has been used with the full array of samplers ranging from the Clarke-Bumpus (Clarke and Bumpus, 1950) to the Gulf III sampler (Gehringer, 1952). Less widely used are the multiplane kite-otter (Colton, 1959) of Figure 2, and the Boothbay depressor (Graham and Vaughan, 1966) of Figure 3. The latter is designed for sampling very close to the bottom and is so built that accidental contact with the bottom alters the 'angle of attack' and prevents the depressor from digging in and damaging the sampler. The V-fin, a stable low-drag depressor of hydrodynamic design, has been used in surveys with echo-sounders towed by helicopters in the Canadian Arctic (Eaton, 1963), but its value as a depressor for plankton samplers appears limited.

Of the depressors which are an integral part of the sampler, the two in widest use are blades. One is associated with the Hardy continuous plankton recorder (Hardy, 1936a) and the other with the Isaacs-Kidd midwater trawl (IKMT) (Isaacs and Kidd, 1953), Figure 4. Several modifications have been made to the IKMT depressor to simplify handling. Taniguchi[1] used a Y-shaped depressor and substituted canvas for steel to reduce weight. Bercaw (1966) described a folding aluminium depressor for the 6-foot net which has proven easy to handle and to store.

Smith et al. (1964) described a modified version of the Gulf I-A sampler (Arnold, 1952) with trim tabs on the horizontal stabilizers, eliminating the need for an independent depressor. This sampler was towed successfully at about 2 metres depth at speeds to about 18 knots. Glover (1967) described an undulating oceanographic instrument which utilizes two depressing planes, inverted aerofoil sections of approximately the same shape and same degree of anhedral as conventional cable depressors. This instrument follows a sinusoidal tow path, achieved

1. Asterisked (*) references denote information presented at the Sydney Symposium.

Figure 5
Tows of the Clarke Jet
net and 1-metre ring net.
Curve *a*, Jet net with 82 kg
weight; curve *b*, Jet net
with Scripps depressor,
both at 4 knots; curve *c*,
1-metre ring net with 45 kg
weight, at 2 knots
(from Aron *et al.*, 1965).
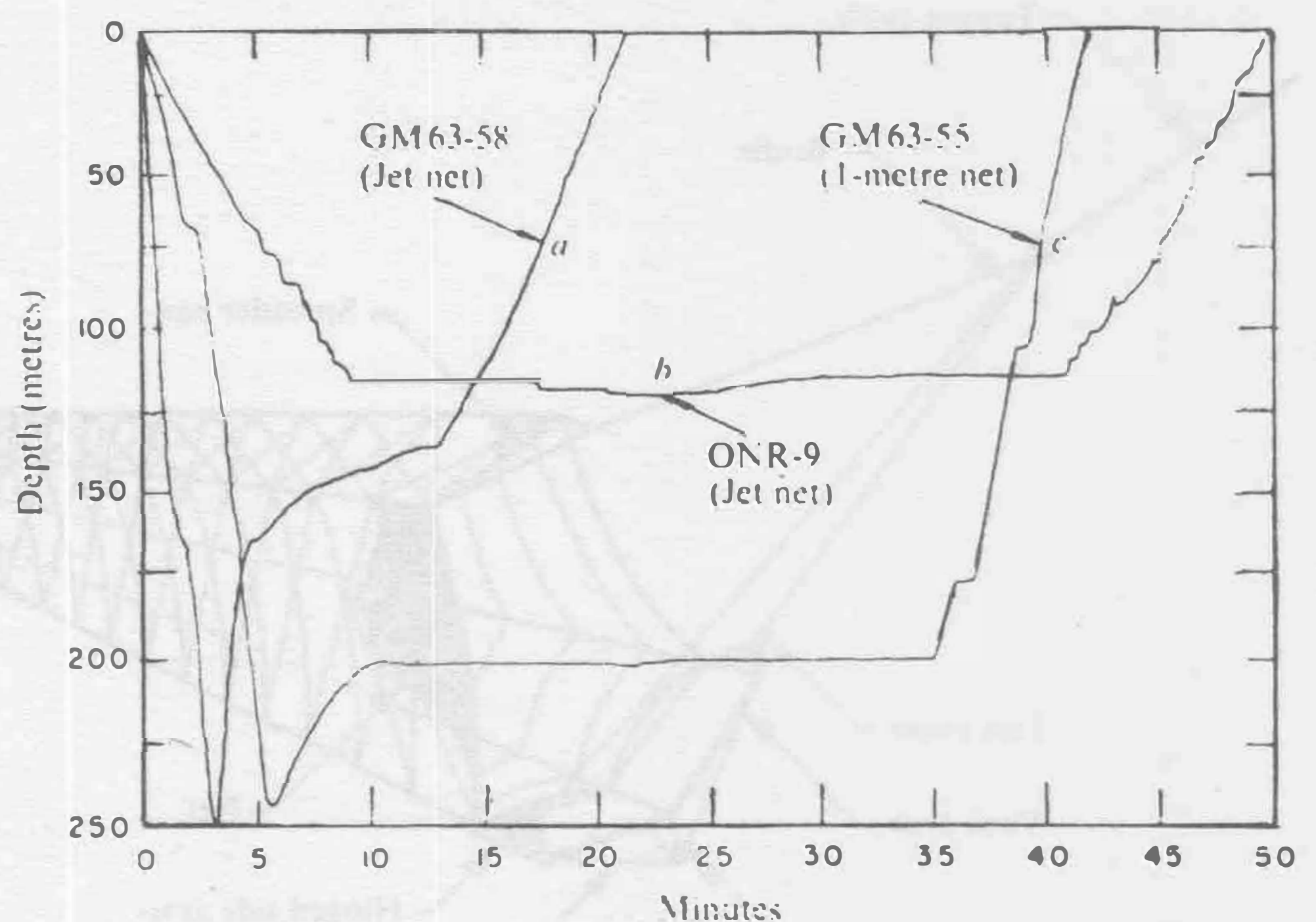
by rotating the diving and tail planes with power taken from a propeller at the after end of the sampler.

Performance studies of depressors. Studies on field performance of depressors have been limited, primarily because instrumentation for monitoring performances has only recently become available. Aron *et al.* (1965) obtained information on the characteristics of a number of the above depressors and several sampling devices.

Hauls made with a 1-metre ring net and the Jet net (Clarke, 1964) are shown in Figure 5. Ship speed was held constant throughout these tows. When a simple weight is used for attaining depth there is a considerable decrease in sampling depth when the winch brake is set at the end of cable payout. The low lift/drag ratio of the dead-weight depressor can also be seen by comparing the two Jet net tows, one with a dead-weight (curve *a*) and one with a Scripps depressor (curve *b*). Approximately the same depth was attained in both tows with the same cable length, despite the fact that the depressor weighed only 20 kg and the dead-weight 82 kg. More important, there was no change in depth when the brake was set during the haul with the Scripps depressor.

In 5.6 knot tows with the Bary catcher (Bary *et al.*, 1958), the Scripps depressor was compared with the multiplane kite-otter (Fig. 6). The high lift/drag ratio of the kite-otter is demonstrated by its much lower ratio of cable length to depth (roughly 2:1) in comparison with the Scripps depressor (4:1). The net path was very erratic in the tow with the kite-otter, however, due to the instability of the depressor. This condition was improved by adjustment of the bridles, to which the kite-otter appears to be very sensitive. If this sensitivity can be reduced, the unit would be most useful.

Bary (personal communication) has compared the Scripps depressor and the multiplane kite-otter used with the Bary catcher. His observations indicate that: (a) the kite-otter has two to three times the down-lift of the Scripps depressor (proportionately increasing in favour of kite-otter as speed increases); (b) the kite-otter will take equipment deeper on a shorter length of warp at any one speed
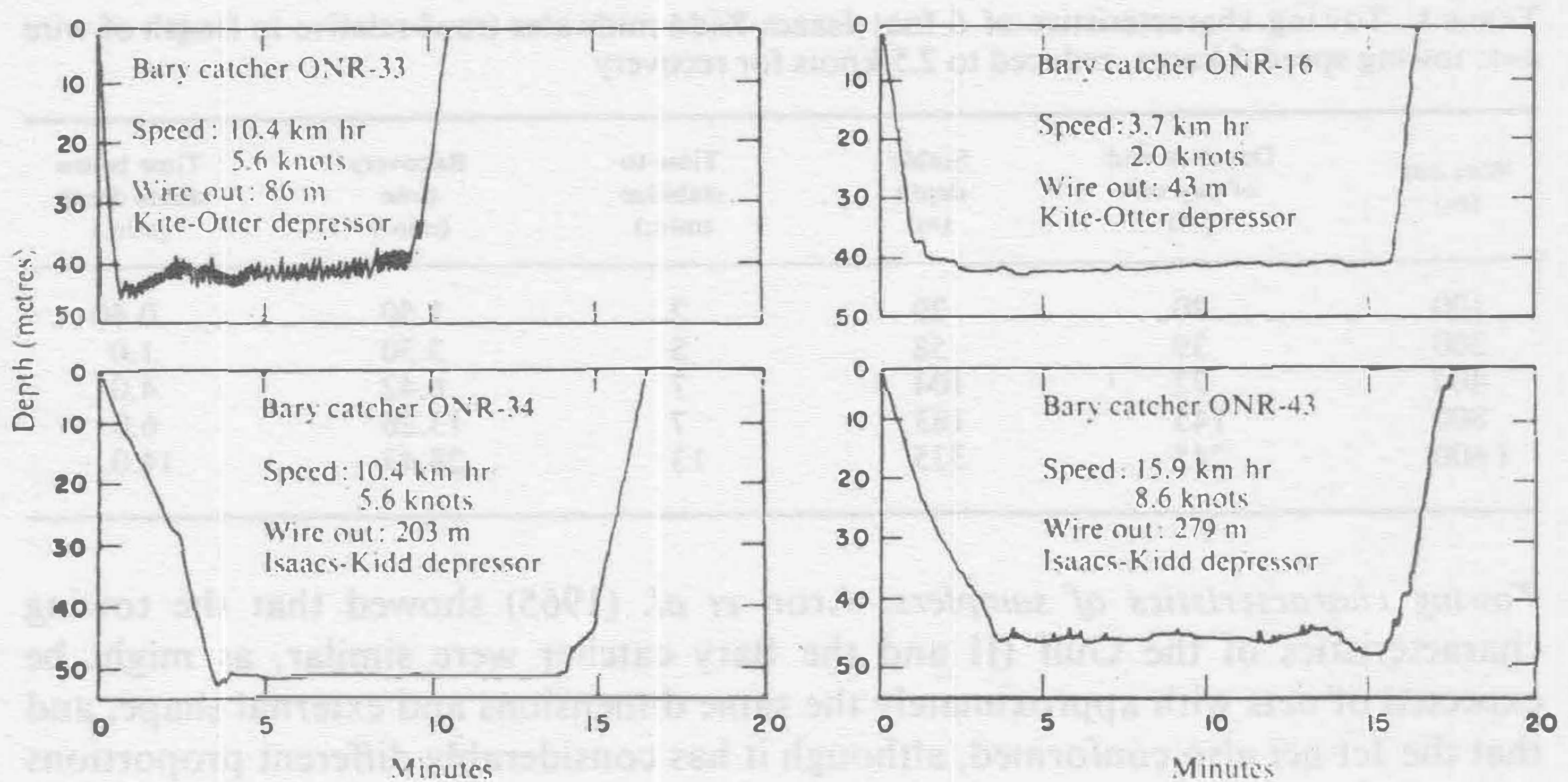
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Figure 6
Bary catcher tows, showing variation in length of wire required
to get same depth at various speeds
(from Aron et al., 1965).

and can descend to much greater depth at all speeds, but is not so convenient to use as the Scripps depressor; (c) the Scripps depressor of 45 pounds (20.4 kg) cannot overcome lift of wire ($^9/_{32}$ inch diameter) at towing speeds above approximately 6 knots for lengths of cable greater than 300 metres; and (d) both depressors show indications of instability, but at lower speeds in the kite-otter than in the Scripps depressor. Colton (1959) gave plans and performance characteristics for several models of the kite-otter depressor.

Aron et al. (1964, 1965) described the towing behaviour of a 6-foot IKMT, in which the depressor is an integral part of the sampler. The data for cable lengths of 100, 200, 400, 800 and 1,600 m show that sampling depth increases with decreasing towing speed, with greater effect at lower velocities. This same observation was made for all of the other depressors which were tested, and it appears to hold for depressors in general.

The dead-weight lost depth when the winch brake was set after all the cable had been paid out, the Scripps and kite-otter depressors seemed to hold depth, and the IKMT increased in depth (up to 50 per cent greater). The time required for the IKMT to attain stable towing depth generally increased with increasing wire length. In a series of hauls at 5 knots, in which towing speed was reduced to about 2.5 knots to facilitate recovery, the IKMT went deeper and for about half the recovery period was below the original depth of sampling (Table 1). Taniguchi et al. (1965) and Imanishi et al. (1965) confirm this increase in depth during recovery. They also showed that the gape height of the net at towing speeds of 5 to 7 knots was 25 to 35 per cent less than that of the stationary net. These papers also include information on the towing resistance of two 10-foot models of the IKMT relative to speed.

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TABLE 1. Towing characteristics of 6-foot Isaacs-Kidd midwater trawl relative to length of wire out; towing speed 5 knots, reduced to 2.5 knots for recovery

Wire out (m)	Depth at end of pay-out (m)	Stable depth (m)	Time to stabilize (min.)	Recovery time (min.)	Time below stable depth (min.)
100	20	29	2	1.50	0.40
200	39	58	5	3.30	1.0
400	72	104	7	6.42	4.0
800	145	183	7	13.26	6.0
1 600	245	335	13	28.43	14.0

Towing characteristics of samplers. Aron *et al.* (1965) showed that the towing characteristics of the Gulf III and the Bary catcher were similar, as might be expected of nets with approximately the same dimensions and external shape, and that the Jet net also conformed, although it has considerably different proportions of length and diameter.

The towing characteristics of other samplers are poorly documented. During an oblique tow with the Bé multiple plankton sampler (Bé, 1962), the path followed by the net during payouts was highly irregular (Fig. 7). The irregularity appeared to start at the time of net opening. Data are sparse, but it might be expected that a change in the configuration of the sampler would alter the tow path, and this appears to occur during tows of the Bé sampler. This possibility and its potential effect on interpretation of data may be relevant to other opening-closing devices that change the effective cross-sectional resistance of the net to the water column. Bary has found that closing the Bary catcher has no effect on the towing path in a few monitored tows (personal communication).

DETERMINATION OF DEPTH OF SAMPLING

After length or duration of tow, depth of sampling is the parameter most often measured by planktologists. The simplest technique is to measure the length of cable in the water with a meter wheel, and the cable angle with a clinometer, and to compute the depth of sampling. This method assumes that the cable forms a straight line from the surface to the sampler. With increasing cable lengths, however, this assumption generally introduces an increasingly greater error as a catenary forms in the cable. A further error in the depth estimate may occur if changes in the angle at the surface remain undetected, or fail to occur in response to depth changes, as for the Bé sampler (Fig. 7) and the kite-otter depressor (Fig. 6).

Maximum depth and depth-distance recorders

The desire for more reliable depth information has led to the development of techniques for obtaining direct measurements. The simplest of these are the Kelvin tube and the bathythermograph which are 'maximum-depth' recorders. These instruments record the maximum depth reached during the haul, but provide no

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Bé sampler ONR 11

Begin recovery

Depth (metres)
0
200
400
600
800
1000
1200
1400
1600

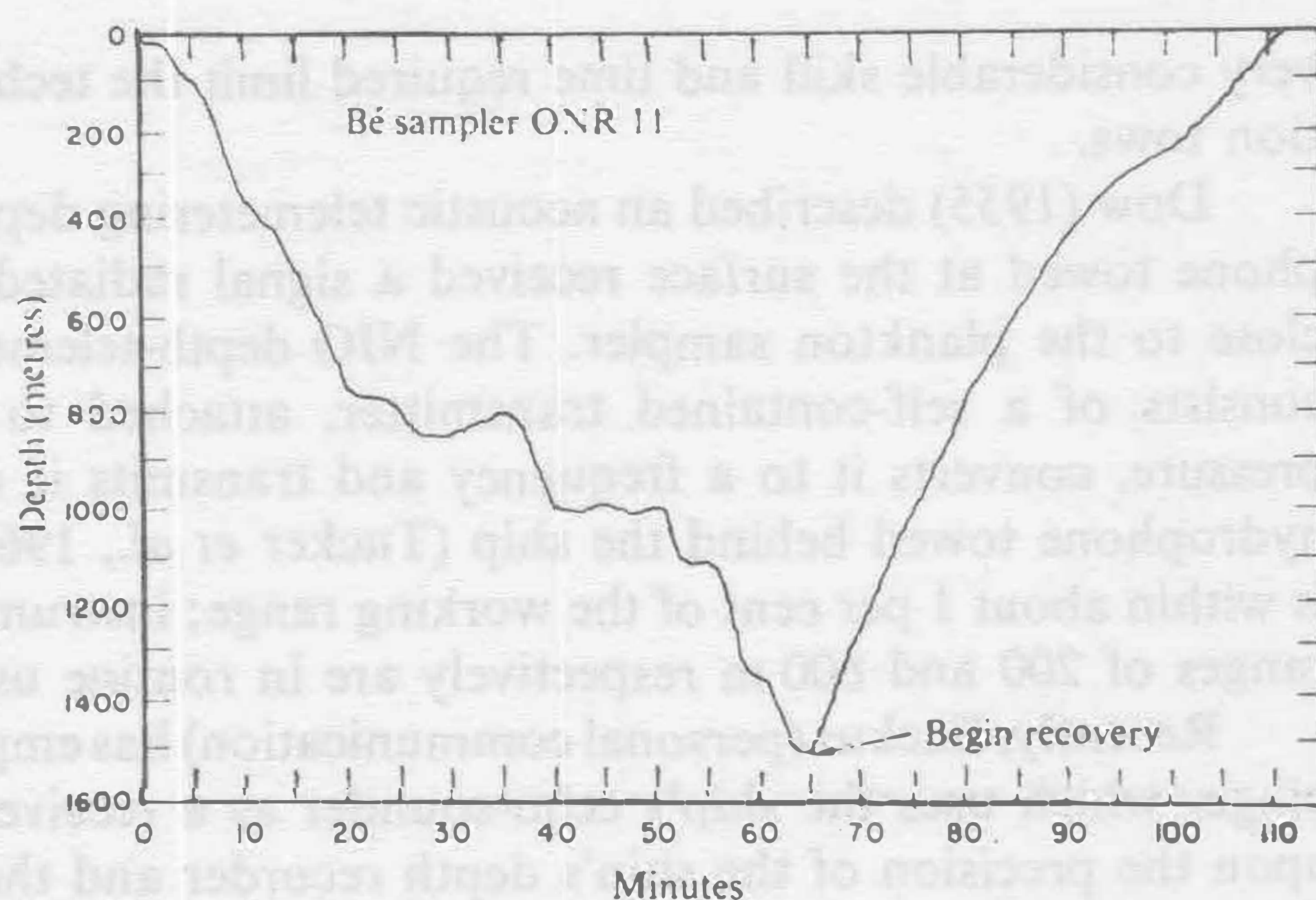0 10 20 30 40 50 60 70 80 90 100 110
Minutes

Figure 7
An oblique tow with
the Bé multiple plankton
sampler, at 1 knot using
45 kg weight
(from Aron *et al.*, 1965).

other information on the tow path, and are generally limited to depths of 500 metres or less. Also, depth is not known until the completion of the haul.

To obtain further information on the tow path, Moore (1952) developed a depth-distance recorder. This device employs a standard bathythermograph slide moved lengthwise by a propeller-driven, worm-operated screw to record distance travelled through the water. Depth is recorded on the slide by a stylus attached to the end of a Bourdon tube. Although this device has not seen wide use, the technique probably provides the least expensive method of recording the sampling path and should not be overlooked. The integrated depth recorder (Hamon, Tranter and Heron, 1963), also used with a Bourdon tube, gives a variable density trace on a fixed photographic film by means of a radioactive source. Maximum and average depths and variation about the average can be read off.

These or other similar types of depth recorders equipped with Bourdon tubes (which can be exchanged according to depth range of operation) are in use with the Gulf III and the IKMT. In the older (but more reliable) type, the recording paper is driven by a simple clockwork motor with a watch spring; the newer type is battery driven. The rather heavy steel casing required for the depth recorder can serve as additional dead-weight.

Another simple method of recording the sampling depth has been designed by D. Brown of the Scripps Institution of Oceanography. This equipment plots depth versus time on an inexpensive battery-powered recorder. This and similar recorders available on the commercial market have been widely used.

Monitoring depth during sampling

In each of the above instruments the depth data are available only after the tow is completed. Because there are obvious advantages to knowing the sampling depth during the haul, a number of monitoring techniques have been used.

Acoustic telemetry. Backus and Hersey (1956) used an echo-sounder from a following ship to determine the cable configuration and depth of an Isaacs-Kidd midwater trawl. This procedure requires no additional special equipment, but the

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very considerable skill and time required limit the technique primarily to calibration tows.

Dow (1955) described an acoustic telemetering depth meter in which a hydrophone towed at the surface received a signal radiated by a transducer attached close to the plankton sampler. The NIO depth-telemeter, based on Dow's unit, consists of a self-contained transmitter, attached to the net, which measures pressure, converts it to a frequency and transmits it over an acoustic link to a hydrophone towed behind the ship (Tucker *et al.*, 1963). The accuracy achieved is within about 1 per cent of the working range; instruments with maximum depth ranges of 200 and 600 m respectively are in routine use.

Recently, Backus (personal communication) has employed a depth telemetering pinger which uses the ship's echo-sounder as a receiver. Quality of data depend upon the precision of the ship's depth recorder and the accuracy of the pressure sensor. Backus used a Precision Graphic Recorder, with greater accuracy than the average echo-sounder, and results appear to be within the accuracy specified by the manufacturer of the pressure sensor (± 3 to 5 per cent, depending upon the sensor used).

The Furuno Net-Sonde, an acoustic-telemetering depth meter, has been used principally in Japan to assist in placing a net at the same depth as fish groups. This has potential in plankton studies.

Electric telemetry. Boden *et al.* (1955) described a depth-recording unit which telemetered data along a single-conductor insulated cable to a recorder on deck. Aron *et al.* (1964) and Bourbeau *et al.* (1966) described a system for telemetering depth electrically by using a single-conductor, load-bearing electrical cable. Their use of a multiplexed FM system allows the simultaneous telemetry of data on temperature, light, and net speed, in addition to depth, and also permits the electrical control of a cod-end sampler. Other sensors can be added without changing the cable or winch requirements. In cost and reliability, the single-conductor cable closely approximates that of non-conductor cable of similar strength.

Acoustic versus electric telemetry. In the consideration of the relative merits of acoustic telemetry and telemetry through a single-conductor cable, several points should be mentioned. The initial costs of acoustic telemetry of a single variable are generally less than those of an electrical conductor system. The transmission of data simultaneously from several sensors, however, is easier, more reliable, and for most purposes less expensive electrically than acoustically. Problems of ambient noise, slant range, and variable sound velocity are eliminated by telemetering electrically. In addition, the limited rate at which information may be transmitted in acoustic telemetry, renders this approach generally unsatisfactory for use with rapidly changing variables such as bioluminescence.

MEASUREMENT OF VOLUME OF WATER FILTERED

A measure of the quantity of water filtered during a plankton tow is essential in

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quantitative sampling. A flowmeter mounted in the mouth of the simple conical net provides a means of estimation. Recent studies of the water velocity at various points across the mouth of the net suggest that a better estimate of the flow through the net is obtained by a meter positioned midway between the centre of the mouth and net rim, rather than centred in the mouth as is commonly done.

A second flowmeter, placed in the free stream outside the net, provides an estimate of the speed of the sampler through the water and, combined with the meter in the mouth, an estimate of the sampler's filtration efficiency. This arrangement is useful in determining the maximum length of time a net of a particular mesh size can be towed in a given body of water before it becomes clogged. Clogging reduces the filtration efficiency of a net, which affects meter readings, and in turn, estimation of the volume of water filtered. Unusually large differences in the readings between the sampler flowmeter and the free stream meter would suggest clogging, and the inaccurate estimate could be discarded. The necessity for rigid standardization of conditions from tow to tow cannot be overemphasized. Without the second meter, we can only speculate on the possibility of clogging.

The simplest flowmeters in use today indicate the number of revolutions of the impeller blades on a series of dials or on a counter. They are commonly supplied with a calibration curve from the manufacturer and are rated for speeds up to 5 knots. These meters provide information after a tow has been completed, and are probably adequate for most sampling programmes. The TSK flowmeter (Nakai, 1954) has proven to be a highly reliable and sturdy meter of the dial type. Tungate and Mummery (1965) described an inexpensive mechanical digital flowmeter. Comita and Comita (1957) described a modification of the Clarke-Bumpus sampler in which a control system can be preset for passing definite quantities of water through the sampler.

Calibration of flowmeters is best done in a testing facility where speed and distance can be closely controlled (Tranter and Smith: see Chapter 3 above). The standard field calibration method is to tow the flowmeter free of the sampler over a known distance and equate impeller revolutions to a measure of distance.

Recent developments in acoustical and electrical instrumentation have provided means of monitoring flow and other sensor data during towing. These systems require either electrical circuits between the sampler and the vessel or acoustical transmission and receiving equipment. One reason for monitoring during a tow is to determine when clogging begins, so a haul may be terminated before further clogging affects the estimate of water filtered. Several manufacturers now offer telemetering ducted impeller current meters, reported to be accurate at speeds up to 5 knots.

The validity of estimates of volume filtered obtained by a meter mounted in the exhaust of the Gulf III high-speed sampler (Gehringer, 1952) is highly questionable. Recent studies of flow velocities across the exhaust of the Gulf III revealed highly variable turbulence which makes estimates of total volume with present meters unrealistic.

There is evidence that flowmeters with impeller blades which nearly fill the mouth or exhaust of a sampler are more accurate than small flowmeters in estimating total flow.

TOWING EQUIPMENT AND PROCEDURES

Most cruises are multipurpose, and the biologist must share available winch, cable, and gear handling facilities with other programmes. These must be adequate for the heaviest gear to be operated, and probably are not best suited for handling and towing plankton gear. Adequate gear-handling facilities are essential to safety, particularly when heavy instruments are used. Figure 8 (from Beverton and Tungate, manuscript) illustrates an adequate arrangement for handling a large multipurpose plankton sampler. For any work at sea the quality of results is in part determined by the ease of operation. Since collections are often made by technicians, who have little personal interest in the results, adequate handling gear and a set of procedures to be rigidly followed should be provided.

Equipment

Winches. Oceanographic winches are subjected to gruelling conditions and are frequently overloaded. It is important to choose a winch of rugged and conservative design. Those not experienced in writing and enforcing engineering specifications would do well to deal only with manufacturers who have produced satisfactory oceanographic winches in the past, and to adhere, if possible, to proved designs. It would be well also to obtain advice and copies of specifications from an organization which has experience in procuring winches. (Many companies cannot be made to realize that winches for long wires differ from winches for short wires.) In general, careful attention should be paid to the following points.

Spools must be exceedingly rugged to avoid crushing of the core and distortion or breakage of the flanges by the many turns of wire. Good durable level-winds (spreaders) must be provided, and special thought must be given to making fair-leading devices which will not be worn excessively by the wire. Power should be adequate for long hauls without overheating the driving mechanism. The brake should be easy to apply and strong enough to break the heaviest wire which is to be used. Similarly, the winch structure, the level-wind, the fastenings to the deck, and the deck itself usually should be strong enough to break the wire without suffering damage.

The size, power requirement, and cost of a winch are determined by the choices of wire size, wire length, hauling speed, and load on the wire. The required horse-power output may be obtained by multiplying the hauling speed in feet per minute by the actual dynamic wire tension in pounds and dividing by 33,000. Since the horsepower efficiency will be only 50 to 75 per cent, the driving motor must be correspondingly larger. And, if the power sources used lack the short-term overload capacity of electric motors (e.g., some hydraulic drives, or internal combustion engines), additional power must be provided for such overloads. It is well to provide for unanticipated long-term overloads, or, more desirably, to have a gear-shift or equivalent mechanism that exchanges torque for speed, to haul heavy loads in emergencies. In estimating the working tension one should add the static pay-load, the weight of all the wire, the drag forces on wire and equipment at the hauling speed, and then multiply by a safety factor (at least 1.5) which includes effects due to surging of the ship and provision for unknown demands of the future.

Warpmeter recorder

Warpmeter transmitter

Depressor

Winch

Accumulator block

Drogue

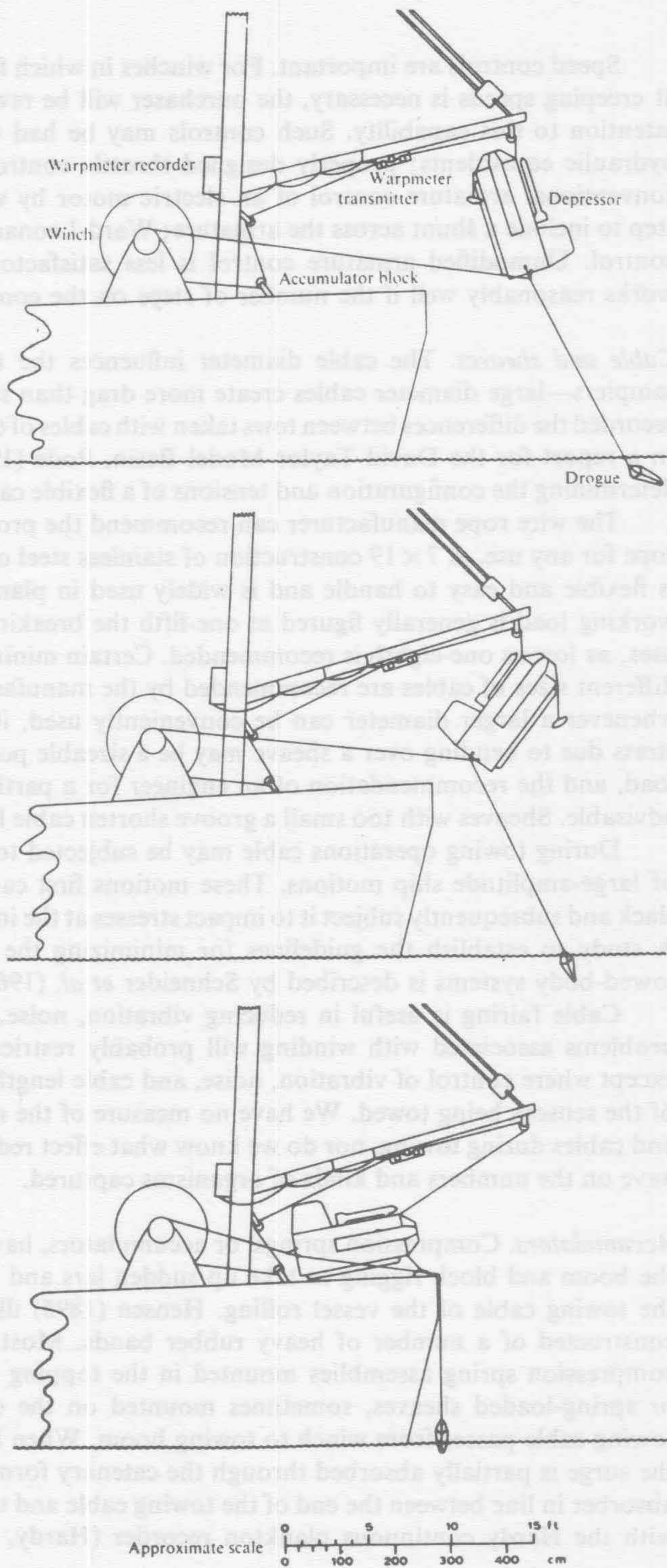Figure 8
Diagrammatic lay-out of winch and towing gear, and three stages of retrieving of the multiple sampler (from Beverton and Tungate).

Approximate scale

0   5   10   15 ft

0   100   200   300   400   cm

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Speed controls are important. For winches in which fine control of wire length at creeping speeds is necessary, the purchaser will be rewarded if he gives special attention to this capability. Such controls may be had with: gear shifts or their hydraulic equivalents; properly designed throttle control of a hydraulic motor; conventional armature control of an electric motor by wiring the first controller step to include a shunt across the armature; Ward-Leonard control; and thyratron control. Unmodified armature control is less satisfactory, but is often used. It works reasonably well if the number of steps on the controller is relatively large.

Cable and sheaves. The cable diameter influences the towing characteristics of samplers—large diameter cables create more drag than small ones. Colton (1959) recorded the differences between tows taken with cables of 6.4 and 12.7 mm diameter. In a report for the David Taylor Model Basin, Pode (1951) produced tables for determining the configuration and tensions of a flexible cable moving in a fluid.

The wire rope manufacturer can recommend the proper size and type of wire rope for any use. A 7×19 construction of stainless steel or galvanized plough steel is flexible and easy to handle and is widely used in plankton sampling. The safe working load is generally figured at one-fifth the breaking strength, but for some uses, as low as one-eighth is recommended. Certain minimum sizes of sheaves for different sizes of cables are recommended by the manufacturers of wire ropes, but whenever a larger diameter can be conveniently used, it is preferable. The total stress due to bending over a sheave may be a sizeable portion of the safe working load, and the recommendation of an engineer for a particular set of conditions is advisable. Sheaves with too small a groove shorten cable life.

During towing operations cable may be subjected to severe loadings because of large-amplitude ship motions. These motions first cause the cable to become slack and subsequently subject it to impact stresses at the instant of tension recovery. A study to establish the guidelines for minimizing the effects of slack-cable in towed-body systems is described by Schneider *et al.* (1964).

Cable fairing is useful in reducing vibration, noise, and drag. The cost and problems associated with winding will probably restrict the use of faired cable except where control of vibration, noise, and cable length are critical to operation of the sensors being towed. We have no measure of the noise created by samplers and cables during towing, nor do we know what effect reduction of the noise might have on the numbers and kinds of organisms captured.

Accumulators. Compression springs, or accumulators, have been incorporated into the boom and block rigging to take up sudden jars and minimize the effect upon the towing cable of the vessel rolling. Hensen (1895) illustrated an accumulator constructed of a number of heavy rubber bands. Most accumulators today are compression spring assemblies mounted in the topping lift of the towing boom, or spring-loaded sheaves, sometimes mounted on the deck, through which the towing cable passes from winch to towing boom. When lengths of cable are great the surge is partially absorbed through the catenary formed in the cable. A shock absorber in line between the end of the towing cable and the sampler has been used with the Hardy continuous plankton recorder (Hardy, 1936a) and the Gulf III

sampler (Anderson and Gehringer, 1957) to reduce cable strain, vibration during towing, and surges.

Standardization of technique

It is impossible to exaggerate the importance of rigorous care in standardizing sampling technique to reduce variability imposed by the sampling procedure.

For oblique and also horizontal tows taken at any significant depth, without a closing device, the winch speed during pay-out and recovery should be regulated. For all tows ship's speed should be kept as nearly constant as possible. Variations in speed lead to variations in sampling depth. Unless suitable closing devices and depth monitoring equipment are used, data interpretation will be biased indeterminably. Further bias is introduced by avoidance in some species at low velocities and escapement at higher speeds.

It should be appreciated that net speed relative to the water column being sampled is frequently very different from ship speed. Since net speed is a significant factor in avoidance and escapement, it is strongly recommended that a flowmeter be installed outside the net. Ideally, the flowmeter should provide a continuous record of time versus velocity; however, even a simple flowmeter such as a TSK can provide a useful measure of average speed during a tow.

Care should also be taken to wash down the nets carefully after each tow. Improper washing causes contamination of samples with collections from previous tows. There is also danger, especially for the nets with finer gauze, that improper washing will hasten clogging and thus prevent the reasonable comparison of successive hauls.

During any long-term or large-scale programme which will require either the replacement of nets or the use of several nets having the same gauze, it is urged that all of the required material be purchased at the same time from the same supplier. It is common to find significant differences in netting of the same specification number, purchased at different times or places. These differences make comparison of collections difficult. Care should also be taken to examine sampling equipment routinely to ensure that ageing and use have not modified the sampling characteristics (particularly, for example, by altering the shape and size of the meshes).

Care of sampling equipment

Nets. The use of synthetic fibres has increased the life of a plankton net, but synthetic materials are subject to abrasion and some, like nylon, deteriorate in sunlight and should be stored in the dark. Silk nets should be thoroughly washed with a mild detergent and scrubbed with a soft brush and rinsed with fresh water after a cruise, or several times during long cruises. Nets of synthetic fibres should be cleaned according to the recommendations of the manufacturer. See Heron (Chapter 2 above) for a comparison of the resistance of silk and synthetic fibres to abrasion and chemicals.

A dilute solution of commercial or household bleach is effective in cleaning nylon, but it will deteriorate silk. A 5 per cent solution of hydrochloric acid brushed

over monel metal netting removes clogging materials and corrosive deposits effectively, but exposure to the acid should be limited to a few minutes and the net thoroughly rinsed with fresh water. The gauze can then be examined under a hand lens to determine if a second application of acid is necessary.

Care should be taken to prevent nets from coming in contact with sharp or rough surfaces. A new net may be strong enough to stand some abrasion, but it becomes increasingly fragile with use. Gear should be thoroughly inspected before use—a weakened net may split during a sudden surge. Discarding nets of questionable strength should be standard procedure. Metal gauze is more resistant than silk or synthetic fibres, but its rigidity makes it susceptible to puncture.

Cables. Cable fatigue can result in loss of gear. It is considered good practice to discard the terminal few feet of a towing cable periodically to eliminate the portion most likely to be affected by fatigue.

Depressors. The efficiency and stability of depressors depend upon their balance. They should be launched and retrieved carefully to prevent damage which might impair their stability. Improperly balanced depressors are not efficient, and unstable depressors can become deadly projectiles if they surface and break free of the water while being towed at high speeds.

Flowmeters. Flowmeters should be checked for damage between tows. Generally, simple adjustments to tension on bearings can be made at sea, but other adjustments should be made only by trained technicians. Meters should be calibrated after repair or adjustment and all meters should be recalibrated periodically.

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Sample design

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INTRODUCTION

The design of sampling for the estimation of plankton populations is at present not well developed. This is not surprising, since previous chapters of this review reveal logistic and technical problems which tend to overshadow the finer points of statistical theory. Elegant and powerful statistical techniques are available, for example to the agricultural biologist, but their utility becomes diluted progressively as one proceeds through the ecological spectrum from plants and sedentary terrestrial animals to the mobile animals of the open ocean. This contribution attempts to introduce some concepts which may be familiar to the statistician but less so to the planktologist. More detailed discussion of certain of the statistical principles involved and more exhaustive references relating to these topics are to be found in Cassie (1962a and 1963b).

It is assumed in the following that the principal aim of the plankton ecologist is to estimate the abundance of plankton, or at least of specified kinds of plankton in a given body of water. 'Kinds' of organism may be classified by using taxonomic or other criteria, or alternatively direct estimates may be made of biomass, productivity, or similar gross variables. The following review will be directed mainly towards the handling of data classified numerically by species.

DEFINITIONS

Parameter. A numerical quantity defining some variable characteristic of the population being studied. Commonly designated by a Greek symbol; for example, μ might be the mean concentration of organisms (e.g., the mean number per litre) in a given body of water. Note that it is the mean which is the parameter and that 'concentration' itself is not a parameter but a variable. The pattern of some variables may be capable of description by one parameter, but commonly two or more will be necessary, e.g., the mean, μ, and the standard deviation, σ, (or the variance, σ^2).

Statistic. A numerical quantity, obtained by sampling, which approximates to or estimates a parameter. Commonly designated by a Latin symbol; e.g. m may be an estimate of μ.

Population. All existing phenomena of the type being sampled in any specified investigation. 'Phenomena' in the present context will usually be the number of organisms (per unit volume), though it could equally well refer to other measurable quantities such as body lengths or water temperatures. Thus, *population* must be regarded as a statistical term with a special meaning, even though it may on occasion appear to be almost synonymous with the ecologist's concept of a population.

Accuracy. An accurate observation is one with little *bias,* i.e., it does not consistently over- or underestimate the true value of the phenomenon being observed.

Precision. A precise observation is one with little *error,* i.e., it can be compared with another precise observation of the same kind and the difference detected, even though small. Such a comparison will be valid in the presence of bias, provided the bias is the same for both observations.

Error and bias may occur independently of one another, so that it is possible to be precise without being accurate, or (at least in the present technical sense) accurate without being precise. Thus, for example, a precise chemical balance might be biased through use of an incorrect 5 g weight. Nevertheless, the difference between two weighings might be both precise and accurate, provided the same 5 g weight was used for each. A less precise balance with correct weights might still be accurate, even though it failed to discriminate between smaller weight differences. Statistical methods are appropriate only for evaluating precision, though they may often be used in conjunction with other methods for evaluating accuracy. Both error and bias may arise, not only in the original observations, but also in the subsequent statistical processing of data—this is, perhaps, one of the most important reasons for employing a statistician.

PATCHINESS

The term 'patchiness' was first made familiar by Hardy (1936c), though Haeckel (1890) was probably first to introduce the concept that plankton was not 'evenly' distributed. Perhaps planktologists are the only group of ecologists who still express some mild surprise that their biota are not randomly distributed in space—surely no terrestrial ecologist would expect anything else but a patchy distribution. It is sometimes implied that patches of plankton have distinct boundaries outside which exist large vacuous regions containing no plankton at all of the kind in question. Thus sampling would become an 'all or nothing' procedure, depending on whether or not the net happens to encounter a patch. Such situations may exist, how frequently we do not know, but there is no doubt that there is a considerable range in the degree of patchiness, ranging from relatively slight fluctuations of abundance to discrete aggregations, schools or swarms. Neither of these two extremes need do violence to any of the mathematical models presented below. The discrete patch situation is merely an extreme form of variation, requiring greater effort to produce the same precision of estimation, but differing from other situations only in degree. While 'patchiness' will undoubtedly remain in the plankton literature, for statistical purposes it is preferable to substitute the term 'overdispersion', which indicates

simply that the variation in plankton density is greater than would be expected from chance alone, but does not imply any particular form or reason for this variability.

MAGNITUDE OF ERRORS

The error of the estimate provided by a single plankton sample may be estimated by replicating the sample. This immediately raises some problems related to the theory of probability. Plankton is not randomly distributed within any spatial frame which is likely to be sampled in practice (Cassie, 1959b, 1963a) and at the same time it is probably impracticable to take truly random replicates without entering into logistics out of all proportion to the problem to be solved. Thus it is not possible to give any clear definition of what population is being sampled by any two or more replicate samples. With the above reservation, it is possible, by standard statistical methods, to make an estimate of the error of samples which, by ordinary standards, are taken in the same place. The error so determined is not attributable to the net alone, but has a large component due to the natural variability of the plankton. The handling of the net may, of course, contribute considerably to the error, and previous chapters have shown the difficulties involved in controlling the path and speed, particularly of deeper hauls. However, there is no reason to believe that two identical nets, if they were towed along the same course at the same speed, and through the same plankton (if it were possible to replace the same organisms in the identical locations and state of activity) would take anything but identical samples. In practice it would probably be difficult if not impossible to distinguish the performance of two nets assembled reasonably competently to the same design, even though a single-tow comparison may sometimes show a startling difference in catch.

Under good experimental conditions (and this very specifically excludes clogging) it seems likely that nearly all the error, or variation in catch, can be attributed to the plankton themselves. One would hardly expect that a common figure could be given for the variability of all plankton under all conditions, but some useful generalizations can be made. Cassie (1963a), drawing information from various authors, finds that the coefficient of variation of a single plankton sample is most often in the range 22-44 per cent, although much larger coefficients are not uncommon. Winsor and Clarke (1940) have drawn attention to the fact that the error is more appropriately expressed in logarithmic units. Thus, if the coefficient of variation is:

$$V = s/m \qquad (1)$$

where m is the mean and s the standard deviation; the 'logarithmic coefficient of variation' is (using logarithms to the base 10):

$$V' = 10^{s'} - 1 \qquad (2)$$

where s' is the standard deviation calculated from the logarithms of the raw data. Using this definition and assuming that the distribution of the logarithms is Normal,[1] the range quoted above becomes 23-53 per cent. The logarithmic coefficient has

1. The term 'Normal', with capital N, is used throughout as referring to the mathematical distribution, sometimes also known as the Gaussian distribution.

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several advantages. Firstly, coefficients of variation greater than 100 per cent (which are not uncommon) can still be meaningful and do not produce a negative lower fiducial limit. Secondly, V' takes cognizance of the nature of the variability. As Winsor and Clarke originally pointed out, V tends to be independent of the mean, so that larger samples are no less variable than small, and the standard deviation is proportional to the mean. In order to compare the performance of various nets, they transformed their data to logarithms. This had the effect of removing the correlation between standard deviation and mean, thus stabilizing the standard deviation (and the variance, s^2) to a more-or-less constant value, so that valid analysis of variance techniques could be applied to their data. Apart from the logarithmic transformation, their technique of analysis follows the same principles used, for example, in agricultural field-plot trials. It permits multiple-factor experiments to be carried out to differentiate variance components arising from different sources and from the interactions between these sources. The technique is well illustrated by Barnes (1951*b*) who identifies the variance components attributable to different nets (Hardy plankton indicators), different taxa, and different tows. The principles underlying logarithmic and other transformations have been discussed by Barnes (1952). Cassie (1962*a*) has shown that the logarithmic transformation has a Normalizing effect upon plankton sample counts provided the mean count is large (50 or more), and has developed a mathematical model which attributes skewing of the transformed data, when the mean is small, to random (Poisson) effects. In practice this skew may not be serious, so that sample counts considerably less than 50 may be often handled in log transformation without serious loss of precision. The ability simultaneously to Normalize the data and stabilize the variance by transformation is of considerable advantage in developing statistical procedures, owing to the large body of theory available relating to the Normal distribution.

Use of the logarithmic coefficient of variation makes sense intuitively when one considers the biological nature of a variable such as plankton density. The number of organisms in a unit volume of water is a function of the *rates* of various biological processes such as reproduction, mortality, selective immigration or emigration, and an increase in density will be related in time to previous densities, or in space to densities in adjacent regions. It is more meaningful to consider a sample having, say, twice as many, or half as many organisms as another, using a multiplicative error factor rather than an additive error expressed in absolute numbers. This is particularly appropriate for very large errors. For example if $m = 100$, $V = 110$ per cent, and the distribution is assumed to be Normal, two-thirds of all sample counts would be expected to fall within the fiducial limits:

$$100 \pm (1.10 \times 100) = -10, 210.$$

The negative lower limit is of course meaningless and the assumption of Normality is untenable. On the other hand, for the same mean, $V' = 110$ per cent, and the logarithms normally distributed, then two-thirds of all samples will fall within the range:

$$100 \overset{\times}{\div} 2.10 = 48, 210.$$

No matter how large the coefficient, the lower limit will always remain positive.

While logarithmic transformation is appropriate for making comparisons, it should be noted that the means obtained from log-transformed data are, after taking antilogarithms, geometric means which will be smaller than the corresponding arithmetic means. Where an absolute estimate of abundance is required, the arithmetic mean is the appropriate statistic, though approximate fiducial limits may still be set using V'. Bagenal (1955) has given a critical account of the inter-relationship between means, coefficients of variation, and fiducial limits using transformed and log-transformed data. Silliman (1946) has applied the concept of logarithmic coefficients of variation in his study of variability in net catches of pilchard eggs, and reaches the conclusion that 'the egg number from one haul may not be considered significantly different from the egg number in another unless it is less than half, or more than double, than that of the other'. It should be noted that fish eggs and larvae are among the more variable in their spatial distribution, probably because they are relatively short-lived members of the plankton, and are initially released in a highly over-dispersed pattern. Thus Silliman's significance criteria can probably be relaxed, at least for some members of the permanent plankton.

If the major part of the variability of a net sample is attributable (at least under optimal working conditions) to the plankton rather than to the net, and if the coefficient of variation is independent of the size of the catch, it might be predicted that nets of different design will give the same coefficient of variation when sampling the same plankton population. This prediction is difficult to test exhaustively, though it seems to be valid at least where the different nets can be handled in a comparable manner. Winsor and Clarke (1940) found that nets of different sizes gave similar coefficients, and concluded that the smaller net was just as affective a sampler as the large. The small and widely-used Clarke-Bumpus sampler is obviously designed with this conclusion in mind. Where different nets are found in practice to give different coefficients of variation, it is often possible to attribute this to specific causes. Barnes and Tranter (1965) found that the Indian Ocean Standard net and the Clarke-Bumpus sampler perform similarly with respect to both catch and variability ($V' = 42\text{-}51$ per cent, which is within the range quoted above), but that the Tropical Juday net has considerably greater variability ($V' = 73\text{-}135$ per cent). They point out that this is probably attributable to the finer gauze of the TJN which induces clogging, as well as to difficulties in washing down the catch. Thus the variance attributable to the overdispersion of the clogging organisms will be added to that of the larger species being estimated.

It may sometimes be found that two nets, though having comparable coefficients for one kind of organism, may have grossly different coefficients for another. No general explanation can be given for this, but it seems likely that many such anomalies are merely another artefact caused by clogging. Each kind of organism will probably have a different threshold at which it begins to take advantage of the water flow pattern to escape or avoid the net. Those organisms which are near this threshold will be more greatly influenced by minor changes in the flow pattern and will hence be more variable.

Errors which commonly reach 50 per cent and may be greater than 100 per

cent are clearly a handicap to accurate estimation. Statistically the most obvious remedy is to increase the number of samples, using the relationship:

$$s_m = s/\sqrt{n}$$

where s_m is the standard error (standard deviation of the mean), and n is the number of samples. This, of course, is exactly what the planktologist wishes to avoid. The labour of collecting samples may, perhaps, be appreciably reduced by technological advances, but as yet there seems to be little prospect of reducing the greatest labour of all, the counting of the plankton sample (reserving judgement for the time being on *in situ* counting techniques such as that of Maddux and Kanwisher, 1965). Thus there is a need for a less costly means of reducing variance.

Where the objective is the comparison of the performances of different nets, the most useful expedient seems to be the towing of nets simultaneously on the same wire and as close together as possible, provided, of course, that the two nets are designed to operate at the same speed. This will not eliminate all variability attributable to the plankton, since it has been shown by Cassie (1959b, 1962b) that non-random variations of plankton abundance occur over distances as small as 5 cm, but there is little doubt that it will result in an appreciable reduction of error and hence of the number of replications necessary for any desired comparison. In a two-net comparison, it would be necessary to employ 2 + 2 nets, two of each kind, in order to estimate the 'within nets' variance, against which the 'between nets' variance is evaluated. If the nets were arranged symmetrically with their centres at the corners of a square or diamond, there is no reason to suspect that any one net should have its catching power changed with respect to any other, at least in a vertical haul. In an oblique or horizontal haul, the situation might be different, since avoidance paths might be vertically oriented. A case of catch differential between upper and lower nets is noted by Winsor and Clarke (1940). Net comparisons on a 1 + 1 basis have been made (e.g., Motoda et al., 1957), but there seems to be no record in the literature of a 2 + 2 trial. A different approach to the same problem was made by Fleminger and Clutter (1965) who endeavoured to avoid effects of patchiness by towing nets along a guided diagonal path in a large sea-water pool. It would be possible to compare three or more nets, suitably arranged, by simultaneous towing. This would result in a further labour-saving on the statistical side, but the gain might be offset by increased technical difficulties.

STATISTICAL DISTRIBUTION OF ERROR

If a series of sets of samples is taken of the same plankton population, each set will probably have a different mean and a different variance. However, the mean and variance do not vary independently of each other. Their relationship can usually be accounted for by the equation:

$$\sigma^2 = \mu + c\mu^2 \tag{3}$$

where μ and σ^2 are the population mean and variance respectively and c is a constant.[1] The mean, μ, may vary either in response to variations in plankton density or as a result of different sizes of net, length of tow, or other variations in technique which change the volume of water filtered. Equation (3) seems to apply regardless of the source of changing mean, provided there is some degree of homogeneity in the population represented by the different set variances.

If the plankton had been randomly distributed, the variance-mean relationship would have been that of the Poisson distribution:

$$\sigma^2 = \mu. \tag{4}$$

Thus overdispersion has added a new component, $c\mu^2$, to the variance. The condition, $s^2 > m$ (substituting the statistics for the parameters) is commonly employed as the statistical criterion for overdispersion (or patchiness). In samples with a very small mean (particularly when $\mu < 1$), μ will be the dominant component unless c is unusually large, so that there is no reason for surprise when a species which is rare in relation to the sample size shows no departure from a random distribution. Randomness in this case implies simply that no determinate distribution can be described, probably because there is insufficient information to do so. As the mean increases, the term $c\mu^2$ becomes predominant, so that:

$$\sigma^2 \sim c\mu^2 \tag{5}$$

or:

$$\sigma/\mu \sim \sqrt{c} \tag{6}$$

so that $\sqrt{c}$ is equivalent to V in (1). In fact, we have merely arrived at a more precise expression of the properties of the coefficient of variation discussed in the last section, and extended those to account for small sample properties. The relationship (3) is by no means unique to plankton, but is common for many natural phenomena, in particular for the distribution of animals and plants in almost any habitat. For plankton, the value of c is commonly in the range 0.05-0.1 (Cassie, 1963a), and it is from these figures that the V and V^l ranges quoted above have been derived. As with V and V^l, higher values of c are not uncommon.

Unfortunately, (3) does not lead to any unique mathematical model for distribution of plankton, and still less does it reveal any causal factor underlying the distribution. Frequency distribution models which have been fitted to plankton data include the negative binomial and Poisson-log-normal (Cassie, 1962a), and the 'Double Poisson' distributions of Neyman and Thomas respectively (Barnes and Marshall, 1951). Barnes (1952) has discussed the implications of the negative binomial and the log-normal distribution on transformations for the analysis of variance. On the whole there is little to choose between the various models. For practical purposes the log-normal does as well as any, at least when the mean is large, and as the mean increases, becomes indistinguishable from the Poisson-log-normal. The appropriate transformation is $\log (X)$, or, for smaller means, $\log (X + K)$ where X is the sample count, and K is a constant, usually 1. The

1. Cf. Barnes, 1952, who uses $1/k$ in the same sense as c is used here.

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constant, K, serves two purposes, firstly to accommodate zero counts, which have no finite logarithm, and secondly to provide a better approximation to normality, since the Poisson component of variance tends to skew the otherwise normal distribution to the log counts.

SAMPLE DESIGN TO ESTIMATE AND MINIMIZE ERROR

Considering the immensity of the ocean and the relatively large and unavoidable error 'built into' natural plankton populations, sampling theory merits a high priority. To study error, one must of course be able first to estimate its magnitude. We are moderately well informed as to the error of a single sample, but have less knowledge of what that sample represents in terms of plankton population. There is a further component of variation, the 'between samples' error to be estimated. Classical statistical theory requires that sampling should be random in order to estimate error. Note that this is the *only* purpose of randomization—there is no increase in precision—indeed in a natural plankton population simple random sampling will almost always reduce precision as compared with a non-random system such as a systematic grid survey. To obtain a compromise between the error-estimating properties of random sampling and the precision of systematic sampling, the usual solution is Stratified random sampling. The region to be sampled is divided into smaller regions or *Strata,* in each of which two or more random samples are taken.[1] To increase precision it is necessary that the error within individual Strata should be less than the over-all error for the region. For most effective Stratification, it is necessary to have some prior knowledge of the region and of the biota being sampled, though, in a pilot survey, an arbitrary choice of Strata is usually better than none at all. In the ocean, we would certainly make use of hydrological data, so that different water masses fell into different Strata. Other divisions would be made perpendicular to well-established gradients associated with latitude, distance from shore and depth. If some Strata have greater variability than others, these should be sampled more intensively. Laevastu (1962) has discussed in detail the principles of Stratification as applied to plankton sampling.

To represent the population at any one instant, it becomes necessary for all samples to be taken at the same instant, or at least sufficiently nearly so that rates of change are negligible. This raises extraordinary difficulties when applied to some of the plankton. For example, eggs of certain tropical and temperate fish have a life measured in hours; some unicellular organisms may double their numbers by binary fission several times a day; while grazing and predation are probably capable, at least in some situations, of producing comparable rates of change. Diurnal variations in vertical distribution (and possibly also in avoidance behaviour) make time differences of even a few hours a substantial source of error. Variations with time may, perhaps, be self-cancelling, but they will nevertheless exist and

1. *Stratified* and *Strata* are used with capital S to distinguish them as statistical terms. Horizontally oriented strata of plankton in the topographical sense might serve as a basis for Stratified sampling, but otherwise the similarity of terminology is a coincidence which cannot conveniently be avoided.

constitute another source of error. It might, perhaps, be feasible for two research ships to take two random samples simultaneously within a single Stratum, but the ship requirements for simultaneous and repeated sampling of quite a modest number of Strata would be enormous. Even assuming the logistic difficulties can be overcome, there remains a considerable technical difficulty in placing research ships on strictly random (not merely haphazard) positions.

Thus it would seem that random sampling of plankton, regardless of its theoretical advantages, is not entirely practicable. It will probably continue to be expedient to sample in systematic grid patterns. Unfortunately, little is known of the theory of error estimation in systematic sampling. Methods which are available (e.g., Cochrane, 1953) depend rather heavily upon a knowledge of the structure of the population, and new methods appropriate to plankton will probably require to be developed, a process which will require the closest collaboration between planktologist and mathematician.

While the estimation of error remains elusive, established methods exist by which the magnitude of this error may be reduced without necessarily increasing the sampling effort. Of the many available techniques and variations, the three which appear to be potentially most applicable to plankton are as follows: (a) selection of the most appropriate sample size; (b) optimum allocation of number of samples per Stratum; (c) regression sampling.

While the theory of these methods is to some extent dependent upon the assumption that samples are taken at random, aspects of error reduction, as opposed to error estimation, will in most cases be applicable to non-random sampling.

Size of sample

The variance-mean relationship (3) leads to an important conclusion which is not necessarily evident intuitively. The mean may be varied at will by variations in technique producing volumetrically larger or smaller samples. For small samples, the Poisson variance component (4) will predominate, so that, substituting the equivalent statistics for the parameters and taking square roots:

$$s = \sqrt{m}$$

and

$$V = 1/\sqrt{m}.$$

Thus, initially, increasing the sample size will decrease the coefficient of variation and increase precision. However, this situation will not continue indefinitely. Taking a range of c values from 0.05 which is about the best which can be expected in practice, to 1.0 which is by no means the worst, tables of V (per cent) may be derived from (3) and (1) (see Table 1).

Clearly there is very little gain at any time in increasing the mean above 100, and for more variable species a mean of 10 is almost as good as one of 1,000 or more.

This phenomenon, which was probably first presented in the marine biological literature by Taylor (1953) in connexion with demersal trawl sampling, has caused

TABLE 1. Values of V (per cent)

m	c		
	0.05	0.2	1.0
0.1	317	319	332
1.0	102	110	141
10	39	55	105
100	24.5	45.8	100.5
1 000	22.5	44.8	100.0
∞	22.3	44.7	100.0

some controversy and is probably still suspect by many. Basically it implies that the larger sample, after a certain minimum level has been reached, does not increase precision. Assuming that the larger sample will cost more in time and effort, the smaller sample is thus preferable. There are a number of requirements of the planktologist which run contrary to this. Large nets are desirable to minimize bias due to avoidance, and, judging from the theoretical treatment by Barkley (1964), the optimum size of net is probably near the upper size range of nets at present in use. Such a net would undoubtedly catch far more of the common species than is necessary for precision. Many also demand a larger net in order that the less abundant species should be adequately represented (e.g., Clutter and Anraku, Chapter 4 above). In the laboratory, the more abundant species may be counted in an aliquot, while the less abundant are often of larger size and may be easily counted in the main sample even without the aid of a microscope. Thus the extra labour of enumeration may not be great.

Unfortunately, there are at present no generalizations available which enable us to reach a compromise between sampling only the common species and sampling *every* species, a result which could only be reached with certainty by filtering the entire ocean. Empirical models such as that of Fisher *et al.* (1943) and Preston (1962) permit the number of species to be related to the number and size of samples. Such a model, if effective, might permit extrapolation to give an estimate of the number of species in the universe (i.e., the ocean in the present instance). Models of this type have not yet been effectively applied to plankton populations. However, it should be noted that, provided the total volume of water filtered by all samples combined is the same, the probability of taking a rare species will be at least as great with small samples as with large.

Longer tows are another means of increasing the sample size, but possibly a more basic concept behind the long tow is the desire to integrate and thus represent a wider range of habitat. There is also an intuitive feeling that a longer tow has a better chance of encountering a patch of plankton, and that the greater part of the plankton population may be located in patches. Since many planktologists express their results in terms of surface area (e.g., plankton under one square metre) there is a particular need for vertical integration by oblique or vertical hauls. Because of vertical migration, horizontal variations in distribution are not comparable unless they are taken at the same time of day, or are integrated from surface to bottom, or at least to the limit of vertical migration. Further, there is some evidence that

vertical distribution is often characterized by dense, horizontally aligned, strata of limited depth range. This has been familiar for some time in the deep scattering layer, but is probably more common than routine echo-sounder records would indicate. Schröder (1962), working in fresh water, has noted many such strata (or *planktonhorizontes*), some of less than a metre in vertical range, while Strickland (personal communication) has found similar phenomena in the ocean. The most obvious remedy for this form of patchiness is the vertical haul which must inevitably intersect every stratum within its range. On the other hand, Banse (1964) has made a plea for the abandonment of vertical integrated hauls in favour of short horizontal tows at specific depths. While some of his arguments may not be applicable in the present context, he makes the important point that most physical data are taken (or at least recorded) at discrete depths and thus would be difficult to correlate with an integrated plankton count. If the main requirement is simply a map of the horizontal distribution of plankton integrated for depth, this may not seem a serious handicap. However, we shall see below that knowledge of the relationship between plankton and physical environment, even if not required for its own sake, may be of considerable significance in reducing sampling error.

The question of the small versus the large integrated sample cannot be solved by theory alone, and for the present, there seems to be insufficient data available to resolve this problem entirely. There is a need for a great deal of detailed small-sample investigation of both horizontal and vertical distribution before this can be done. Compromise will have to be made between the many conflicting requirements outlined above.

Number of samples per Stratum

We have already noted the benefit of Stratification in increasing the precision of random sampling. In non-random sampling some of the same principles apply. There will usually be some benefit in dividing the sampling area or volume into smaller, more homogeneous units. Even so, it will usually be found that some Strata have more variability than others. To obtain maximum precision for a given amount of effort, samples should be allocated to Strata so that:

$$n_i = (N_i \sigma_i / \sqrt{C_i}) \times \text{a constant}$$

or:

$$n_i \propto N_i \sigma_i / \sqrt{C_i} \tag{7}$$

where n is the number of samples, N is the total number of samples possible, σ is the standard deviation of sample counts (estimated by s), and C is the cost of taking a sample. The subscript, i, is the serial number of the Stratum, and implies that any term to which it is appended is a variable which may have a different value for each Stratum. We may, for example, refer to the cost, C_i, of a sample in the ith Stratum, or more specifically to, say, the cost, C_4, of sampling the fourth Stratum. For plankton application, N is the area or volume of the Stratum, divided by the area or volume of a sample. In the ocean, the cost factor will be mainly a function of weather, time and distance, and all but the most dedicated of seafarers will probably apply this correction automatically, at least in a crude fashion. We have seen from (6)

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that the standard deviation, σ, tends to be proportional to the mean, μ. Substituting m, the estimated mean, in (7):

$$n_i \propto N_i m_i / \sqrt{C_i}. \qquad (8)$$

This implies that the number of samples in a given Stratum should be proportional to the concentration of plankton, a conclusion which makes sense intuitively, and may be some help in elucidating the 'Size of sample' theorem (above). In practice, the concentration is not usually known until it is estimated by taking a sample, though there are some occasions when hydrological or other information indicates that certain regions will have particularly dense or sparse plankton populations. It would also be feasible in some instances to establish a certain minimum intensity of sampling, to be increased in selected Strata on the basis of the plankton concentration in the initial sample. Even a crude volumetric estimate using, say, a three-level scale would give appreciable gain in precision, although obviously some discretion would be necessary, as when the change in volume is attributable to a change in taxonomic composition, say, from copepods to salps or coelenterates. In some techniques, such as the Hardy plankton recorder, it may be relatively easy to take more samples than are actually enumerated. The application of (8) is then very much simpler since the initial analysis may be made on the basis of widely spaced samples, and this information used as pilot data to select regions of more intense sampling.

Up to this point, it has been assumed that the component of cost represented by laboratory enumeration is either negligible or the same for all samples. This is not necessarily true. If, for example, the counting time is proportional to the mean ($C_i \propto \mu_i$), the appropriate number of samples per Stratum is obtained by substituting m_i for C^i in (8):

$$n_i \propto N_i / \sqrt{m_i}. \qquad (9)$$

This is the reverse of the situation in (8), the lower cost of counting less concentrated samples outweighing the greater amount of information given by the more concentrated. In practice, the situation will probably be nearer (8), since concentrated, dense samples can usually be subsampled, thus reducing the labour of counting. In the case of biomass-type measures, of course, the cost will be much the same for all samples. The relative weightings to be placed on field and laboratory costs will depend greatly upon the techniques and upon the relative value placed upon field and laboratory time, but some increase in precision can usually be gained by application of the principles above.

Regression sampling

This technique is well known in a number of fields of statistical application, but seems only rarely to have been applied in any branch of ecology. While certain variables studied in the field are laborious to estimate directly, these may nevertheless be correlated with other variables which are more easily estimated (or may even be already known). For example, the horizontal distribution of plankton concentration might be correlated with the temperature of the water. If, to take the

simplest case, the correlation was positive and linear, the relationship could be expressed by the equation:

$$Y_j = \alpha + \beta X_j + \varepsilon_j \tag{10}$$

where Y is the plankton concentration, X the temperature, α and β are regression parameters (estimated in practice by a and b), and ε is an error term, and j refers to the jth sample. Once this relationship is established, it will be fairly obvious that a greater density of plankton is to be expected in water parcels of higher temperature, provided these are within the population of water parcels represented by the equation. By means of (10) an estimate of plankton concentration in the jth sample can be made from temperature alone. The precision will not be as great as from a direct sample count because of the new error term, ε, but, on the other hand, temperature is so much more easily measured that a great many more sample estimates can be made at the same cost as one plankton count, and the *mean* of a number of regression estimates may be more precise than the mean of a smaller number of direct estimates.

The regression estimate, $\bar{y}'$, of the mean plankton concentration is made from the equation:

$$\bar{y}' = \bar{y} + b(\bar{x}' - \bar{x}) \tag{11}$$

where $\bar{x}'$ is the mean temperature from all temperature samples, x is the mean temperature from a smaller number of temperature samples which coincide with plankton samples, for which the mean is $\bar{y}$. Provided both the smaller and the larger set of samples are representative of the same population, the mean, $\bar{x}'$, being derived from a larger number of samples, will be more precise than $\bar{x}$. If X and Y are correlated, $\bar{y}'$ will also be more precise than $\bar{y}$. For random sampling, assuming the errors of x' and b to be relatively small, the standard error of $\bar{y}'$ is:

$$s_{\bar{y}'} = \sqrt{(1 - r^2)} s_{\bar{y}} \tag{12}$$

where $s_{\bar{y}}$ is the standard error of $\bar{y}$ and r is the coefficient of correlation between X and Y. The gain in precision is related to the magnitude of the correlation. If, for example, $r = 0.95$, $s_{\bar{y}'}$ is about $1/3 s_{\bar{y}}$, and by simple random sampling this precision would be achieved only by taking ten times as many plankton samples. The following table gives the relationship between r and the number of samples, n_r, required for equal precision by random sampling.

r	n_r	r	n_r
0.99	50	0.70	2.0
0.90	5.3	0.50	1.3
0.80	2.8		

The gain is slight if r is less than about 0.7 and only becomes spectacular when r exceeds 0.9.

In practice, it is often found that plankton concentration is correlated to physical properties of the water which are easily (and often routinely) measured.

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The reason for the correlation may be obscure, so that no useful causal interpretation can be made, but this is unimportant for regression estimation. All that is necessary is that a correlation should exist and that it should preferably be 0.7 or higher. The simple linear model of (10) is, in fact, seldom appropriate, and is better replaced by the exponential form:

$$Y_j = Ae^{bX_j} + \varepsilon_j \tag{13}$$

or in log transformation:

$$\ln Y_j = a + bX_j + \varepsilon_j \quad (a = \ln A). \tag{14}$$

The correlation need not be based upon a simple linear model; indeed, it is probable that a number of regression techniques may need to be brought into this application, including multiple, curvilinear, and periodic regression. Apparently the only use of a regression estimate in the plankton literature is that of King and Hida (1954), who employed the relationship:

$$\log Y_t = a + b \cos t + \varepsilon_t \tag{15}$$

where t is the time of day expressed in angular measure ($360^\circ = 24$ hours). It was found that diurnal fluctuations in plankton density in the upper 200 metres were approximately sinusoidal with a maximum at midnight ($t = 0$), and thus fitted the above equation with a correlation of up to 0.8. It was thus possible to adjust the plankton densities taken at different times of day to the expected (and maximal) value, $\hat{Y}_o$, at midnight:

$$\hat{Y}_o = Y_t \exp(-b \cos t). \tag{16}$$

The application of this estimate is not identical with that given in (11), but the principles are the same in that a correlated variable (time of day) is used to increase the precision of an estimate.

A multiple regression model has been used by Cassie (1960) (though for a different purpose):

$$Y_j = a \exp(b_T T + b_S S) + \varepsilon_j \tag{17}$$

where T, S are temperature and salinity respectively, and b_T, b_S the partial regression coefficients on temperature and salinity. This has produced multiple correlations greater than 0.9 some occasions. As with previous models, this would normally be handled by linear regression methods, with plankton density transformed to logarithms.

It would be premature to predict whether high correlations with commonly and easily measured variables such as temperature, salinity, dissolved oxygen, light, etc., will be found sufficiently frequently to make regression estimates profitable. The most promising situations will probably be those where these variables have a considerable range of values, e.g., coastal and estuarine regions, regions of hydro-

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logical discontinuity, or where the survey covers a range of latitude, or a wide vertical range. More powerful models may perhaps be developed by incorporating non-linear regression techniques (in addition to the log transformation which is almost universal). For example, the equation:

$$Y_j = A \exp(b_1 X_j - b_2 X_j^2) \tag{18}$$

describes the Normal curve, which seems a reasonable model for the distribution of organisms through a range of values of the environmental factor X which extends both above and below the optimum for the organism. Transforming to logarithms:

$$\ln Y_j = a + b_1 X_j - b_2 X_j^2 \tag{19}$$

which is a simple quadratic. More complex models, such as higher order polynomials may also be used, though here the application is rather more empirical, since the curve will not usually remain a realistic model when extrapolated beyond the range of the data. Some experimentation with the data may be necessary to find the most appropriate model, but the ultimate results may be spectacular. For example, Cassie (in preparation) has derived a canonical expression for 100 plankton samples taken in an estuary in which an exponential function of 11 species of plankton has a correlation of 0.97 with a quadratic function in temperature and salinity. Relationships of this type may seem formidable on first acquaintance, but are relatively easily handled by computer. The above-mentioned function was derived in about ten minutes on an IBM 1620, which is a relatively slow machine by modern standards.

Possibly one of the most promising fields for the application of regression estimates is in the vertical pattern of distribution. Schröder (1962) finds that *planktonhorizontes* in lakes frequently coincide with discontinuities in the vertical profile of temperature. The reason for this relationship is not entirely understood, but it seems likely that, while the gross pattern of vertical migration is controlled by light, the response to light stimulus may be modified or even reversed by changes in temperature. There would be a tendency for vertical migrants to be retarded at temperature discontinuities, thus forming horizontal layers. Such a situation would probably be amenable to mathematical model treatment in which plankton density is expressed as a function of light (or perhaps simply time of day), temperature, and possibly other physical variables if they are found to be significant. A sampling programme utilizing data of this type would require a relatively small number of detailed vertical plankton profiles accompanied by a much larger number of profiles of physical water properties. Various instruments are currently available or in development which may permit the above type of application. Longhurst *et al.* (1966) have developed a modification of the Hardy plankton recorder which will take 50 plankton samples at intervals down to 680 m, and record temperature and depth. Glover (personal communication) is currently developing a continuously undulating version of the Hardy recorder which ranges from 10 to 100 m and records depth, salinity, filtration rate, light intensity, turbidity and chlorophyll

concentration. Cassie (1964) is developing a pump-type sampler to take a continuous series of samples at vertical intervals, which are limited only by the facilities for lowering and raising, and to record depth, temperature, salinity and (tentatively) other variables such as light and dissolved oxygen. A rather more direct approach is the 'in situ particle counter' of Maddux and Kanwisher (1965). While such a device may never replace direct plankton identification and enumeration, there is little doubt that it will measure a variable or variables which have a direct and causal correlation with plankton abundance, and could be used to increase the precision of direct estimates. Longhurst (personal communication) is planning to incorporate this instrument in his sampler.

STATISTICS AND AVOIDANCE

Avoidance in itself is not a statistical problem, since it involves accuracy rather than precision. However, any given mathematical model for avoidance may be tested against appropriate data by statistical methods. Thus, if a series of nets of standard design but different sizes are towed under standardized conditions, the catches would be a function of net diameter and diameter of the peripheral escape zone, and might be expressed by the equation:

$$N_k = c(R_k - \Delta_k)^2 \tag{20}$$

where N_k = catch of the kth net; R_k = radius of the kth net; Δ_k = peripheral escape radius of the kth net; c = a constant incorporating length of tow and density of plankton. The simplest possible assumption is that Δ is constant between all nets. Taking square roots:

$$\sqrt{N_k} = \sqrt{c}(R_k - \Delta); \tag{21}$$

Two simultaneous equations, and hence two sizes of net, are necessary to solve for c and Δ. The independent variable, R, can be measured to any required degree of accuracy, but the dependent variable, N, is subject to the usual errors of sampling, so that in statistical terms we have a regression equation:

$$\sqrt{N_k} = \sqrt{c}(R_k - \Delta) + \varepsilon_k. \tag{22}$$

The standard error of ε may be estimated by suitable replication, using two sizes of net, but to test the reality of the model (e.g., its linearity, or the constancy of Δ) three or more net sizes would be necessary.

At present, the nearest approach to suitable data for the solution of the equation is that of Fleminger and Clutter (1965). Unfortunately, the data published contains too much error (in the technical sense) to yield a useful solution. A further analysis of the raw data of Fleminger and Clutter might shed some light on the problem, but it is likely that unusually generous replication, or (preferably) refinements in sample design will be necessary before a final solution can be reached.

FURTHER PROCESSING OF DATA

The ultimate analysis and interpretation of plankton data are outside the scope of this review. However, satisfactory sample design can never be achieved if the objective of sampling is not kept clearly in mind. A few of the new mathematical developments in interpretation deserve mention, not only for their bearing on sample design, but also as an indication of what can be achieved by computer data-handling methods. The 'biomass-type' plankton estimate, though simplifying the appearance of the initial data, does not lend itself well to the development of statistical theory, since so many different sources of error are lumped together. Detailed enumeration of plankton by taxa is, of course, time-consuming, and leads to ponderous tables of data which are not readily comprehensible. The first of these two difficulties is not at present completely soluble, though it may perhaps be minimized by application of some of the principles discussed above under 'Sample design to estimate and minimize error'. On the other hand, the objective reduction of large data tables is rapidly coming within our grasp. Recent computer-oriented contributions to plankton data handling include Williamson (1961), Cassie (1963b), Fager and McGowan (1963), and Colebrook (1964).

Terminology

Plankton catch (x): the quantity of plankton of a particular kind taken by a plankton net.

Volume filtered (w): the volume of water filtered by a plankton net in collecting plankton from a natural body of water.

The catch per unit volume filtered (X) is given by the equation

$$X = \frac{x}{w}.$$

Plankton sample: a collection of plankton that is believed to be representative of the natural body of water from which it is taken.

Plankton samples are usually biased because some plankters avoid the net (*avoidance*) and others are lost through the meshes (*escapement*). An estimate ($\hat{y}$) of the number of plankters of a particular kind in an unbiased sample is given by the equation

$$\hat{y} = \frac{x}{C \cdot S}$$

where S is the *mesh selectivity* of the net, and C is the *catching efficiency* of the sampler of which the net is a part.

Plankton concentration (Y): the quantity of plankton of a particular kind per unit volume of a natural body of water. An estimate ($\hat{Y}$) of the plankton concentration is given by the equation:

$$\hat{Y} = \frac{\hat{y}}{w},$$

the accuracy of the estimate depending not only on the sampling bias, but also on the plankton distribution within the water body.

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Filtration efficiency (*F*): the ratio of the volume of water filtered by a plankton sampler to the volume swept by the sampler mouth. That is,

$$F = \frac{w}{A \cdot D} \tag{a}$$

where *A* is the mouth area of the sampler and *D* is the distance towed. The relation may also be expressed as:

$$F = \frac{A' \cdot D}{A \cdot D} = \frac{A'}{A} \tag{b}$$

where *A'* is the *effective mouth area,* or as:

$$F = \frac{A \cdot V'}{A \cdot V} = \frac{V'}{V} \tag{c}$$

where *V* is the towing velocity, and *V'* is the mean velocity of the flow through the sampler mouth.

Mesh: one of the open spaces (pores) in a net, enclosed by the strands of a meshwork which may be termed the *gauze.*

Porosity (*β*): the open area fraction of the gauze comprising the filtering surface; *β* may be calculated from the equation:

$$\beta = \frac{m^2}{(d + m)^2}$$

where *m* is the *mesh width* and *d* is the diameter of the strands in the meshwork.

Open area ratio (*R*): the ratio of the open area of a net to the area of its mouth; *R* is given by the equation:

$$R = \frac{a \cdot \beta}{A}$$

where *a* is the porous area of the net.

Clogging: the process by which the porosity and filtering area ratio of a net are progressively reduced by particles which adhere to the strands of gauze during filtration.

Mesh velocity (*v'*): the mean velocity at which the water discharges through the meshes of a plankton net; *v'* may be calculated from the equation:

$$v = \frac{A \cdot F \cdot V}{a \cdot \beta} = \frac{V'}{R}$$

Approach velocity (*v*): the effective velocity at which the water approaches the immediate environs of the filtering surface before its acceleration through the meshes; *v* is given by the equation:

$$v = v' \cdot \beta.$$

Filtration pressure (ΔP): the pressure of the water flowing through a plankton net upon its filtering surface; *P* may be calculated from the equation:

$$\Delta P = K \cdot \tfrac{1}{2} \varrho v^2$$

where *K* is the *resistance coefficient* (pressure drop coefficient) of the gauze.

Drag (*D*) is the total resistance to the free passage of the sampler through the water; *D* is given by the equation:

$$D = C_D \cdot \tfrac{1}{2} \varrho V^2 \cdot A$$

where C_D is the *drag coefficient* of the sampler.

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Part II

Standardization of zooplankton sampling methods at sea

Introduction

Plankton has been sampled by such a variety of methods that direct comparison of results has been impossible to achieve. Various international and national bodies have expressed keen desire to consider the possibilities of standardization of zooplankton methods where it was reasonably practical to do so.

A joint working group (WG-13) was therefore set up by SCOR, Unesco and ICES to deal with this problem and at their first meeting in Paris 1964 a general plan was prepared.

Present were the convener, J. H. Fraser (ICES), Dr. G. Humphrey (then president of SCOR), Dr. T. Parsons (Unesco) and Professor J. Krey (then chairman of the Plankton Committee of ICES). As plankton covers such a great range of organisms, in size, shape, consistency and behaviour, no single standardized collecting method is possible and arbitrary divisions become necessary. Of these size was chosen as the most practicable and innocuous and the following *terms of reference* were agreed:

To set up small working parties from experts in their particular fields of work, who will examine and consider the methods used at sea and in the laboratory in sampling zooplankton of various categories, and to make recommendations concerning the methods they consider the most satisfactory for general adoption. Where they consider present methods inadequate new methods should be recommended, based if necessary on new hydrodynamic or other research. Where it is possible to do so the working parties should compile a series of intercalibration factors between the methods most frequently in current use, and should consider the inclusion of factors for past methods especially where much data have been published.

There should be four such working parties in zooplankton to deal with:

1. The microzooplankton, at present sampled by water-bottle, very fine-meshed nets and pump filters.
2. The zooplankton now sampled by a great range of techniques, but largely dependent on filtration through a No. 3 mesh (about 60 meshes per inch).
3. The larger zooplankton, often sampled by stramin or other coarse-meshed nets.
4. The fast-moving macroplankton, such as the larger euphausiids and small fish.

It is important to emphasize that while standardization of plankton methods would assist greatly in the comparisons of one area with another, and would help in the selection of gear by those needing such help, standardization should in no way be interpreted as a bar to progress towards further improvements of methods, nor as a discouragement in the use of other more specialized gear for purposes where this is considered desirable.

Although the working parties could be expected to do much of their work by correspondence, the finances incurred by necessary meetings would be shared on an equal basis by ICES, SCOR and Unesco.

It was agreed that there should be five members to working parties 1, 3 and 4 but seven for WP-2 which has more complex problems. All the countries represented in SCOR were asked to nominate suitable personnel for consideration by the convening committee and these lists were very helpful in selecting the working party members. Not all these first selected were able to give their services and those finally selected were:

Working Party 1. R. Currie (convener), Marine Laboratory, Millport, United Kingdom; J. Krey, University, Kiel, Federal Republic of Germany; K. Banse, University of Washington, Seattle, U.S.A.; V. Hansen, Charlottenlund Slot, Denmark; I. McLaren, McGill University, Montreal, Canada.

Working Party 2. A. W. H. Bé (convener), Lamont Geological Observatory, Palisades, N.Y., U.S.A.; N. Della Croce, University of Genoa, Italy; A. Boudillon, Station Marine d'Endoume, Marseille, France; A. de Decker, Division of Sea Fisheries, Cape Town, South Africa; B. Kimor, Sea Fisheries Research Station, Haifa, Israel; E. Hagmeier, Helgoland, Federal Republic of Germany; B. Bogorov, Institute of Oceanology, Moscow, U.S.S.R.

Working Party 3. D. Tranter (convener), CSIRO, Cronulla, Australia; M. Vannucci, Instituto Oceanografico, São Paulo, Brazil; J. Gehringer, Bureau Commercial Fisheries, Brunswick, Georgia, U.S.A.; M. Vinogradov, Institute of Oceanology, Moscow, U.S.S.R.; M. Anraku, Seikai Fisheries Laboratory, Nagasaki, Japan.

Working Party 4. P. Foxton (convener), National Institute of Oceanography, Wormley, United Kingdom; W. Aron, General Motors, Santa Barbara, California, U.S.A.; M. Legand, ORSTOM, Noumea, New Caledonia; T. Nemoto, Whales Research Institute, Tokyo, Japan.

SYMPOSIUM ON THE HYDRODYNAMICS OF ZOOPLANKTON SAMPLING

The suggestion to hold this symposium was first proposed by David Tranter as a valuable way to provide the background knowledge necessary to the proper functioning of WP-3. It was logical to recommend that it be held at Sydney, where the right facilities were readily and freely available at the University of Sydney through the courtesy and co-operation of the Department of Aeronautical and Mechanical Engineering, and where all the prior organization could be done on the spot without additional expenditure.

The idea was strongly supported by WP-2 and by ICES, and thanks to help from SCOR and Unesco it was possible to hold the symposium at Sydney in February 1966. There were 27 participants plus 7 observers from Australia, and 38 contributions were given.

The symposium started with two days' practical testing at the University of Sydney. Here experimental work was carried out:

1. Using model nets in wind-tunnels with visible smoke trails. Models of various meshes and length of cone were tested without and with clear perspex cases to represent encased nets such as the Gulf III; nets were held at different angles using various degrees of artificial clogging.

2. Testing the prototype WP-2 net in a larger wind-tunnel. A hot-wire anemometer was used to give a full picture of the flow and turbulence over the whole diameter of the net at various distances in front of it. Tests with bridles were made to ascertain the best position for the flowmeter.

3. Testing the Clarke-Bumpus net for flow and filtration efficiency using various meshes, net lengths and towing speeds in the water test tank.

The WP-2 net was also tested at sea to ascertain wire-angles and towing behaviour.

Microzooplankton.
Report of Working Party No. 1

Working Party No. 1 adopted an upper size limit of 200 μ for the organisms considered, as WP-2 had chosen this for their lower limit. The size group dealt with includes all the smaller animal constituents of the plankton community variously described as nanoplankton, microplankton, etc., and includes everything from the smallest protozoa to the eggs and larvae of a wide range of organisms and the adults of many smaller forms such as the copepods.

OBJECTIVES OF INVESTIGATIONS

These can be classified as follows:
Qualitative: systematic; distributional; life histories; community structure.
Quantitative: production; biomass; population dynamics; physiological studies.

REQUIREMENTS FOR A STANDARD METHOD

There is a very pressing need to find out more about the composition of the micro-zooplankton and to find out its importance in the general ecology of the sea. These organisms are undoubtedly a very important link between the bacteria and phyto-plankton and the zooplankton organisms and it is possible that a substantial part of the energy transfer is conducted by the microzooplankton. Qualitative information is required about their systematics, their distribution in time and space and their community structure and trophic relationships. Quantitative measurements of their biomass, information on their physiology, particularly of feeding, respiration and excretion, and information about their behaviour are needed.

The main fields in which some unification of methods might help would seem to be in distributional and quantitative studies.

EXISTING METHODS

Field methods

Water-bottle samples varying in size from 100 ml to 100 litres.
Pump samples.
In situ filtration with: membranes; micro-mesh nets; fine nets ($> 40 \times 40 \mu$ aperture).

Laboratory methods

Fixation and preservation: formalin; lugol; osmic acid, etc.
Concentration: none; sedimentation; centrifugation; filtration (membrane, paper or mesh).
Subsampling.
Counting: staining; haemacytometers; larger squared slides; inverted microscope.
Biomass determination: dry weight; protein, carbohydrate, etc.; total carbon, phosphorus, nitrogen, etc.; electronic volume measurement; computation from microscopic size measurements.

RECOMMENDED METHODS

The terms of reference gave no opportunity or time to conduct experimental work and make comparisons of different methods and the following comments are the majority opinions of the working party.

Field sampling. The majority preference is for the use of water samples and it is generally felt that a 10 litre water-bottle should give a significant sample of forms up to about 150 μ in size. The main disadvantage of water-bottles, however, is that many samples must be taken to cover different depth ranges and for certain purposes water samples integrated over a depth range may be preferable (as used by Lohmann, Strickland and Parsons and others).

Some members of the working party expressed a preference for nets for sampling organisms at the larger end of the size range (75-200 μ) and for the more sparsely distributed organisms. In particular, nets have the advantage of eliminating the effects of marked vertical stratification. At the same time, existing fine-mesh nets are difficult to operate in bad weather, they inevitably lose the smaller organisms through the meshes and they clog easily.

LABORATORY METHODS

Buffered formalin[1] is the most satisfactory general fixative but is of questionable value for use with calcareous forms. Rhodhe's iodine fixative is preferable for use

1. See also p. 158.

with the smaller naked forms but is a poor substitute for the examination of living material. Clearly there is a great need for further research in this field and some liaison with phytoplankton workers dealing with the same problem would seem desirable.

The occasions on which no concentration of material for counting is required are the exception rather than the rule, and generally some technique is required to present the material in a suitable form for counting. Sedimentation appears to be the method most widely favoured because of the uncertainty of other methods. Evidence both for and against the reliability of centrifugation has been produced, and filtration, while adequate for larger forms, cannot really be considered satisfactory as a quantitative technique for many of the smaller organisms as they are either disrupted or disappear optically.

Subsampling and counting can, for convenience, be considered together. Generally it is felt that, to obtain an acceptable numerical estimate, one should count a sample of such size that some 30-40 organisms of the particular species of interest can be counted. It is thus inevitable that the sample size chosen must be varied in accordance with the object of the count. The working group is in favour of using a mechanical form of subsampling (as, for example, by means of a Stempel pipette) to make this possible. There seems to be sufficient evidence to cast doubt on the reliability of making counts on only part of the area of a squared slide or a filter owing to the non-random distribution of material.

The technique of counting must inevitably depend on the size of organism being dealt with. The Sedgwick-Rafter cell is satisfactory for the larger organisms and haemocytometers are adequate for the smallest, but care must be taken to avoid counting, say, nanoplankton on a Sedgwick-Rafter cell about 1 mm deep as many specimens can be overlooked. A useful half-way measure is a squared slide with a cell of coverslip thickness and having a capacity of about 0.5 ml. This has the advantage that moderately high-power objectives can be used for examination. Inverted microscopes overcome some of these difficulties, but, when a long settlement column is used, it is difficult to make detailed examination of an object from different aspects. Beyond aiming to make counts as quantitative as possible and avoiding these more obvious difficulties little else can be said with regard to counting.

The estimation of biomass is perhaps the field calling most for standardization but at the present time no one method seems to offer the potential for widespread adoption. The basic difficulties of separating dead from living material and phytoplankton from zooplankton seem to forestall any completely satisfactory approach, and any method adopted would at best be a compromise. Similarly, some uniformity of approach to the problem of estimating production must be sought, but again little progress has been made towards agreement and at best we can only recommend active investigation in this field.

Smaller mesozooplankton.
Report of Working Party No. 2

The working party recommended a standard sampler of simple, practicable design as one of a series of instruments for quantitative, comparative biomass studies of marine plankton in the upper 200 m of water. A preliminary design of net was agreed upon and this net, after some modification, is referred to as the *WP-2 net* (see Fig. 1); it can be considered to sample the planktonic organisms in the size spectrum from 10 mm downward to a width of at least 200 μ. The retention of motile organisms by a mesh screen depends largely on their largest cross-section or width dimension, so that a copepod 600 or 700 μ in length, having a cross-section of 150 μ, has a better chance of escaping than a spherical radiolarian of 210 μ diameter.

TESTS

The prototype net was tested in a wind-tunnel using a hot-wire anemometer and in a towing channel at the aeronautical and hydrodynamic laboratories of the University of Sydney in February 1966 under the direction of Mr. David Tranter of CSIRO, Cronulla. Profiles of velocity and turbulence in front of the mouth opening were obtained with and without bridles. These measurements yielded data on flow patterns, filtration efficiencies at various towing velocities, and the optimum site for flowmeter placement. The results of the hydrodynamic tests in Sydney are presented in more detail in Appendix 1.

In addition, the prototype net was field tested on several cruises in waters of widely variable plankton standing crops. The tests were conducted by Dr. Paul Smith of the United States Bureau of Commercial Fisheries in the eastern North Pacific during the spring of 1966. Using two telemetering flowmeters, one mounted outside and the other inside the mouth opening of the net, he was able to monitor the water flow through the net at various velocities. Ten-second readings were taken simultaneously for both meters every 30 seconds on an electronic event counter.

The field tests demonstrate that the filtration efficiency of the WP-2 net changes during towing due to clogging. From a limited number of observations it was noted that the filtration efficiency of the prototype WP-2 net decreased from 94 per cent efficiency at the start to 85 per cent (level at which clogging is considered to begin)

after a period of 4 minutes towing at 2 knots in very rich, neritic California Current waters. In relatively clear waters outside the California Current enrichment, 200 miles off Point Conception, the WP-2 net began to clog (filtration efficiency dropping to 85 per cent) after 16 minutes of towing at 1 ½ knots.

AMENDED RECOMMENDATIONS

In the light of the field results, cha..ges in the preliminary recommendations were suggested. The net should have a cylindrical front section and a conical end section, each having a filtration ratio of 3 : 1, thus giving a filtration ratio for the total net of 6 : 1 and a considerable margin of safety against clogging. The cylindrical portion will act as a self-cleaning section and has a superior sustained filtration efficiency (Smith, Counts and Clutter, 1965), while it simultaneously helps to shorten the length of the net without altering the filtration area. The net should be towed in a vertical (rather than oblique) manner in the upper 200 m of water, so as to reduce the towing period, and, hence, avoid the possibility of clogging. Since plankton-rich waters often occur over continental shelves where water depths are less than 200 m, the vertical tows are consequently limited to correspondingly shorter water columns in these regions.

SPECIFICATION

Shape: cylindrical-conical. Length of cylindrical section: 95 cm; side length of conical section: 166 cm.

Mouth opening: 57 cm internal diameter, circular, maintained by a brass or galvanized-iron ring made of metal rod, 1.5 cm in diameter thickness. To give an area of 0.25 m² the diameter should be 56.4 cm; the diameter of 57 cm is intended to make up for the thickness of the canvas.

Mouth area: 0.25 m².

Net material: Nylon Nytal 7 P, or similar net material, basket weave, with mesh aperture width of 200 μ. Porosity (= ratio of mesh aperture area to total mesh area = mesh transparency): 55 per cent.

Canvas attachment to ring: 10 cm width.

Canvas band for throttling line: 10 cm width (57 cm below upper canvas band).

Bridle (3): 57 cm long each, attached to swivel.

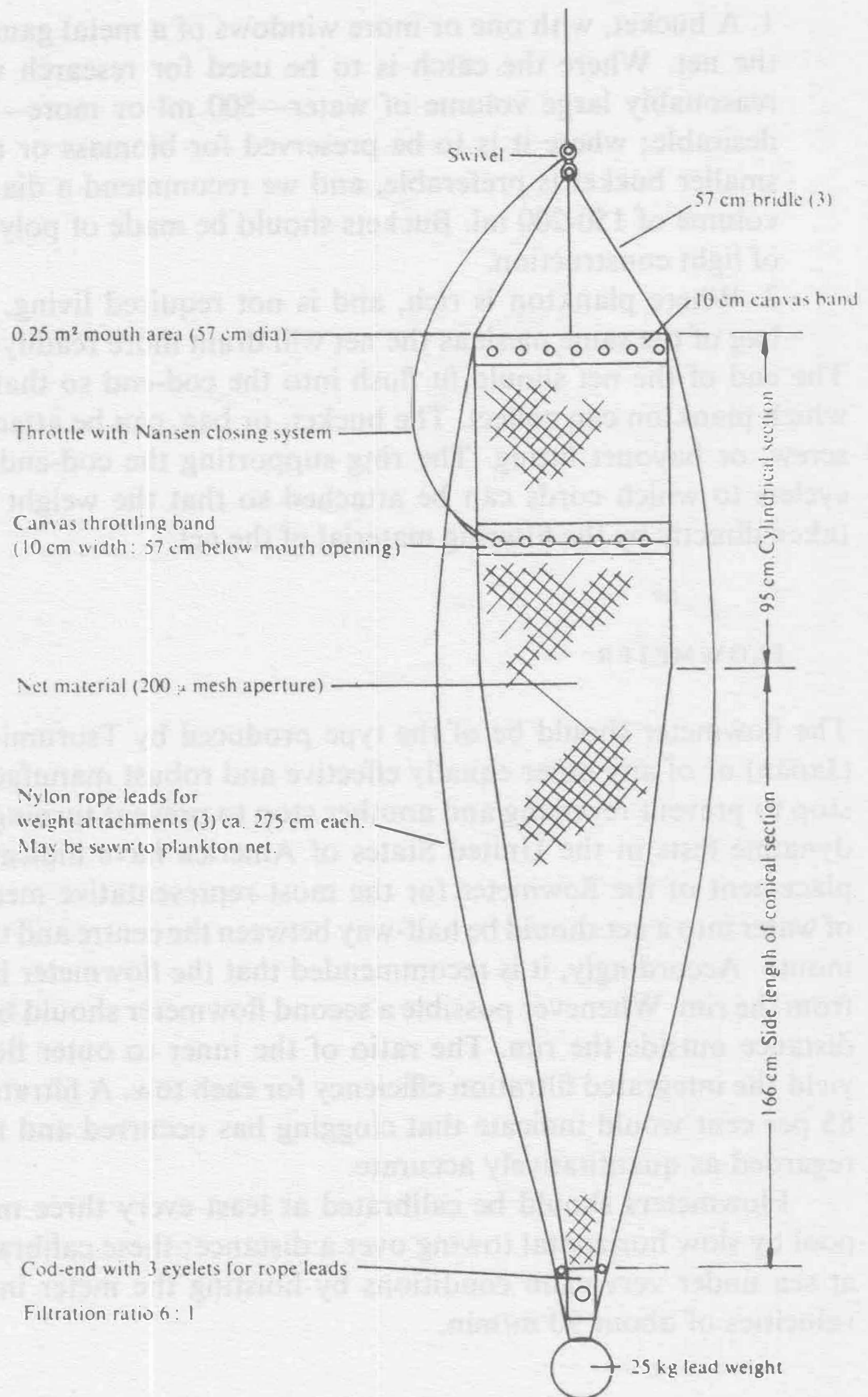Filtration ratio (ratio of mesh aperture to mouth area): 6 : 1.

Filtration efficiency: 0.94 (94 per cent).

Lead weight: 25 kg (40 kg or heavier when wire angle tends to exceed 25º).

Flowmeter: TSK or equivalent, to be attached from three points on mouth ring and centred at 14.25 cm from rim.

Cod-end: (a) bucket with window of same mesh as net (7.5 cm diameter; volume 150-200 ml) for biomass or taxonomic purposes; polyvinyl chloride or light brass; or (b) bucket with window of same mesh as net (7.5 cm diameter; volume 500 cc) for living plankton catches; or (c) bag of same mesh as net (for tows in very rich waters).

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Figure 1
The WP-2 net: modified
version.

Swivel

57 cm bridle (3)

10 cm canvas band

0.25 m² mouth area (57 cm dia)

Throttle with Nansen closing system

Canvas throttling band
(10 cm width: 57 cm below mouth opening)

95 cm Cylindrical section

Net material (200 µ mesh aperture)

Nylon rope leads for
weight attachments (3) ca. 275 cm each.
May be sewn to plankton net.

166 cm Side length of conical section

Cod-end with 3 eyelets for rope leads

Filtration ratio 6 : 1

25 kg lead weight

Ring: 57 cm internal diameter, 1.5 cm diameter thickness; with three eyelets, 120° apart, for bridles and rope lead attachments.

COD-END ARRANGEMENTS

The hydrodynamics of a conical net are such that precise details of the cod-end arrangement are not of great importance and laboratories can use the method they find most suitable for the condition in which they operate. If there are no special preferences the following are recommended:

1. A bucket, with one or more windows of a metal gauze of the same mesh as the net. Where the catch is to be used for research with living material, a reasonably large volume of water—500 ml or more—below the windows is desirable; where it is to be preserved for biomass or taxonomic purposes, a smaller bucket is preferable, and we recommend a diameter of 7.5 cm and a volume of 150-200 ml. Buckets should be made of polyvinyl chloride or brass of light construction.

2. Where plankton is rich, and is not required living, a detachable cod-end bag of the same mesh as the net will drain more readily than a bucket.

The end of the net should fit flush into the cod-end so that there is no pocket in which plankton can collect. The bucket, or bag, can be attached by a simple band, screw, or bayonet fitting. The ring supporting the cod-end should be fitted with eyelets to which cords can be attached so that the weight of the cod-end is not taken directly by the filtering material of the net.

FLOWMETER

The flowmeter should be of the type produced by Tsurumi-Seiki Kosakusho Co. (Japan) or of any other equally effective and robust manufacture. It should have a stop to prevent reversing and another stop to prevent turning in air. Recent hydro-dynamic tests in the United States of America have indicated that the optimum placement of the flowmeter for the most representative measurement of the flow of water into a net should be half-way between the centre and the rim of the sampler's mouth. Accordingly, it is recommended that the flowmeter be centred at 14.25 cm from the rim. Whenever possible a second flowmeter should be placed an equivalent distance outside the rim. The ratio of the inner to outer flowmeter readings will yield the integrated filtration efficiency for each tow. A filtration efficiency less than 85 per cent would indicate that clogging has occurred and the tow should not be regarded as quantitatively accurate.

Flowmeters should be calibrated at least every three months in a swimming pool by slow horizontal towing over a distance; these calibrations may be checked at sea under very calm conditions by hoisting the meter in a vertical manner at velocities of about 90 m/min.

NET MATERIAL AND MESH SIZE

Nylon has several advantages over silk as netting material. The former is more durable and does not shrink when wet, although its meshes are subject to considerable deformation in shape under stresses. WP-2 recommends nylon monofilament, basket-weave netting material because of its good resistance against friction and moderate deformation (e.g., nylon Nytal 7 P and the polyester Estal Mono P.E.). The mesh should be entirely basket-weave rather than alternate basket and twist weave, which are deformed more easily. The mesh opening should have an aperture of 200 by 200 μ when the net is wet and used, and the threads should be 70 μ in

diameter. If these measurements differ, the filtering efficiency of nets of otherwise the same design will also differ.

DEPTH OF TOWING, TOWING SPEED, DURATION AND TIME OF TOWING

In view of the field tests results which have shown that clogging of the WP-2 net can occur rapidly in rich, neritic waters, WP-2 recommends that this net be towed in a vertical manner in the upper 200 m of water. In shallower waters, the vertical tows should be taken from just above the sea bottom to the surface.

In order that the tows be taken in as vertical a manner as possible, a lead weight of 25 kg is recommended when sea conditions are relatively calm. When the ship drifts rapidly, a lead weight of 40 kg or more may be required to keep the wire angle below the suggested maximum of 25°.

The net may be lowered at 60 m/min. and raised at 45 m/min. Since the net will be lowered with weight and cod-end first and the mouth opening is not presented to the direction of water flow, it is assumed that no plankton is collected in the net during lowering. The plankton is collected during hoisting, which should give a towing duration of about 4½ minutes for the 200 m water column at a hauling speed of 45 m/min.

In order to minimize the influence of diurnal migration on biomass studies, it is recommended that sampling be done as far as possible during the three-hour period after sunrise and after sunset. This does not preclude sampling at other times, but these may not be so strictly comparable in biomass studies.

OPENING-AND-CLOSING SAMPLER

For vertical distributional studies, sampling should preferably be carried out in accordance to the water structure.

When hydrographic information is not available, the following water columns should be sampled by vertical tows while the boat is drifting: 0-200 m; 200-500 m; 500-1,000 m; 1,000-1,500 m; 1,500-2,000 m; 2,000-3,000 m.

Two alternative ways of obtaining such samples are by:

1. Modified Nansen method. A throttling line can be attached to the lower canvas band of our standard sampler and linked to the release mechanism.[1] A weight should be used below the cod-end for vertical series.

2. Multiple opening-and-closing plankton sampler[2] for obtaining larger quantities of plankton by oblique towing. Three quantitative samples from three predetermined depth ranges can be collected during a single lowering.

1. *Discovery Report*, vol. 1, 1929, p. 151-222.
2. Bé, *Deep-Sea Research*, vol. 9, 1962.

GENERAL CARE AND MAINTENANCE

Nets should be intensively hosed before being brought aboard to wash plankton into the cod-end.

Nets that show signs of clogging can be washed by towing the net without a cod-end or when clogging is more severe the nets should be washed in detergent. Nets should be washed in fresh water after each cruise, before storage.

Nets should not be left in the sun for prolonged periods nor left where there is risk of unnecessary damage by frictional wear and tear.

Flowmeters should be washed with fresh water after use unless they are to be used again in successive hauls.

PRESERVATION OF PLANKTON SAMPLES

Pending any recommendations to be made by a working party considering laboratory methods, WP-2 makes the following recommendations.

The use of formaldehyde as a fixative and preservative. The saturated solution known as 'concentrated formalin' contains 38-40 per cent formaldehyde. One part of concentrated formalin should be added to nine parts of sea water including the plankton sample, and this should be done as soon as possible after collection. As a precaution against the dissolution of calcareous plankton in highly concentrated samples, the strength of buffered formalin should be doubled in such samples.

It is essential that the formalin be neutralized before use by addition of either borax (sodium tetraborate), marble chips or another suitable buffering agent. Marble chips have the advantage of dissolving gradually in the same measure as acid is produced in the formaldehyde solution. Periodic checks of the presence of undissolved marble chips or checking with pH indicator paper are two simple ways of ascertaining whether the solution is still neutral. Hexamine, apart from being expensive, has the disadvantage of easily crystallizing around organisms when the sample is subject to even a slight amount of evaporation, e.g., while being examined under the microscope in an open dish.

Commercial formalin is often contaminated with iron compounds which, on neutralization, produce a brown precipitate of iron hydroxide. This precipitate spoils the sample by sticking to the surface of the organisms and obliterating their finer structures. It is therefore recommended that analytical grade formalin be used and stored in glass or plastic containers.

DETERMINATION OF BIOMASS

If possible, two identical plankton samples should be taken simultaneously—one for biomass study, the other for taxonomic use. If only a single sample is taken it should be split in half.

The first sample (or subsample, in case of splitting) is preserved in formalin for taxonomic and counting purposes.

The second sample (or subsample) is deep-frozen, then dried at 60°C according to the technique recommended by Lovegrove[1] and finally weighed. The organic matter will be determined on this sample by loss upon ignition. The results (dry weight and organic matter) are expressed in milligrammes per cubic metre.

A scheme for estimation of total biomass, i.e., including organisms both smaller and larger than those sampled by the WP-2 net, is given by Bé in Appendix 3.

Tests should be made to determine the effect of formalin fixation upon dry weight and organic matter content. If formalin preservation should be found to have no undesirable effect, it could be used as a routine technique and samples preserved in formalin could be split in the laboratory ashore, one-half to be used for dry-weight and organic matter measurements.

WP-2 recommend for future work:

Hydrodynamic and field testing of standard samplers and high-speed samplers to acquire basic knowledge of net design in relation to water flow, plankton behaviour, concentration, and patchiness.

Research on materials (e.g., net material).

Development of a telemetering depth-flowmeter, electrically opening-closing samplers, a shipboard flowmeter calibration tank, and a flowmeter with digital dial operated magnetically.

Research towards elimination of bridle and other obstructions in front of net—as related to plankton avoidance of nets, and on the effect of ship's shock wave and noise on plankton sampling.

That a bibliography on sampling gear, sampling methods and processing plankton samples be compiled and kept up to date.

Two other recommendations of WP-2 have already been put into effect: (a) the development of a standard method of processing plankton samples in the laboratory is to be considered by a working group to be set up by SCOR; (b) the manual of plankton sampling methods has been prepared and is included with this monograph.

The working party also discussed the necessity of making comparative tests of plankton sampling material, and it is hoped to prepare a list of suitable equivalents after testing. Facilities for this have been made available through the kind co-operation of Professor A. von Brandt, Bundesforschungsanstalt für Fischerei, Institut für Netz- und Materialforschung, Palmaille 9, Hamburg-Altona 1, and Dr. Erik Hagmeier, Biologische Anstalt, Helgoland. Some results of tests are included in Appendix 2.

1. In: H. Barnes (ed.), *Some Contemporary Studies in Marine Science,* 1966, p. 29-467.

Larger mesozooplankton.
Report of Working Party No. 3

The group considered problems associated with the sampling of the larger plank-
tonic organisms which are relatively more scarce. The main purpose of WP-3 was
then to recommend a sampler of coarse mesh that would sample the larger organisms
in as quantitative a manner as possible from a large quantity of water and not retain
the smaller, more numerous, organisms. Collections made with a fine-meshed net
are too overcrowded with the small organisms. Sieving in the laboratory does not
overcome this problem as the small organisms stick to the larger ones in the pre-
servative, so masking their characteristics—this is specially true of coelente-
rates.

To minimize loss of time, and to filter adequate quantities of water, high-speed
nets are desirable. Most high-speed nets of current design have very reduced mouth
apertures and filter relatively small quantities of water. However, this has the
advantage that the flow through the actual meshes of the net is reduced, with the
consequent improvement in condition of the catch. A design of sampler was needed
which would filter a large quantity of water at high speed yet keep the catch in
good condition, and be as easy to handle as possible. They recommend a design
of net for use during the interim period while a suitable high-speed sampler was
designed and tested.

WP-3, like WP-2, considered intercalibration factors for samplers in current
use impracticable.

The following recommendations were made.

ENCASED SAMPLER

A. *That an encased sampler with a net of mesh aperture 1 mm be designed to sample
the larger zooplankton.* Its specifications should fulfil as far as practicable the
following considerations:

1. The sampler should filter at a rate of 20 m³/min.
2. The flow through the sampler should be metered.
3. The mesh velocity (exit velocity from the meshes) should be as slow as
possible, and preferably not greater than 10 cm/sec.
4. There should be no obstructions ahead of the sampler mouth.

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5. The sampler should tow in a stable manner and the drag should be as low as possible.

6. The sampler should be fitted with a depressor capable of taking it to a depth of 200 m at a speed of 6 knots.

7. The sampler should be fitted with an acoustically operated opening-closing action and a depth sensor telemetering to the surface, and space should be left available for further modules if required.

8. The sampler should be robust and non-corrodible.

9. The net and the catch should be easy to remove and the flowmeter easy to read.

10. The sampler should be as small as possible consistent with the above requirements.

INTERIM SAMPLER

B. *That a simple unencased net with the following specifications would serve as the best interim sampler for the larger zooplankton* (see Fig. 2):

1. Mouth of 1 m^2 consisting of a $\frac{3}{4}$ inch (approximately 2 cm), outside diameter, ring of galvanized tubing.

2. Net with a cylindrical forward part, 57 cm long, and a conical after part, 200 cm long, strengthened with six longitudinal tapes not more than 2 cm wide.

3. Gauze of monofilament nylon of mesh aperture 1 mm.

4. Throat of dacron sailcloth not more than 12 cm wide to be wrapped around the ring. Notches at three equidistant points to take the bridle lugs.

5. Bridle of three legs equal in length to the mouth diameter.

6. Flowmeter to be placed 25 cm inside the ring. It would be useful also to have a second flowmeter outside the net to measure the speed of the net through the water.

7. Bucket to be light in weight.

8. Towing speed to be 2-3 knots.

9. Sinker to be either a dead weight of approximately 40 kg or an equally efficient depressor.

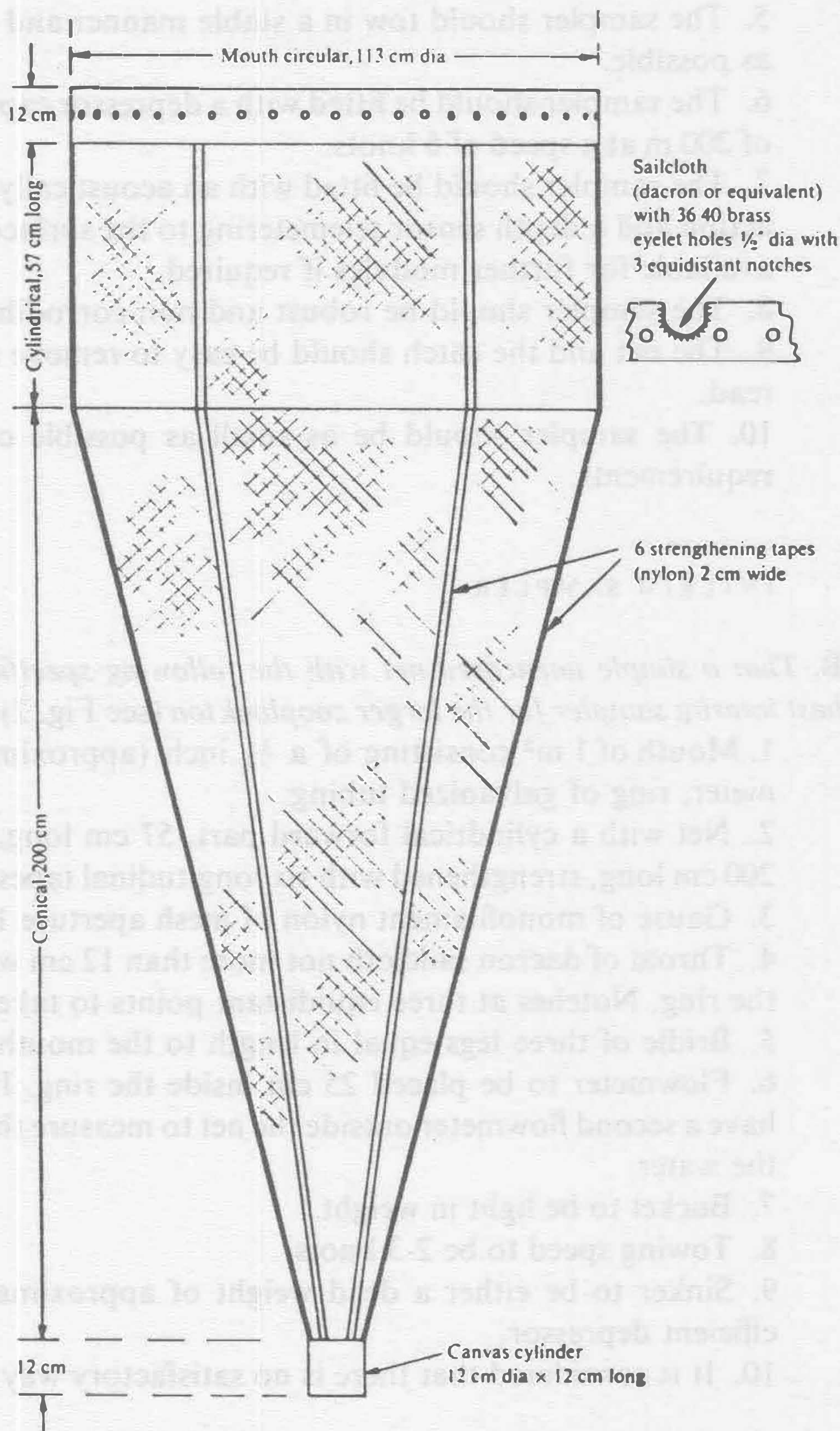10. It is considered that there is no satisfactory way of closing this net.

TESTING FACILITIES

C. *That a list be made of the facilities available throughout the world,* suitable for testing plankton nets, e.g., test tanks, circulating water channels, wind tunnels, etc.

TELEMETRY

D. *That further research be undertaken* to find the best practical means of telemetering information from the sampler to the surface and telemetering control signals from the surface to the sampler.

Figure 2
The WP-3 interim net.

Mouth circular, 113 cm dia

12 cm

Cylindrical, 57 cm long

Sailcloth
(dacron or equivalent)
with 36 40 brass
eyelet holes ½" dia with
3 equidistant notches

Conical, 200 cm long

6 strengthening tapes
(nylon) 2 cm wide

12 cm

Canvas cylinder
12 cm dia × 12 cm long

It is hoped that laboratories with the necessary facilities will give consideration to the design of an encased sampler to meet, as far as practicable, the recommendations of WP-3.

POSTSCRIPT

Since these recommendations were issued in *SCOR Proceedings* the recommended nets have been tried out. The most important of the results obtained were communicated to the Hamburg meeting of ICES in October 1967 by Mr. J. A. Posgay of the Woods Hole United States Bureau of Commercial Fisheries, and these indicate

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that the bridles in front of the WP-3 net seriously affect its efficiency for the capture of larval fish. This note is added here to emphasize this warning.

The probability of this had been considered by the working party, and hence their emphasis on the need for a new and convenient design of a high-speed sampler that would filter a large volume of water. The interim design of net should nevertheless serve a useful purpose as suitable, and convenient for use by less well-equipped vessels, for sampling those species of macroplankton that are not so fast-swimming and are sparsely distributed, necessitating the filtration of a large volume of water.

Experience from the Aberdeen laboratory suggests that the recommended ring is of too light a design for use in bad weather from a large vessel and a solid, instead of a tubular construction would be more satisfactory under these conditions.

Micronekton.
Report of Working Party No. 4

The development of sampling methods for capturing the larger plankton and smaller nekton in a quantitative manner is in its infancy and although some progress has been made not much gear has been designed specifically for this purpose. A plea for standardization might thus appear inopportune at this stage. However, one promising design—the Isaacs-Kidd midwater trawl—is already in use and already a large body of catch data is available. Our recommendations are therefore directed towards introducing some degree of acceptable uniformity in the construction, dimensions, and operation of this sampling device, so that valid comparisons can be made with data from different sources. It is also hoped that these recommendations will serve as a guide to those initiating new sampling programmes.

CATEGORY OF ANIMALS CONSIDERED

WP-4 considered methods by which a representative sample can be taken of pelagic organisms lying within the arbitrary size range 2.0 to 10.0 cm. No single term as yet defined (macrozooplankton, micronekton, forage organisms) is strictly applicable under this definition but if a term is to be used, then 'micronekton' is recommended since it implies less of an overlap with the planktonic animals considered by WP-3.

Within the size range 2.0 to 10.0 cm large decapods (Sergestiids, Penaeids, Oplophorids), fish larvae, small adult fish, small cephalopods and large euphausiids will predominate. Gelatinous organisms and animals lying outside the size range will occur in the catches and these must be considered separately from the main sample.

TYPE OF SAMPLER

Of the methods available it is apparent that one type of sampler, the Isaacs-Kidd midwater trawl (IKMT), is in widespread use. Its advantages include a large mouth opening relatively free of bridles and other obstructions; it is self-depressing, it is versatile and easier to fish than conventional conical nets of comparable mouth

area, and it can be towed at great depth and at high speed. A cod-end closing device is available. Of its disadvantages, perhaps the most important is that there is no measure of the volume of water filtered so that it is only semi-quantitative. Nevertheless, with the realization that it falls short of the requirements of an ideal sampler, WP-4 recommend, at this state in the development of sampling devices, the IKMT as a basis for standardization.

Size of sampler

There are advantages in having as large a net as possible but shipboard facilities vary to such an extent that absolute size could be a limiting factor. For this reason two sizes are recommended: 6 foot and 10 foot, this dimension referring to the spread of the depressor.

Over-all physical dimensions and method of rigging

Specifications of net, depressor, spreader bar, etc., and method of rigging can be found in the following reports:

6 foot: ARON, W. 1962. Some aspects of sampling the macroplankton. *Rapp. Cons. Expl. Mer,* 153, p. 29-38.

10 foot: ISAACS, J. D.; KIDD, L. W. 1953. *Isaacs-Kidd midwater trawl. Final report.* Scripps Institution of Oceanography. (Ref. 53-3, 1-18.)

Mesh size

0.5 inch (12.5 mm) stretched mesh nylon, preferably knotless. It is usual to support this finer mesh within an outer net; meshes of about 2½ inches (6.5 cm) knot to knot are suitable. The use of nets having mixed or graded meshes is strongly deprecated.

Cod-end

There is evidence that the catch is maintained in better condition if the trawl terminates in a metal or plastic container preceded by a short fine-mesh section, of 3 mm mesh aperture. It must be emphasized that this finer mesh will superimpose on the main catch a fraction of animals smaller than 2.0 cm which must be excluded in the final treatment of the sample.

TYPE OF HAUL

Whether an oblique or horizontal tow is used depends largely upon the nature of the problem under investigation since they meet different requirements. Oblique tows are best suited to small- or large-scale regional surveys aimed at delimiting distributional patterns, of species or biomass, within the top 200 m. Horizontal tows are applicable to studies of variation in vertical distribution, sampling with

respect to thermoclines and scattering layers, and sampling more sparsely distributed organisms.

In the circumstances, WP-4 can only recommend procedures that should be followed in making these two quite different types of haul. The importance of adopting and maintaining rigorously a standard sampling procedure cannot be overemphasized, since only in this way can valid comparisons be made between a series of hauls.

Oblique haul. Pay out at 40 m/min. Haul in at 40 m/min. Ship's speed throughout tow: 3 knots (except for shooting and recovering the trawl). Depth of haul: 200-0 m.

Horizontal tow. Pay out at 40 m/min. Haul in at 60 m/min. Ship's speed 3 knots. Duration of tow: 2 hours at fishing depth. Depth of tow: at 50 m intervals down to 1,000 m; at 250 m intervals below 1,000 m.

SHIP'S SPEED

Recent work has shown that the IKMT is extremely sensitive to variations in ship's speed. It is therefore important to maintain a constant speed throughout the tow if the depth of fishing is to remain uniform.

DEPTH OF FISHING

The use of a depth-time recorder or a depth telemeter is a prerequisite of midwater sampling, since an accurate knowledge of the depth of fishing is essential to a proper interpretation of the data.

DISTANCE OF TOW

Methods of metering the flow of water through the IKMT have yet to be evolved. However, as a first approximation of volume filtered, estimates can be made based on mouth area times distance towed through the water (which equals the length of the sampled column). A flowmeter mounted in the cod-end can be used to give a relative measure of the length of water column sampled.

TREATMENT OF CATCH

Animals falling outside the size range 2-10 cm should be treated separately from the main catch. Consider catch by taxa: measure displacement volume or wet weight and enumerate. If possible, pool taxa and consider by trophic level.

CONCLUDING REMARKS

It must be emphasized that, while the recommendations refer to existing gear, it is not implied that the methods available are adequate. On the contrary, it is clear that they leave much to be desired and progress in the quantitative study of these more active pelagic organisms will largely depend upon technical improvements in the IKMT and in the evolution of new devices and approaches. This work must be encouraged; it is long overdue, and WP-4 strongly urges that support be given to the following:

1. Field and laboratory studies of the hydrodynamics and catching efficiency of the IKMT. An objective appraisal of this sampling device can only be made as a result of such work.

2. Studies to evaluate the effectiveness of existing opening-closing systems and, if necessary, to design and produce new ones.

3. The design and production of reliable, accurate depth-telemeters, operative to 5,000 m.

4. The design of devices that can be incorporated in the sampler to telemeter or record environmental parameters (light, temperature, etc.).

Concluding remarks

Members of both WP-1 and WP-2 have commented on the lack in these recommendations of equipment to deal with those organisms too big to be adequately sampled by the water-bottle and yet small enough to escape through the meshes of the WP-2 net. Choosing arbitrary divisions by size inevitably means overlapping or, as in this instance, a gap. WP-2 considered that to reduce their mesh to less than 200 μ would introduce too serious a problem in filtration and clogging, and WP-1 considered that it would be impracticable to make the water-bottle technique big enough to sample sufficient water. A net of 25N mesh, with a mesh aperture of about 60 μ, is therefore desirable where this field is to be covered. No special recommendations are made in this report concerning the precise design, but it should have a comparatively small mouth aperture and, with a porosity of about 25 per cent, the area of filtering material should be about 24 times the area of the mouth. The general design could follow that of the WP-2 net recommended above.

WP-2 were primarily concerned with the selection of the proper mesh and the size range of organisms to be collected. The net chosen for their collection has no basically new features but is an attempt to produce an efficient and acceptable standardized version from the many types in current use. At present not enough is known about the properties of existing fine nets, and studies to produce a really satisfactory design should be initiated. Working parties 3 and 4 have made it clear, too, that more satisfactory methods are also needed for sampling the larger organisms. Much was done on these lines at the Sydney symposium and the relevant details are included in this monograph.

None of the working parties considered that any satisfactory series of figures could be produced to enable quantitative intercalibrations to be made for the many existing types of net. The methods of working and details of design were extremely variable and the effect of these variations was too complicated for any confidence to be placed in an arbitrary intercalibration figure.

Working Group 13 has therefore completed its task in formulating the recommendations given in this report.

ACKNOWLEDGEMENTS

Appendixes

1. Hydrodynamic tests on the prototype net of Working Party 2

By David Tranter and Andrew Heron, CSIRO, Cronulla, Australia

During the Symposium on the Hydrodynamics of Plankton Samplers, at Cronulla in February 1966, a net, made to WP-2 specifications, was tested at the Engineering School of the University of Sydney. The purpose of the tests was to examine the flow in front of the net, with a bridle in place, to determine the best position for a flowmeter.

WIND-TUNNEL TESTS

Measurements of velocity and turbulence were made with a hot-wire anemometer, with and without a bridle. The values are shown in Figure 3. These values only indicate the disturbance caused by the shackle itself, as the traverses were done between two legs of the bridle. The proportions of the water column represented by the different values are shown in Table 1. There can be some variation in interpretation of the peripheral region. Due to the angle at which the flow turns and the close proximity of the ring, the 0.78 value may not represent water going through the net. However, the range of probable filtration efficiencies is between 0.930 and 0.945. The value of 0.93-0.945 for filtration efficiency shows that the site for a flowmeter is critical. Even the region which is not affected by the shackle or the ring is biased by being up to 5 per cent too high. However, this would still seem to be the best place for a reliable comparative reading.

TABLE 1. Proportions of volumes represented by velocity values across the mouth of the WP-2 net in the wind tunnel (with bridle)

Traverse	Distance from centre (in.)	Area represented (in.)	Proportion of area	Proportion of volume (propr. area × vel.)
T_1	0	0—0.5	0.25	22.75
T_2	1	0.5—1.5	2.0	200
T_3	2	1.5—2.5	4.0	388
T_4	3	2.5—3.5	6.0	579
T_5	4	3.5—4.5	8.0	772
T_6	5	4.5—5.5	10.0	1 010
T_7	6	5.5—6.5	12.0	1 200
T_8	7	6.5—7.5	14.0	1 351
T_9	8	7.5—8.5	16.0	1 520
T_{10}	9	8.5—9.5	18.0	1 638
T_{11}	10	9.5—11.2	35.25	2 745

WATER TANK TESTS

A profile across the mouth of the net at the level of the rim was made, using a laboratory flowmeter with a diameter of 1 cm. The results for a towing speed of 93.6 cm/sec are shown in Table 2. As expected, they closely parallel the wind-tunnel results. However, the profile differs in that the water at the periphery, when it is deflected around the net, is presented to the flowmeter at a sharp angle which gives a low reading. This means that from a point about 2 cm in from the ring out to the free stream, the low values represent a change in direction of the water more than a change in velocity. Otherwise the pattern appears to be the same.

Some tests were made to compare filtration efficiency at various velocities. The results are shown in Table 3. There was little change in the ratio of the velocity at the site of the flowmeter to the free stream velocity.

TABLE 2. Velocities across the mouth of the WP-2 net in the water tank (free-stream velocity (carriage) = 1.94 knots; free-stream velocity (meter) = 1.94 knots)

Distance from centre (in.)	Meter reading	Velocity of carriage. V_2 (knots)	Velocity of meter. V_1 (knots)	V_1/V_2
		WITHOUT BRIDLE		
0	6.0—	1.94	1.88	0.959
2	6.05—	1.94	1.89	0.965
4	6.0 ±0.2	1.94	1.88	0.959
6	6.05±0.15	1.94	1.88	0.959
8	5.9 ±0.1	1.94	1.85	0.954
9	5.75±0.15	1.94	1.80	0.928
10	5.55±0.15	1.94	1.74	0.897
11	5.45±0.15	1.93	1.71	0.886
12	5.6 ±0.2	1.93	1.76	0.911
14	5.9 ±0.2	1.93	1.85	0.958
16	6.0 ±0.2	1.93	1.88	0.974
		WITH BRIDLE		
0	5.65±0.15	1.93	1.77	0.917
1	6.05±0.15	1.93	1.89	0.980
2	6.05±0.15	1.93	1.89	0.980
6	5.95±0.15	1.93	1.86	0.964
8	5.70±0.2	1.93	1.79	0.928
9	5.65±0.25	1.93	1.77	0.917
10	5.55±0.25	1.93	1.74	0.902
11	5.45±0.15	1.93	1.71	0.986
12	5.60±0.2	1.93	1.76	0.912
14	5.90±0.2	1.93	1.85	0.959

TABLE 3. Filtration efficiency and velocity in the WP-2 net in the water tank (with bridle)

Distance from centre (in.)	Meter reading	Velocity of carriage. V_2 (knots)	Velocity of meter. V_1 (knots)	V_1/V_2
6	1.55±0.15	0.556	0.555	0.980
6	3.25±0.25	1.061	1.060	0.998
6	4.7 ±0.2	1.546	1.490	0.965
6	6.5 ±0.2	2.090	2.025	0.970
6	8.2 ±0.2	2.680	2.530	0.945

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Velocity – proportion of free stream velocity
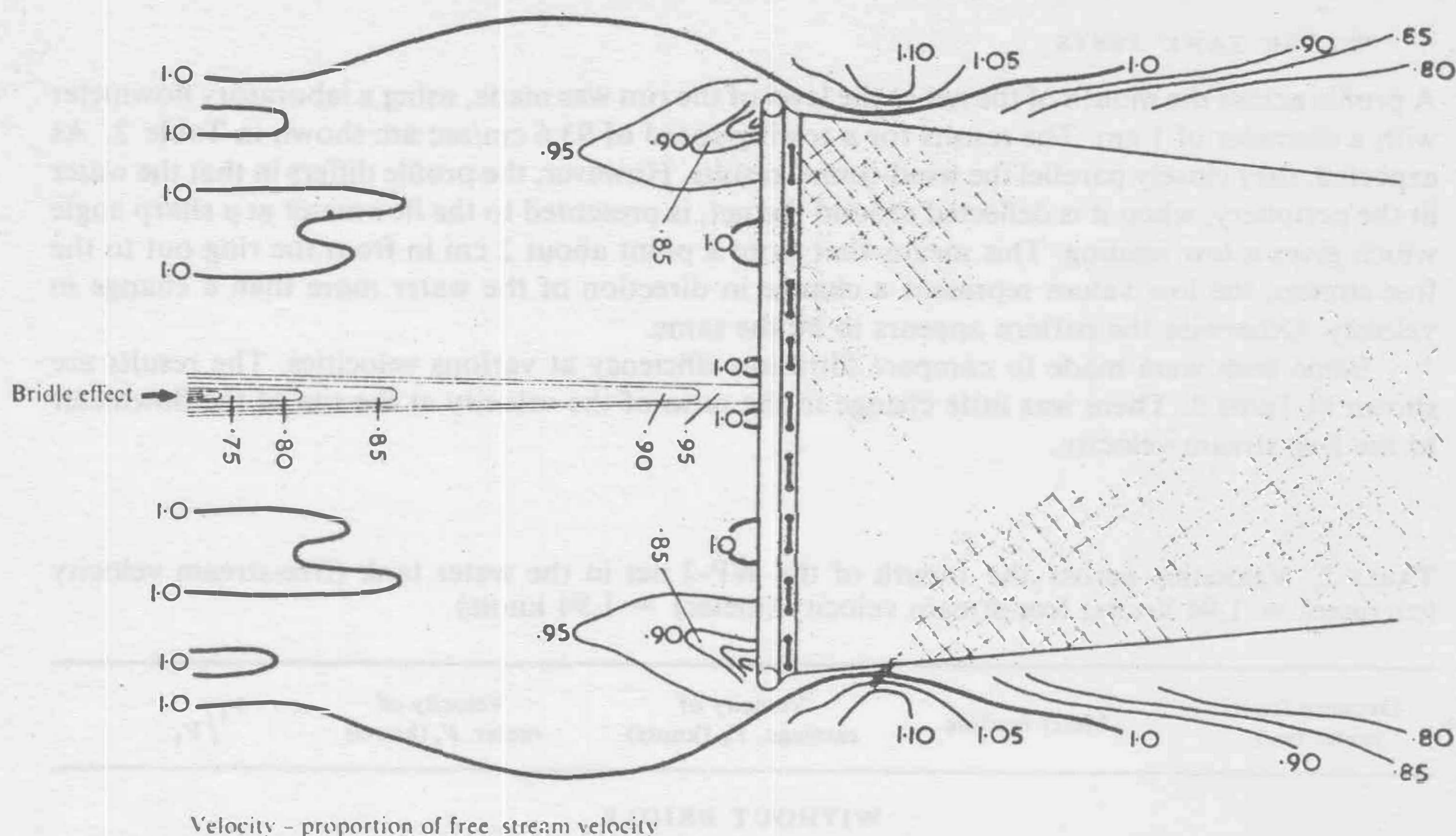
Appendix 1
Figure 3
The WP-2 net.

2. Observations on synthetic gauzes for plankton nets

By E. Hagmeier, Helgoland

Some data have been collected on the properties of synthetic gauzes used for plankton sampling. I am indebted to Professor Dr. B. Kimor, Haifa, for his kind co-operation, and to Miss A. Fehse for her careful assistance with experiments and measurements.

EXAMINATIONS OF GAUZE BEFORE AND AFTER USE

The mesh sizes in used nets showed no significant deviations in synthetic material from new. However, the filtering efficiency is reduced by particles which tend to stick to the filaments (especially in twist-type weave). Careful cleaning of the nets after use is recommended. To facilitate thorough washing, an easy method of separating the gauze from ring and bucket would be welcome (e.g., by a zip fastener, as practised at the Kiel laboratory).

MEASUREMENTS ON 200 μ GAUZES

There is some variety in the synthetic bolting cloth of 200 μ mesh size which is on sale. The samples obtained (there are certainly more types) are listed in Table 4; the data given are partly furnished by the manufacturers, but are completed and controlled by my own measurements.

The material of the filaments is nylon, save in Estal Mono P.E., where it is a polyester, and in Monodur, where it is perlon; both are more resistant than nylon. The actual mesh opening varied around 200 μ; larger deviations appeared in Monodur. The percentage of open area in the tissue surface ranges from 34.5 to 55 per cent, dependent on the diameter of the filaments. All the netting listed is monofilament, mostly of basket-weave; in Nytal 7-200 μ and Nitex 202 the warp consists of alternate single and double twisted filaments. The prices of all tissues listed are around U.S.$5 per square metre.

TABLE 4. Some characteristics of 200 μ bolting material on sale

Gauze	Mesh openings of sample (μ)	Sifting surface (%)	Diameter of filaments (μ)		Manu-facturer [1]	Whether tested
			Warp	Woof		
Nytal DIN 1171 30-200 μ	190—220	34.5	140	140	A	No
HD 200 μ	180—200	41.5	110	110	A	No
*7xxx 200 μ	200—215	43	110	100	A	Yes
*7 200 μ	190—215	47.5	$80 + 2 \times 60$	80	A	Yes
200 μ	200—215	47.5	90	90	A	No
*7P 200 μ	190—210	55	70	70	A	Yes
*Estal Mono P.E. 200 μ	205—215	44.5	108	108	A	Yes
*Monodur 200	200—250	40	127	127	B	Yes
Nitex 202	195—210	45	$88 + 2 \times 64$	88	C	Yes

1. Manufacturers: A: Schweizer Seidengasenfabrik A.G., 9425 Thal, St. Gallen, Switzerland; B: Vereinigte Seiden webereien A.G., 415 Krefeld, Federal Republic of Germany; C: Swiss origin, dealer Tobler, Ernst & Traber, 71 Murray Street, New York 7, N.Y., U.S.A.

INFLUENCE OF FRICTION

Samples of the gauzes marked by an asterisk in Table 4 were dragged over the edge of a glass slide; the sample was moved to and fro 240 times per minute, with a weight of 500 grammes fastened to one end.

After 10 minutes, the most obvious change appeared in Nytal 7 and Nitex, when the sample was chafed transversely to the course of the twisted filaments: the threads became displaced. No shifting of the filaments appeared when the sample was moved in the direction of the twisted filaments. The amount of wearing was different: in Nitex, Nytal 7, and Nytal 7xxx more losses of material were registered than in Monodur, Estal Mono P.E., and Nytal 7P.

Two samples were treated for one hour, when the filaments of Nytal 7 broke, but Estal Mono P.E. was still in a rather good state.

DEFORMATION OF MESHES

A drag of 1,000 grammes was applied to six samples at an angle of 45° to the course of the filaments. The deviations of the diagonal diameters from normal were shown to be largest (about 20 per cent) in Nitex and Nytal 7, moderate (± 14 per cent) in Nytal 7xxx, Nytal 7P, and Estal Mono P.E., and not substantial (3 per cent) in Monodur.

CONCLUSIONS AND SUMMARY

Measurements and experiments were carried out on 200 μ gauze of different materials, strength, and texture. Of the samples tested, the most suitable for plankton nets appeared to be the nylon gauze Nytal 7P and the polyester texture Estal Mono P.E. (both of basket weave), because of their good resistance against friction and moderate deformation values. The perlon gauze Monodur, with similar advantages, is less accurate in mesh size and has a rather rigid structure, which makes sewing difficult.

3. Measuring total plankton biomass

By Allan Bé, Lamont Geological Observatory

This scheme was proposed at the Symposium on the Hydrodynamics of Plankton Samplers, CSIRO, Cronulla, Australia, 14-16 February 1966 and its validity as well as the 'sampling suitability' of each of the recommended plankton samplers need to be investigated more thoroughly.

Assuming that agreement can be reached on standardization of a set of plankton samplers of different dimensions and mesh apertures, we are then faced with the problem of integrating our various catches to obtain 'total biomass'.

The plankton catches from these various samplers will overlap with one another with respect to kind and size. A net can theoretically select the lower size limit of organisms, but cannot discriminate for the upper size limit which depends largely on the kind of plankton present, the towing speed, and the area of the mouth of the net.

A scheme is proposed for eliminating the overlapping upper size fractions from each haul that are duplicated in the samples from the coarser-meshed nets by means of a series of graded sieves whose meshes are equivalent to those of the standard samplers used. Each plankton catch is filtered through a separatory column and is divided into as many size classes as there are standard samplers. For a series of four standard samplers the theoretical total would be sixteen fractions as shown in the following arbitrary model:

Separatory column with graded sieves	Water-bottle ($\theta\ \mu$)	$200\ \mu$ net	$1\ 000\ \mu$ net	$5\ 000\ \mu$ net
$5\ 000\ \mu$	A^3	B^2	C^1	D
$1\ 000\ \mu$	A^2	B^1	C	D^{-1}
$200\ \mu$	A^1	B	C^{-1}	D^{-2}
$0\ \mu$	A	B^{-1}	C^{-2}	D^{-3}

The fractions A, B, C and D theoretically contain the plankton organisms that are most ideally collected by each of the standard samplers, and their sum (after correcting for the volumes of water filtered by each sampler) should give us the best estimate of 'total plankton biomass'.