

A NEW METHOD OF DETERMINING THE EFFICIENCY OF  
TOWED PLANKTON SAMPLERS

by

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## ABSTRACT

In recent years interest has increased concerning the accuracy with which collections made with plankton samplers describe the size and species composition of zooplanktonic communities. The indications are that errors arising from the avoidance of sampling devices by zooplankton may be important, especially when precise data are required.

A model is proposed to describe the processes by which zooplanktonic organisms escape or avoid a sampler in terms of the radius of the mouth of the sampler, the speed at which it is towed, the effective speed the organisms can attain in order to escape, and the distance at which the organisms can detect the sampler. The model is capable of being fitted to field data to provide a curve of percentage catch plotted against speed of towing. The results presented indicate that the model gives a good representation of the processes of biological escapement. Implications of the results are embodied in recommendations respecting the design of plankton samplers.

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## INTRODUCTION:

The goal of the planktologist is to understand the structural and functional aspects of the planktonic community. Because he is unable to observe this community directly he is largely committed to gathering his data at a distance, and for information regarding the size and species composition of the planktonic community, has to rely on samples collected by a variety of devices. Although pumps, traps, and even purse seines have been and are being used to obtain such samples, almost all are collected with towed plankton samplers. In the present study several samplers designed to catch zooplankton ranging from about one millimetre to several centimetres in length are discussed.

Almost without exception plankton samplers operate by passing a large volume of water through a filtering surface. This surface, which is usually in the form of a conical net, is expected to retain much of the particulate matter which is larger than the mesh aperture (Wiborg, 1948). In the simplest type of sampler the filtering surface is a truncated cone supported by a ring at the mouth and terminating in a collecting bucket towards the apex of the cone. This design is basic to nearly all plankton samplers, but has a number of disadvantages. Chief of these is the lack of any provision for obtaining uncontaminated samples from a particular stratum of the water column, and a general clumsiness when using more than one sampler at a time. However, the basic principles of its

operation are common to all towed plankton samplers.

Two sorts of information should be obtained when using a plankton sampler. These are, firstly, a representative sample of the community or population of a species or group of species of zooplankton present; and, secondly, information leading to a determination of the volume of water filtered. A plankton sampler may fail to provide either of these for a variety of reasons and, if the inadequacy is not recognised, errors in the interpretation of the data may result. These errors can be divided into two broad categories.

Firstly, there are those sources of error originating internally to the sampler, including those arising from inaccurate determination of the volume of water which has passed through the filter. These errors can be largely overcome by the use of a flow meter which has been carefully calibrated. Losses of catch resulting from extrusion of animals through the meshes of the filter can be minimised by selecting a filter which will retain all specimens of the species to be studied.

In the second category are sources of error originating externally to the sampler, including those arising in the estimation of the size of a zooplankton population because of the non-homogeneous distribution of its constituents (Barnes, 1949; Barnes and Marshall, 1951; Cassie, 1958, 1959). Attempts to compensate for the non-homogeneous distribution of zooplankton can be made, if necessary, in the design of the sampling program. This category also

includes errors in the estimates of the size of zooplanktonic populations which may arise from the detection and avoidance of the sampling device by individual animals. These errors are not easily detected, and they lead to non-quantitative data which can be troublesome to any program requiring exact information concerning the size of the population of each species in a community.

Data from studies in the field by Sheard (1941), Aron (1962), Hansen and Anderson (1962), Regan (1963), and Le Brasseur and McAllister (1966)\* indicate not only that problems arise from the reactions of zooplanktonic organisms to the presence of the sampler, but also that the problems are compounded because the effects of the reactions vary according to the varying powers of perception and locomotion possessed by each species. In this connection Flemminger and Clutter (1965) have postulated the existence of a zone around the periphery of the mouth of the sampler from which the species of zooplankton they studied were able to escape. Barkeley (1964) has analysed the kinematics of the reaction of individual animals to the presence of the sampler.

In the present study a mathematical model, based on Barkeley's analysis of the reaction of individual animals to the presence of a plankton sampler, is proposed. This model treats the peripheral zone of escape as a function of the speed of hauling and can be fitted to field data to provide a

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\* Courtesy R. Le Brasseur, Pacific Oceanographic Group, Nanaimo, British Columbia, Canada.

plot of percentage catch against speed of hauling. The results of this study indicate that the model accounts for the major features of loss in catch resulting from the detection and avoidance of the plankton sampler by individual organisms.

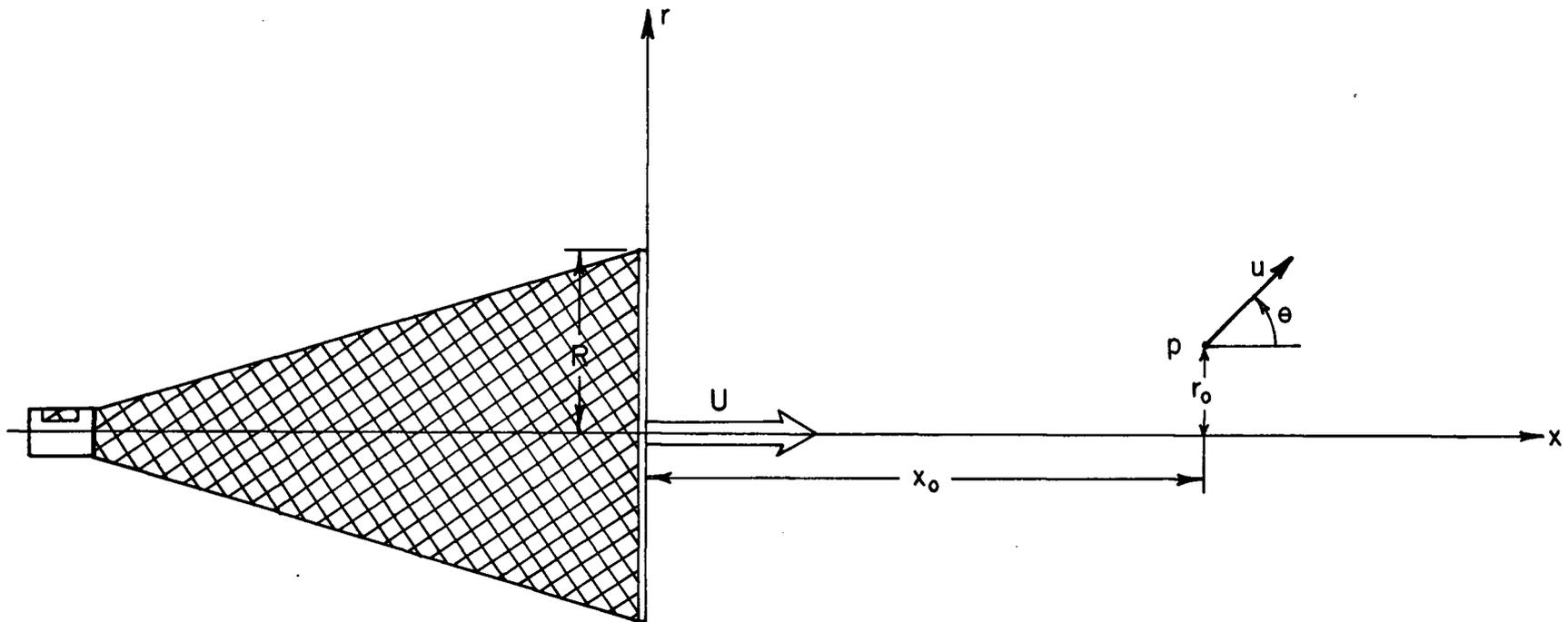


Figure 1. The kinematic basis of Barkeley's model for assessing the efficiency of a towed plankton sampler.  $U$  = the speed of towing,  $R$  = the radius of the sampler,  $X_0$  = the distance at which organisms can detect the sampler,  $r_0$  = the initial offset of the organism,  $u$  = the minimal escape velocity of the organism,  $p$  = the original position of the organism,  $\theta$  = the angle at which the organism swims with respect to the axis of the sampler.

## CONCEPTS AND SURVEY OF LITERATURE:

For the purpose of this study biological escapement is defined as the avoidance of an approaching plankton sampler by zooplankton by means of their own exertions. The consequence of biological escapement is underestimation of the size of zooplanktonic populations. Another effect of biological escapement is that, as a result of the varying powers of perception and mobility possessed by different species of zooplankton, the proportions of animals caught may not be the same as the proportions of those species in the community. This contributes to the selectivity of a sampler, where selectivity is defined as the differential capture of one or more species or size ranges of zooplankton.

If Barkeley's (1964) analysis of the kinematics of biological escapement is correct (Fig. 1) it is to be expected that the number of specimens of a species captured per unit volume of water will increase if the speed of hauling is increased. As the speed of hauling is increased the zooplankton will have less opportunity to evade the sampler because they will have less time in which to move before the sampler overtakes them. This increase in catch can be expected to be greatest for those animals which are best able to escape capture at the original speed of hauling. However, other factors may affect the estimates of the numbers of each species present; mostly these originate in errors arising in the collecting technique.

The usual method of operation of a plankton sampler is to pass a large volume of water through the filtering surface (net). One source of error is in the determination of the volume of water which has been filtered. This volume can be determined either with a flow meter which has been calibrated in the sampler in which it is to be used, or by assuming that the sampler filters some constant fraction of the water presented to it over the length of the tow. If the volume of water filtered is to be determined by assumption it is essential to know what the length of the tow was and, in most instances, what proportion of the water presented to the sampler is filtered. However, the distance that the sampler has moved through the water is not always easy to determine. In horizontal or oblique hauls unknown effects of currents should be accounted for. Even in a vertical haul, should the ship move relative to the wire, the distance that the sampler moves through the water is difficult to determine.

Another cause of errors, in the determination of the volume of water which has passed through the sampler, is clogging of the meshes of the filter, often by phytoplankton. When sampling is carried out in productive waters clogging can be a serious problem. When clogging occurs the amount of water filtered per unit distance may be greatly reduced. The severity of clogging can be reduced by increasing the amount of open area of the filter in relation to the area of the mouth of the sampler, e.g. by greatly increasing the length of the sampler, or by increasing the size of the meshes of the

filter. (Smith, pers. comm.).\*

Because it is important to determine the volume of water which has been filtered many plankton samplers employ flow meters. A flow meter consists of an impeller, geared to a counter, which records the number of revolutions made by the impeller. The use of a flow meter introduces many problems because it actually measures the length of a column of water which has passed through the sampler; not volume. Therefore, it is necessary to calibrate the flow meter before the number of revolutions can be converted to volume filtered.

The calibration is made by towing the sampler over a known distance both with and without the filter in place. The results from tows made without the filter give the calibration with respect to distance moved through the water. Comparison of the results given with and without the filter gives an estimate of the percentage of the water presented to the sampler which is accepted by it. What is actually measured by the difference between the readings obtained with and without the filter is the reduction in the velocity of flow through the sampler caused by the presence of the filter, or the length of the water column which passed through the sampler at the position of the flow meter. In small samplers like the Clarke-Bumpus Sampler (Clarke and Bumpus, 1950) in which the impeller occupies most of the diameter of the sampler, a good estimate of the amount of water which has passed through the

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\*Dr. P. Smith, U. S. Bureau of Commercial Fisheries, La Jolla, Calif.

sampler may be obtained. In larger samplers such as the N.I.O. 70-cm sampler (Currie and Foxton, 1957) or the one-metre conical sampler the flow meter occupies only a small portion of the mouth of the sampler and the assumption must be made that the flow through the sampler is everywhere the same as it is at the position of the flow-meter. Further, flow-meters have traditionally been mounted in the centre of the mouth of the sampler. Recent experimental studies have shown that the wire, and especially the terminal shackle (Fig. 5a) which is attached to the bridles of the sampler, create a turbulent wake which passes into the centre of the mouth of the sampler (Bary, pers. comm.).\* Because the flow meter must be in a region of laminar flow in order to give accurate results, the wake may cause centrally mounted flow-meters to give inaccurate results.

Errors in estimates of the number of organisms per unit volume of water resulting from inaccurate estimates of the volume of water which has been filtered could obscure the effects of biological escapement.

In Fig. 2 flow-meter readings recorded during the field trials undertaken in the course of this study are plotted against the speed of hauling (see Table 1). When the field trials were carried out the effect of the turbulent wake passing into the centre of the mouth of the sampler was not appreciated, and therefore all data were obtained with

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\*Dr. B. Mck. Bary, Institute of Oceanography, University of B. C., Vancouver, Canada.

Figure 2 (facing) Mean flowmeter counts plotted against speed of hauling. The results for the 1-m conical sampler, the 70-cm N.I.O. sampler, and the Catcher were obtained during the field trials of August, 1965; those for the two experimental samplers were obtained during the field trials of January, 1966.

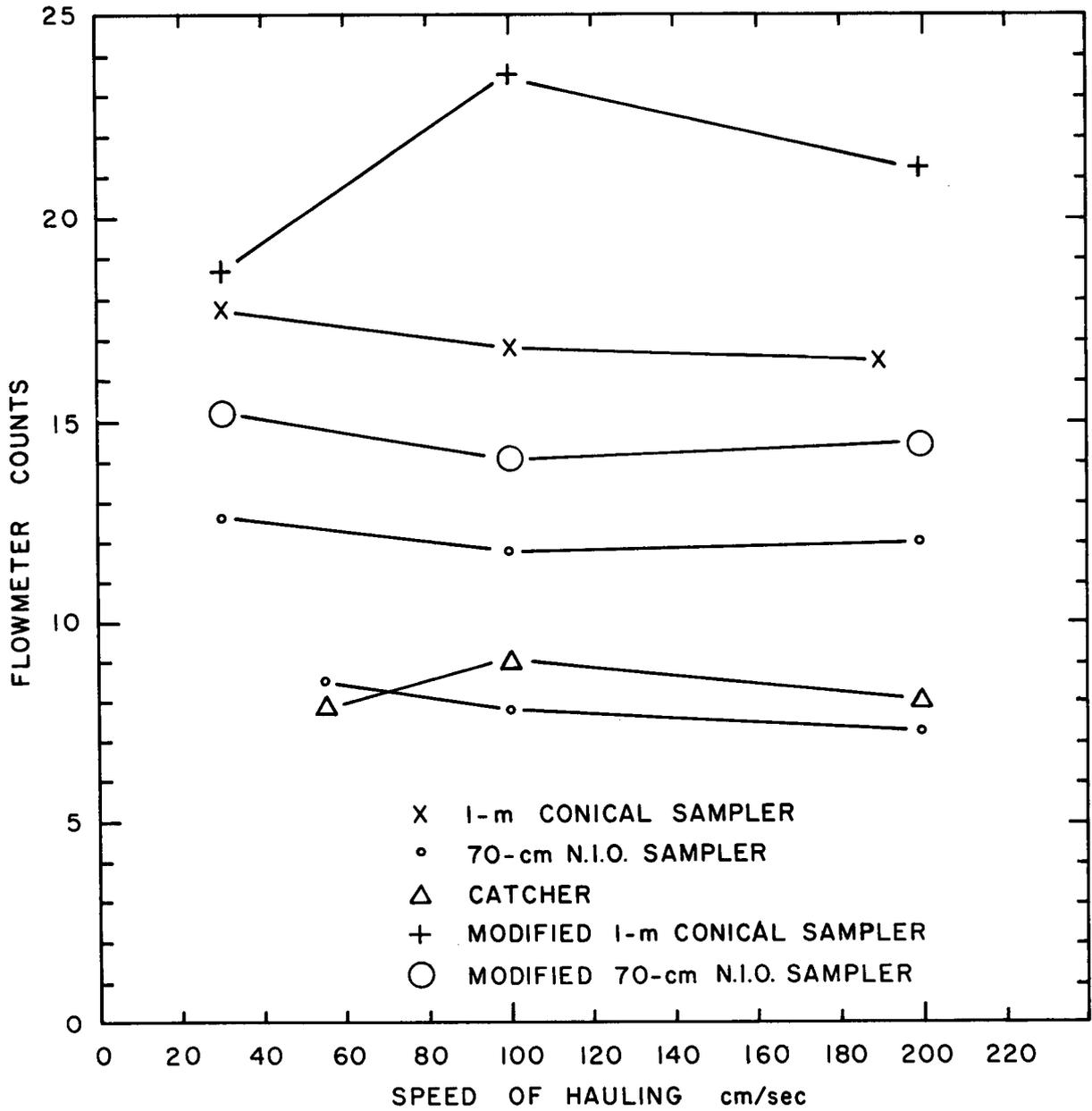


Table 1. Flow Meter Counts (per haul)

	August, 1965		
	25 cm/sec	Speeds 100 cm/sec	200 cm/sec
One-metre conical sampler			
	18.0	16.5	16.5
	17.0	14.5	16.5
	18.0	17.0	15.0
	18.0	18.5	16.0
	17.5	17.5	17.0
	18.0	17.5	16.0
	18.5	17.0	17.0
	17.0	16.5	16.5
70-cm N.I.O. sampler			
	6.5	7.5	7.0
	9.5	8.5	7.0
	9.5	7.5	7.5
	9.0	8.0	6.5
	8.0	8.5	7.5
	9.5	7.5	8.0
	7.5	9.0	6.0
	8.5	8.0	7.0
Catcher (50 cm/sec)			
	6.0	9.5	9.0
	8.0	8.5	10.0
	8.0	9.0	9.5
	9.0	8.5	9.5
	8.0	9.0	7.0
	8.5	9.0	9.0
	7.0	9.0	10.0
	8.0	8.0	9.0
January, 1966			
Modified one-metre conical sampler			
	19.0	24.0	17.0
	14.0	26.5	30.0
	23.5	25.0	15.0
Modified 70-cm N.I.O. sampler			
	15.0	14.0	14.5
	15.5	14.0	14.5
	15.0	14.0	14.0

centrally mounted flowmeters.

The impeller of the flow meter used in the Catcher (Fig. 7a) (Bary et al., 1958) occupies nearly the whole diameter of the tail piece. The impeller of the flowmeter used in the N.I.O. 70-cm sampler (Fig. 6a) and in the one-metre conical sampler was about 15 cm in diameter (Currie and Foxton, 1957). Only large deviations in flow such as those caused by clogging, can be detected readily. In the present study a large deviation was obtained using the one metre conical sampler (Fig. 5b) when it was modified by adding a cylindrical lead weight 80 cm in front of the mouth of the sampler. It is most probable that this deviation was caused by the wake from the weight affecting the flow meter.

Because the flow-meters in the two large samplers were not only in the turbulent zone, but also were unable to monitor more than a small portion of the flow through the sampler, the results from them have been used only as an assurance that large changes in the volume of water filtered per haul probably did not occur.

In the present study the volume of water filtered was calculated by assuming that the samplers filtered 100% of the water presented to them over the course of the tow. Clogging is believed not to have occurred. In the field trials the samplers were hauled vertically over a known distance. In the protected location in which they were carried out the wire never strayed more than a few degrees from the vertical. In the special circumstances of this study the method of assuming

a volume filtered appears to be the most useful one. It is probable that the samplers did not filter 100% of the water presented to them, but this is not important because the model being evaluated requires only that some constant proportion of the water be filtered. That a constant volume is filtered over a range of speeds has been demonstrated for the Catcher by Bary et al. (1958) and for the Clarke-Bumpus Sampler by Tranter and Heron (1965) and by Gilfillan and Pease (in prep.).

Errors in estimates of the number of specimens present per unit volume, when a known volume of water has been filtered, can arise from two sources. Firstly, organisms small enough to pass through the meshes of the filter will not be sampled quantitatively. This situation can be avoided by choosing a filter with a small enough mesh aperture to retain individuals of all those species which are to be studied. However, decreasing the size of the mesh aperture increases the rate at which the filter will clog. Therefore a compromise is often necessary when sampling in productive waters.

A further source of variation results from the non-homogeneous dispersion of individuals, or 'patchiness', of a species in the sea (Barnes, 1949; Barnes and Marshall, 1951). These patches may be several kilometers in lateral extent (Cushing, 1954) and have a substructure on the order of several metres in all dimensions (Cassie, 1958, 1959). These patches may also be only a few metres in thickness (Bary, 1966).

Hauls several hundred metres long will tend to average out the effects of the patchy substructure and provide a

better sample of the population present. Vertical hauls will yield the most reliable sample when the aggregations of zooplankton are primarily in horizontal layers. A further precaution which should be taken to attempt to reduce the effects of patchiness is to follow the same parcel of water rather than to sample at the same geographical position.

Few reliable data concerning biological escapement are available in the literature. In many of the reported investigations of the problems connected with plankton sampling, inadequate measures were taken to reduce those other sources of error which can obscure the effects of biological escapement. Accordingly interpretation of the results is difficult at best (e.g. Hensen, 1895; Kunne, 1933; Gibbons, 1939). A brief review of the pertinent literature is given below.

Winsor and Clarke (1940) concluded that estimates of the size of copepod and chaetognath populations given by a conical sampler having a mouth opening of 12.5 cm (all samplers such as this one are subsequently referred to in the text in the form: 12.5-cm conical sampler) were comparable to those given by a conical sampler with a mouth opening of 75 cm (i.e. a 75-cm conical sampler). Such estimates are open to question because the field trials not only were carried out at a geographical location rather than in a single parcel of water, but the area (Georges Bank) is one of strong circulation. Thus errors may have been introduced by patchiness.

Sheard (1941) towed a 70-cm Discovery sampler (Kemp and Hardy, 1929) at speeds ranging from 2 to 6 knots (kt) i.e. 1 to 3 m/sec. As the speed of towing was increased, the size of the catch also increased. At 6 kt fish up to 7.5 cm in length were caught. Fish were not caught at 2 kt. Sheard attributed the increase in catch and the changes in the composition of the samples collected at the higher speeds of towing to decreased biological escapement.

Aron (1962) compares the catching power of an Isaacs-Kidd midwater trawl having a 3 ft (.9m) mouth opening and a Clarke-Bumpus sampler (Clarke and Bumpus, 1950) with a 12.5 cm mouth opening with respect to euphausiids. He states that, in thousands of samples collected with Clarke-Bumpus Samplers from the North Pacific, euphausiids were very rare, while nearly all samples collected with the Isaacs-Kidd midwater trawl from the same area were dominated by euphausiids.

Hansen and Anderson (1962) compared the catch collected by a 50-cm conical sampler and by a 38-cm Hensen sampler (Jenkins, 1901) with the catch obtained with a 8-litre water bottle. Efficiencies were calculated with respect to total zooplankton present. The catch of the 8-litre water bottle was taken as 100%. On this basis the efficiency of the Hensen sampler was 65%; that of the 50-cm conical sampler only 18%.

Regan (1963) investigated the suitability of the Clarke-Bumpus Sampler as an instrument for collecting euphausiids. Regan's data show a tendency toward increased catches at higher speeds of towing. The increase in catch at

the higher speeds becomes greater for life history stages of increased age and size and is greatest for adults. Regan's data also show that the average increase in catch was greater by day than by night. This suggests that vision may be important in the detection of samplers by euphausiids.

Barnes and Tranter (1965) conducted a series of trials in order to compare the abilities (i.e. the "catching power") of the Australian version of the Clarke-Bumpus Sampler (Tranter, 1966), the Indian Ocean Standard Sampler (Currie, 1962), and the Tropical Juday Sampler (Juday, 1916) to collect organisms. Statistical comparison between replicate samples failed to show any difference which could be ascribed to biological escapement.

Fleminger and Clutter (1965) conducted a study designed to furnish information about biological escapement. They sampled two captive zooplankton populations with three conical samplers of similar design, having mouth areas in the ratio 1:2:4. These samplers were towed in a tank on a specially built runway at constant speed. The effects of two levels of population density and light intensity were evaluated. In all comparisons involving two samplers the smaller caught relatively fewer animals than the larger. In the denser populations this trend was accentuated. The ratios of the catch of the smaller to the larger sampler for copepods were not affected by light intensity. The same ratios for the catches of mysids, which possess compound eyes, were increased at higher light intensities; the disparity between catches

for samplers of varying size was greater in the light than in the dark. From these results the authors postulated the existence of a zone around the periphery of the mouth of the sampler from which the animals could escape and that this zone was broader in the light for those animals which detected the sampler by visual means. In the present study this concept is enlarged upon to treat the width of a peripheral zone of escape as a function of the speed of towing.

Le Brasseur and McAllister (1966)\* studied the effects of the size of the sampler, the speed of hauling, and light intensity on the catches of a wide range of zooplanktonic species. They interpreted their results as showing that increasing the area of the mouth of the sampler increased the estimates of population density. Increasing the speed of hauling also increased the estimates of population density for some species, but not for others. The increased catch ascribed to increased speed was most pronounced for euphausiids. Dark-coloured samplers gave considerably larger estimates of the size of the euphausiid population than light coloured samplers. Estimates of the size of the euphausiid population were larger by night than by day for all samplers. Only the catches of euphausiids were affected by the colour of the sampler and by changes in light intensity. The authors concluded that these results demonstrated the effects of biological escapement, and that

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\* Unpublished manuscript, courtesy of R. Le Brasseur, Pacific Oceanographic group, Nanaimo, B. C., Canada.

for euphausiids biological escapement was mediated visually.

Recent investigations (Smith, pers. comm.)\* have established that one-metre conical samplers, which are accepting 95% of the water presented to them, are preceded by acceleration fronts extending up to one and one-half metres in front of the mouth of the sampler. Laboratory studies have shown (Smith, pers. comm.) that of copepods tested, stage V Calanus helgolandicus are capable of speeds in excess of 67 cm/sec for distances up to 7 cm, and Labidocera trispinosa and L. acutifrons of speeds of 70 and 80 cm/sec respectively for distances up to 15 cm. The large copepod Euchirella galatea can swim at a rate of 100 cm/sec for up to one and one-half metres. The stimulus which evoked these responses was the injection of 0.1 ml of sea water at a velocity of 7.5 cm/sec into the sea water medium 5 cm distant from the animal. Smith has also said that the acceleration fronts preceding a plankton sampler would probably be greater than the acceleration fronts produced by this relatively small jet of water.

In addition to the literature surveyed above, concerned with biological escapement of zooplanktonic species, there exists a large body of literature dealing with the errors introduced into the estimates of the size of larval fish populations by the effects of biological escapement (Silliman, 1943; Ahlstrom, 1954; Bridger, 1957; Colton, 1958; Aron, 1962;

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\*Dr. P. Smith, Bureau of Commercial Fisheries, La Jolla, Calif.

Isaacs, 1965; and Percy, 1965). In all of these reports the authors conclude that biological escapement is a serious problem in obtaining a representative sample from populations of larval fish.

Thus, the evidence for the existence of biological escapement is strong. However, none of the investigations reported in the literature gives any proper indication of the magnitude of the errors introduced by biological escapement, other than the suspicion that these errors may be large.

It is clear, therefore, that the planktologist is in the difficult position of knowing that data derived from collections may be in error, but of not knowing how large these errors may be. The possibility exists, also, that collections made with different samplers may not be subject to the same errors.

These several considerations, namely the effects of biological escapement of the size and species composition of a sample, have led to the development of a mathematical model which describes biological escapement in such terms that the model can be fitted to data derived from collections made in the field to give an estimate of the catching power of a plankton sampler. Evidence is presented which indicates that the model is capable of giving a good estimate of the catching power of a plankton sampler provided that certain assumptions are valid.

## THE MODEL:

Barkeley (1964) has proposed a mathematical model (Fig. 1) which will yield the minimum speed that an animal must attain to completely escape from a plankton sampler under specified conditions. These conditions include the radius of the mouth of the sampler, the speed at which the sampler is moving, and the distance at which the animals can detect the sampler. The detection distance would be difficult to determine and is unknown for any zooplanktonic organism. In addition, Barkeley's model, although it analyzes the problem of biological escapement in general terms, namely the situation where all the organisms escape from the sampler, it is incapable of dealing with the situation where a fraction of a zooplanktonic population escapes. In sum, his model indicates those steps which must be taken to minimise the effects of biological escapement, but it cannot be fitted to data derived from collections made in the field, with any sort of plankton sampler, to give information about the performance of the sampler.

The model which follows is formulated in terms of the same four quantities considered by Barkeley's model. However, the following model can be fitted to field data to provide an estimate of the ability of a plankton sampler to capture any zooplanktonic species. In this model the plankton sampler is regarded as filtering some constant proportion of the water presented to it over the range of speeds for which the model

is to apply. Implicit in this assumption is the further assumption that the model is to apply only in the absence of clogging of the meshes of the filter.

The kinematic basis of the model is shown in Fig. 3. The radius of the mouth of the sampler is  $r_0$ . The speed of towing is  $S_0$ . The distance at which the animals, i.e. the population of any species or life history stage of any species, can detect the presence of the sampler by any means and respond to it is shown as the plane,  $x$ , perpendicular to the longitudinal axis of the sampler. The distance to the plane,  $x$ , from the mouth of the sampler is assumed to remain constant as the speed of towing increases. This is reasonable in view of the fact that the sampler filters the same amount of water per unit distance over the range of speeds to be used. Possibly a more realistic representation of the surface of response,  $x$ , is shown by the dashed curve. The basis of this curve is the result of a wind tunnel study of flow through plankton samplers carried out at the SCOR - ICES-UNESCO symposium on Zooplankton Sampling Methods held in Australia in 1965 (Bary, pers. comm.). The study showed that the pressure gradients preceding the mouth of the sampler approximate to this form. The representation of the surface of response shown by the broken curve is to apply only when the animals detect the sampler, by means of the acceleration fronts preceding it.

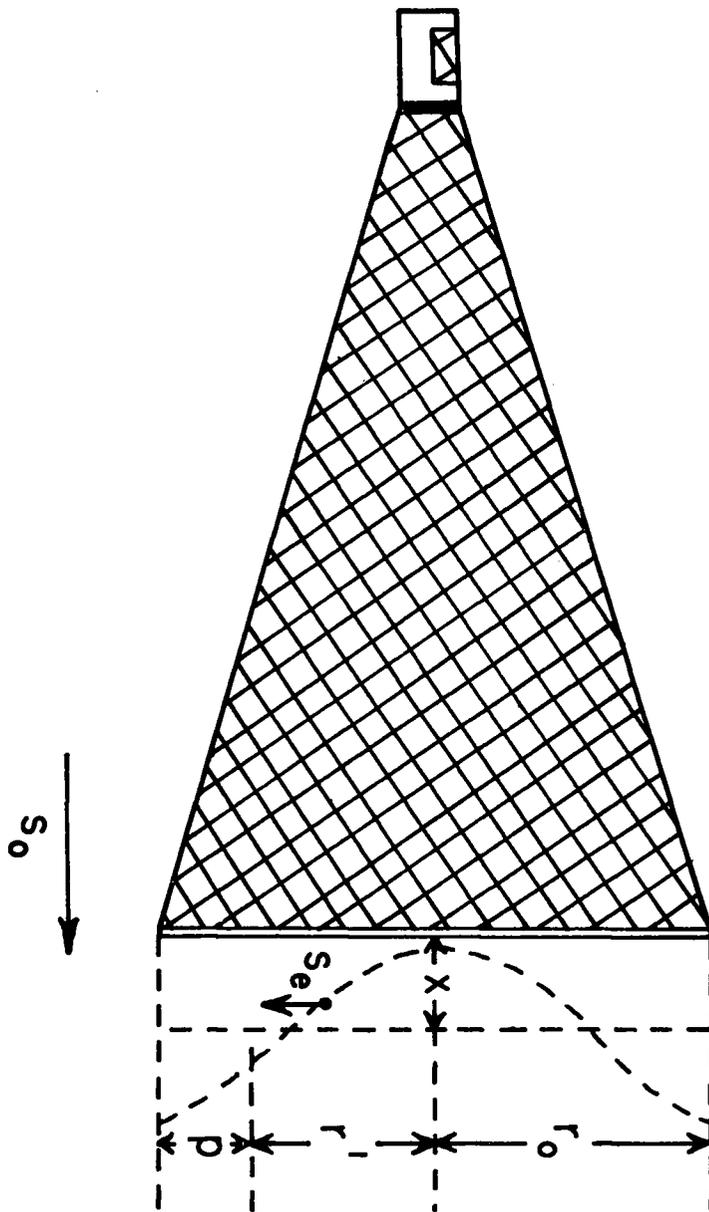
Treatment of the surface of response as a plane is not an important departure from reality because there will be some

plane,  $x$ , in which it will appear that all the animals have reacted. This is true because the model deals with the reactions of a population of animals presented to the sampler, and not with the reactions of any one animal. For the same reason the animals' speed of escape,  $S_e$ , does not represent the highest speed that any individual animal can attain. Instead  $S_e$  represents the mean of all the components of all the animals' speeds perpendicular to the longitudinal axis of the sampler. The width of the zone around the periphery of the mouth of the sampler from which animals can escape is  $p^1$ , the radius of the area from which animals cannot escape is  $r^1$ .

If it is assumed that at any one time the individuals of a species are randomly distributed across the mouth of the sampler, although not necessarily throughout the water column, then the proportion of animals caught can be expressed as the ratio of the area of the zone from which animals cannot escape to the area of the mouth of the sampler. This ratio multiplied by 100 can be referred to as percentage catch ( $p$  below).

The width of the zone from which animals can escape is the product of the speed that the animals can attain perpendicular to the longitudinal axis of the sampler,  $S_e$ , and the time that the animals have in which to move before the sampler overtakes them,  $x/S_o$ . This width is a function of the speed of towing. The area from which the animals cannot escape,  $A_1$ , can be expressed as  $\pi$  times the square of the difference between the radius of the mouth of the sampler and

Figure 3 (facing) The kinematic basis of the model.



$s_0$  — speed of towing

$s_e$  — mean speed of escape

$r_0$  — radius of net

$x$  — mean distance at which net can be detected

broken line curve — more realistic representation of  $x$

$r'$  — radius of zone from which escape is impossible ( $r_0 - p$ )

$p$  — peripheral zone of escape (before net can overtake)

the width of the zone from which animals can escape.

$$A_1 = \pi (r_o - X S_e / S_o)^2 \quad \underline{1}$$

Equation 1 when divided by the total area of the mouth of the sampler,  $A_2$ , and multiplied by 100 yields equation 2 which expressed percentage catch, P.

$$p = \left( \frac{\pi (r_o - X S_e / S_o)^2}{\pi r_o^2} \right) \times 100 \quad \underline{2}$$

Equation 2 can be rearranged to yield:

$$p = (1 - X S_e / r_o S_o)^2 \times 100 \quad \underline{3}$$

which is the working equation for percentage catch.

If  $S_o$  is the only variable in this equation, 3, it is possible to solve for percentage catch when two or more samples taken at different speeds are available.

Substituting a quantity, Q, for  $X S_e / r_o S_o$  in equation 3 the basic equation becomes:

$$p = (1 - Q)^2 \quad \underline{4}$$

If the number of animals actually caught is represented by B then it is true that there exists some factor, z, which is equal to P/B. The factor, z, can be obtained provided that  $S_o$  is the only variable. If this is true, then:

$$(zB)^{1/2} = 1 - Q = P \quad \underline{5}$$

from which it follows that:

$$1 - (zB)^{1/2} = Q \quad \underline{6}$$

Bearing in mind since  $Q = xS_e/r_o S_o$ , then:

$$S_o = x S_e / r_o \quad \underline{7}$$

which is an identity. If  $S_o$  is the only variable in equation 7 then the quantity  $QS_o$  is constant. Therefore, from equation 6 the expression  $S_o(1 - (zB)^{1/2})$  is also constant and when two or more values of  $S_o$  and  $B$  are available the resulting equation of the form:

$$S_{o1} - S_{o1}(zB_1)^{1/2} = S_{o2} - S_{o2}(zB_2)^{1/2} \quad \underline{8}$$

can be solved for  $z$ . Once  $z$  has been obtained  $P$  is calculated from equation 9.

$$P = zB \quad \underline{9}$$

When values of  $P$  have been calculated, equation 3 can be expanded and solved for  $X S_e$  (i.e. see eqn. 10).

$$(X S_e / R_o S_o)^2 - 2(X S_e / R_o S_o) + 1 - p = 0 \quad \underline{10}$$

The values of  $X S$  which are calculated from equation 10 are substituted back into equation 3, from which a plot of percentage catch against speed of hauling is generated.

This method of fitting the model to field data is recursive. The only absolute check on the validity of the assumptions made in the formulation of the model is internal. This internal check is given by the values of the proportionality constant,  $z$ . If the assumptions made in the formulation of the model are not valid,  $z$  can be expected to vary in some systematic manner. If the assumptions are valid  $z$  will be constant.

## MATERIALS AND METHODS:

The field trials undertaken in the course of this study were designed to yield two sorts of information. The primary task was to assess the ability of the mathematical model to describe the processes of biological escapement. The secondary task was to determine, by means of the model, the magnitude of the errors attributable to biological escapement which are introduced into estimates of population size and species composition in samples collected by various plankton sampling devices.

Every effort was made in the design of the field trials to ensure that the only variable factor was the speed at which each sampler was to be hauled through the water. It was essential that the speed of hauling be accurately known, that the volume of water filtered did not change from haul to haul, and that the same community of zooplankton was sampled by each haul. These requirements are best met by vertical hauling of the sampler in a particular body of water at one position or location. The distance that the sampler moves through the water as well as the time taken can be accurately measured. Errors introduced by the failure to sample the same zooplanktonic community with each haul because of the tendency of zooplankton to form layerlike or lenslike aggregations (Bary, 1966) and to perform diel migrations are reduced by vertical hauling. However such precautions will be of no avail if it is not possible to sample from the same parcel of water in the course

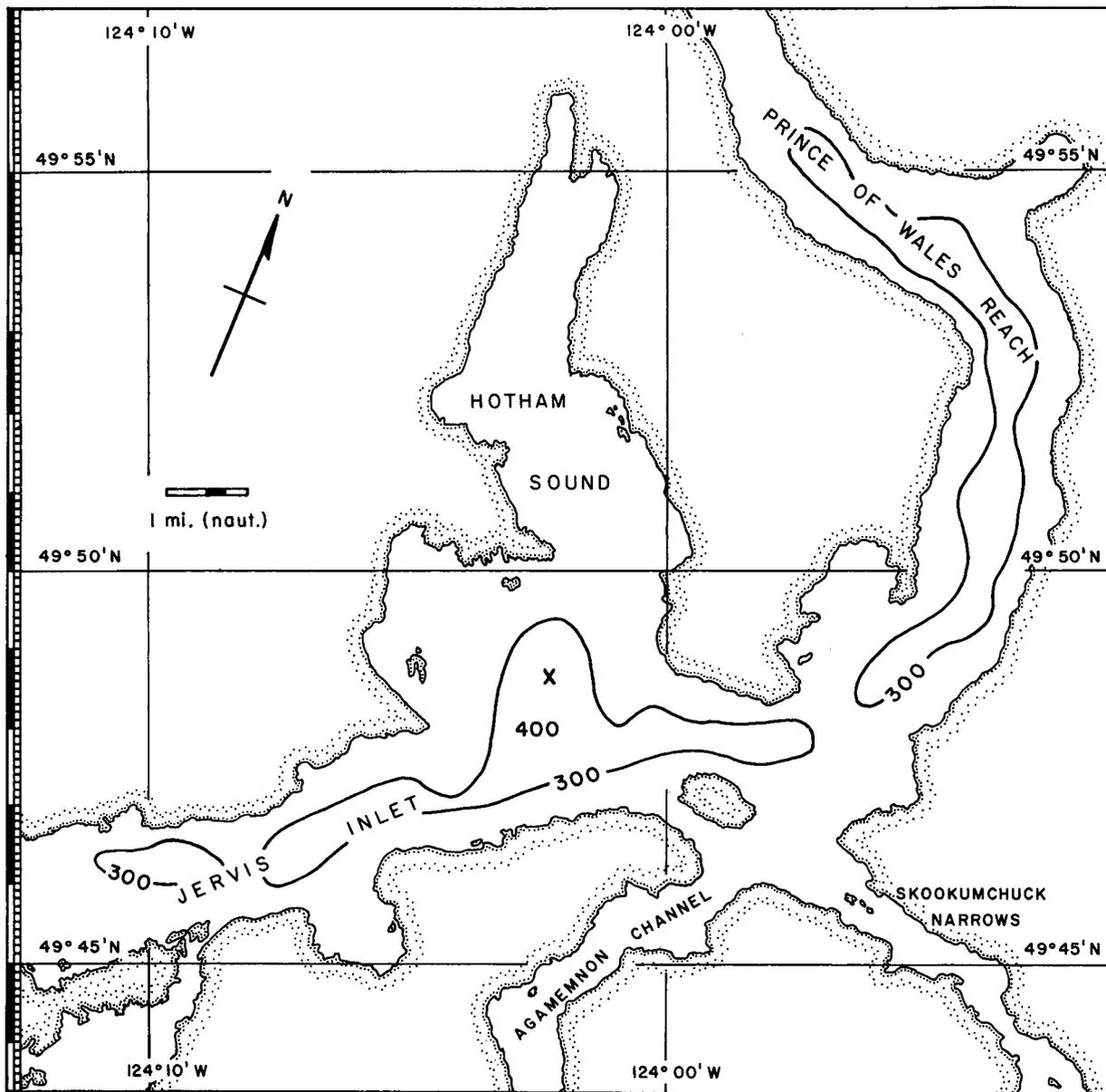
of field operations and to keep the wire from straying from the vertical.

An ideal location for field trials would be a deep, isolated basin in a protected location in which water movements, and therefore movements of planktonic organisms, would be minimal. In B. C. coastal waters an area which, on present knowledge, is most likely to fulfil the above requirements is that portion of Jervis Inlet, British Columbia, Canada, lying between  $49^{\circ}45'$  N. latitude and  $49^{\circ}50'$  N. latitude and between  $124^{\circ}00'$  W. longitude and  $124^{\circ}06'$  W, longitude (Fig. 4). In this area is a deep basin with a maximum depth of 732 m (400fm).

#### Field Procedure:

During the trials every effort was made to sample from the same parcel of water each day. The ship was brought on station each morning and allowed to drift with the tide. If the ship was blown by wind more than one-quarter mile from the station position it was moved back on station. Positions were taken every hour. It was seldom necessary to move the ship more than two or three times each day. However, strong winds were experienced only once during the course of the field trials and, for the most part, the weather was calm. In these conditions the ship was allowed to drift with the tidal currents. Movement back and forth across the designated station position resulted, to a total distance of about one-half mile. It is believed that by this procedure the collections of organisms were likely to have been from the same parcel of

Figure 4 (facing) The location of the field trials of August, 1965 and January, 1966. Site of sampling is indicated by an X.



water during any one day. It could only be assumed, because the tidal currents were demonstrably weak during any one day, that from day to day in the course of the field trials the water body did not change appreciably. The subsequent analysis of the results suggest that this assumption was reasonable.

The design of the field trials was the same for each sampler. The sampler was hauled vertically from 400 or 500 m, at one of three speeds, namely, 0.30 m/sec (0.50 m/sec for Catcher), 1.0 m/sec, or 2.0 m/sec. Eight replicate hauls were made at each speed. It was possible to complete only one half of each series with any one sampler in one day. Therefore each series is a composite of tows made on two days. The order in which the speeds of hauling occurred was randomized each day to avoid systematic errors. The depth to which the sampler descended was determined by paying out the wire over a metering sheave and checking that the meter returned to zero when the sampler had been retrieved. The total time required for each haul was recorded with a stop watch. Any haul for which the assigned speed was not reached within the first 50 m, or which stopped before reaching the surface, was repeated.

When the sampler reached the surface its filter (net) was carefully washed down using a high-pressure jet of seawater from a hose. The sample was preserved in 5% neutralized formalin. The number of revolutions made by the impeller of the flow meter was recorded. Then the process was repeated.

The first set of field trials was carried out in August, 1965. A second series was undertaken in January, 1966,

in which the same procedures were followed except that only three replicate hauls were made at each speed.

#### The Plankton Samplers:

Five plankton samplers were used during the field trials. These were selected as being representative of three widely used classes of plankton samplers, namely, the conical sampler, the conical sampler modified by the addition of an impervious cylindrical portion anterior to the filter, and the encased high-speed sampler.

The simplest of these is the original design of conical sampler (Fig. 5a) which consists of a circular ring supporting a conical filter which terminates in a bucket in which the sample collects. The conical sampler used in this study has a mouth diameter of 100 cm, and is towed by three bridles extending 80 cm in front of the mouth. The filter is 305 cm in length. The mesh aperture approximates to 0.7 mm square. During the January, 1966, trials this conical sampler was modified by the addition of a cylindrical lead weight 15 cm in diameter and 30 cm in length, which was suspended at the apex of the bridles, 80 cm in front of the mouth of the sampler. In all tows with the one-metre conical sampler a flow meter was fitted in the centre of the mouth aperture.

The 70-cm N.I.O. sampler (Currie and Foxton, 1957) (Fig. 6a) is typical of a large class of plankton samplers.

These samplers are all basically the simple conical sampler modified by the addition of an impervious, cylindrical portion, ahead of the filter. They can be closed by "strangling" this cylindrical portion. This design originated with the Nansen sampler (Nansen, 1915). It was modified in the discovery samplers (Kemp and Hardy, 1929), in the Norpac sampler (Marumo, 1958) and again in the Indian Ocean Standard sampler (Currie, 1963).

The N.I.O. sampler used in the field trials has a mouth diameter of 70 cm. A canvas cylinder 122 cm in length is attached to a sheet metal drum 30.5 cm in length which, in turn, precedes and is attached to the filter. The filter has an anterior cylindrical portion 100 cm in length followed by a conical portion 150 cm in length, which terminates in a collecting bucket. In the present study a flow meter was mounted within the mouth of the canvas cylinder. The aperture of the meshes approximates to 200 micra square. The filter in the sampler used in the field trials was new. During the January, 1966, trials this sampler was used without the canvas cylinder (Fig. 6b). The results obtained with the standard sampler in its original form in January, 1966, were the same as those obtained in August, 1965, and are not reported.

The Catcher (Bary et al., 1958) is typical of a fairly new class, the encased, high-speed plankton samplers. Other samplers of this type include the Gulf I (Arnold, 1959), the Gulf III (Gheringer, 1952), the Gulf V (Arnold, 1959), and the Jet Net (Clarke, 1964). The Hardy Plankton Recorder

(Hardy, 1936) is towed at high speeds, but is in all other respects dissimilar to the above-mentioned samplers. Remarks made below probably do not apply to the Hardy Plankton Recorder. In the construction of all of these samplers an outer, rigid casing encloses the filtering surface, which is usually conical. A consistent feature of these samplers is that the mouth opening is less in diameter than the casing. A result of this feature is to reduce the speed of flow of the water after it has entered the mouth and, as a consequence, lessens the damage done to the zooplankton when they contact the filter. Because of the reduced diameter of the mouth, encased samplers usually have a larger total area of mesh aperture than conventional conical samplers. Most, but not all, of the encased samplers are provided with flow meters in the rear part for metering the flow after it has passed through the filter. Finally, the construction of the high-speed samplers is much more robust than is usually in uncased samplers. However, the primary raison d'etre of the high-speed samplers is that it has long been thought that, if the speed at which the sampler is towed is increased, zooplanktonic organisms of a wider range of sizes and swimming ability will have less chance to avoid the sampler. Thus the sample collected is believed to be more representative of the community of zooplankton present.

The Catcher (Fig. 7a) consists of a cylindrical fibre-glass housing 215 cm (84 in.) in length and 30 cm (12 in.) in diameter. This housing can be disassembled into two main

parts. The forward portion, or 'body', contains the filter (Fig. 7b). The after portion contains the flow meter and bears stabilizing fins attached at right angles to its outer surface. The diameter of the mouth opening is 22.5 cm (9 in.). The model of the Catcher used in this study differs from that described by Bary et al. (1958) in that the opening-closing mechanism is in the form of a metal disc which is rotated to open and close the mouth opening, and that the tail of the sampler is of equal diameter to the body, rather than reduced to 22.5 cm (9 in.).

#### Laboratory Methods:

In the laboratory the organisms in the samples were sorted into four groups. Each of these groups consists of organisms of similar size which were present in numbers large enough for an accurate analysis. They are representative of the medium- to large-sized zooplankton. The first group consisted of copepods of the genus Calanus. This group was the most numerous; over 90% of the specimens were stage V C. plumchrus with a few specimens of adult Calanus spp.. These specimens range from 4 to 5 mm in length. The second group was composed of specimens of the copepod Eucalanus bungii var. bungii most of which were stage III or stage IV copepodites ranging from 3 to 5 mm in length. The third group was composed of specimens of the copepod Euchaeta japonica, most of which were adult, ranging from 5 to 6 mm in length. This species is much more robust than C. plumchrus or



Figure 5a. The 1-metre conical sampler rigged as it was used during the field trials of August, 1965.

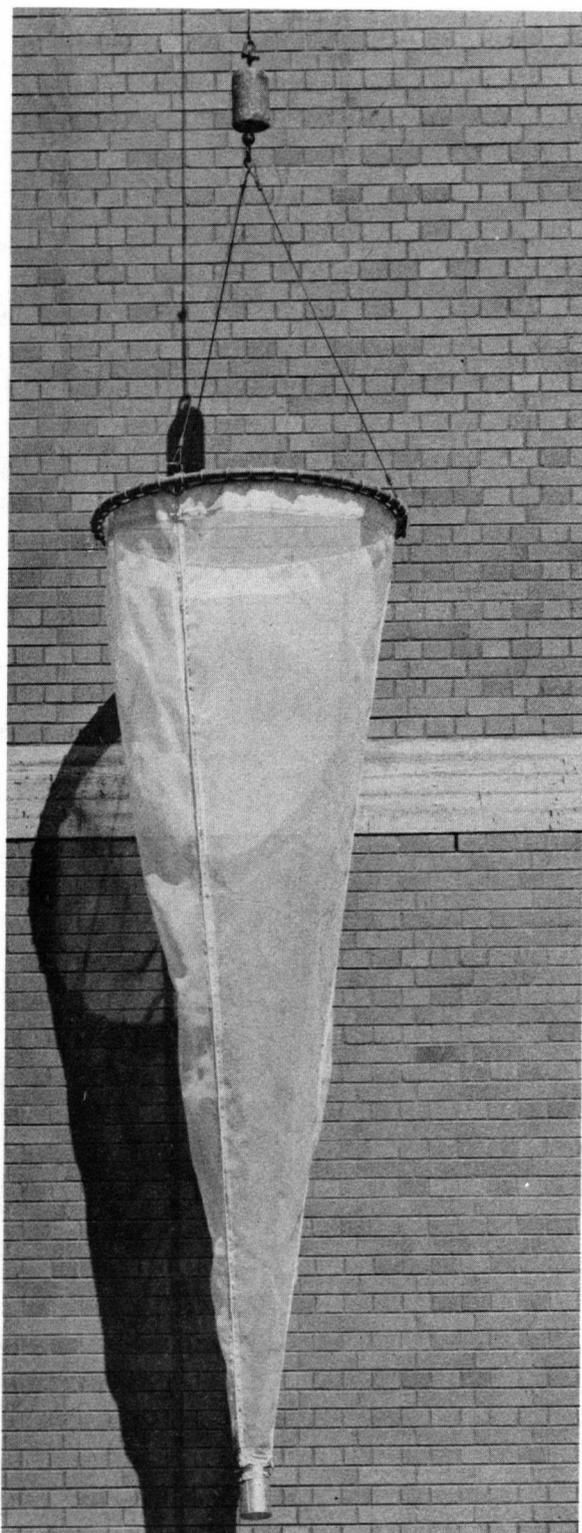


Figure 5b. The 1-metre conical sampler modified by the attachment of a weight to its bridles. The sampler was used as illustrated in the field trials of January, 1966.

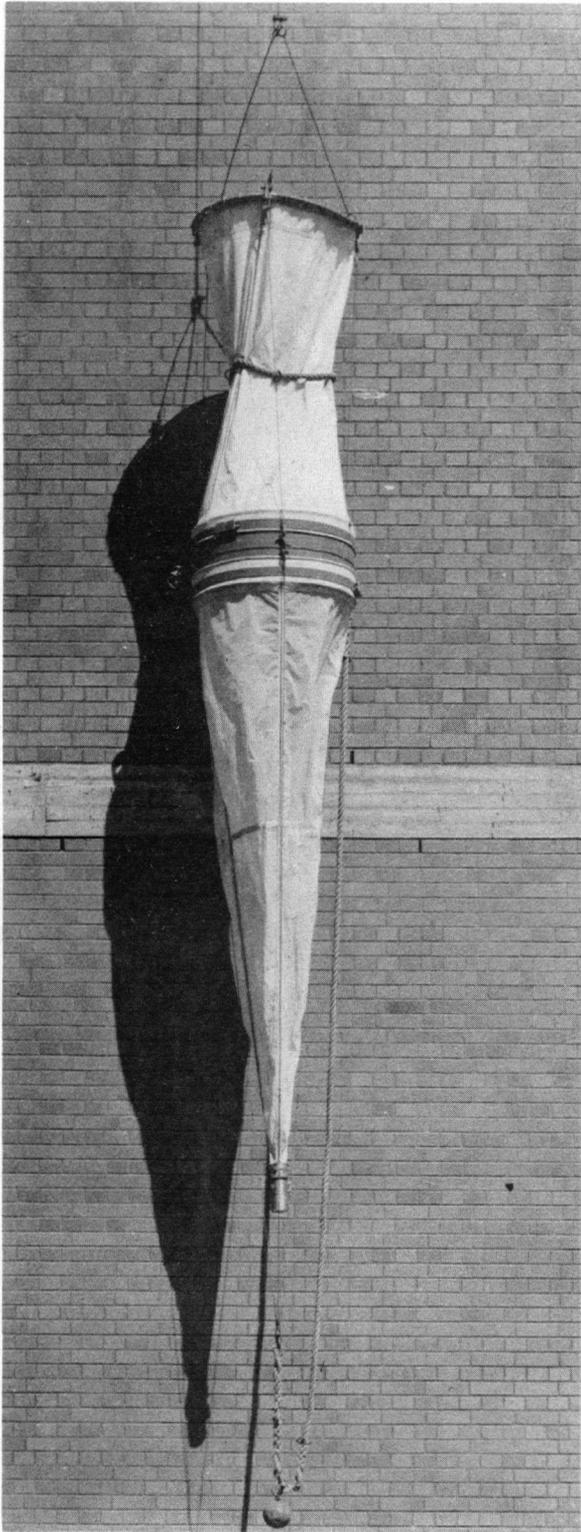


Figure 6a. The 70-cm N.I.O. sampler as it was used in the field trials of August, 1965.

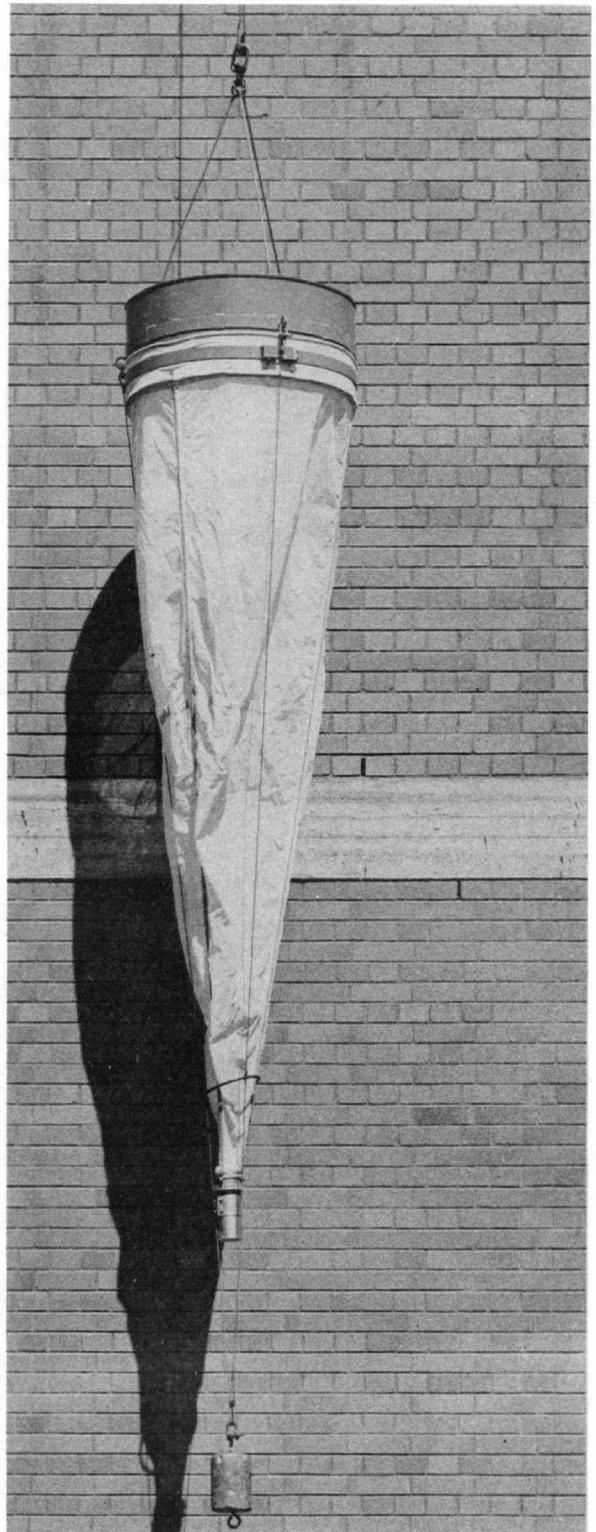


Figure 6b. The 70-cm N.I.O. sampler modified by the removal of the canvas cylinder. The sampler was used as illustrated in the field trials of January, 1966.

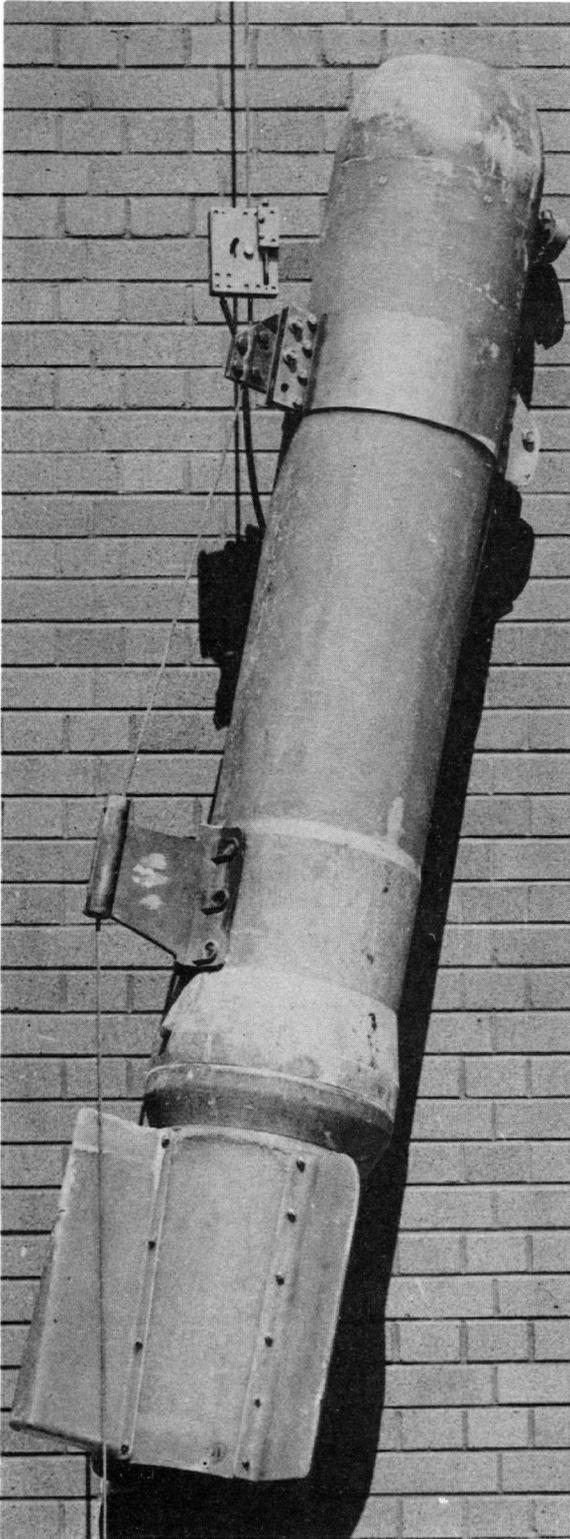


Figure 7a. The Catcher as it was rigged during the trials of August, 1965

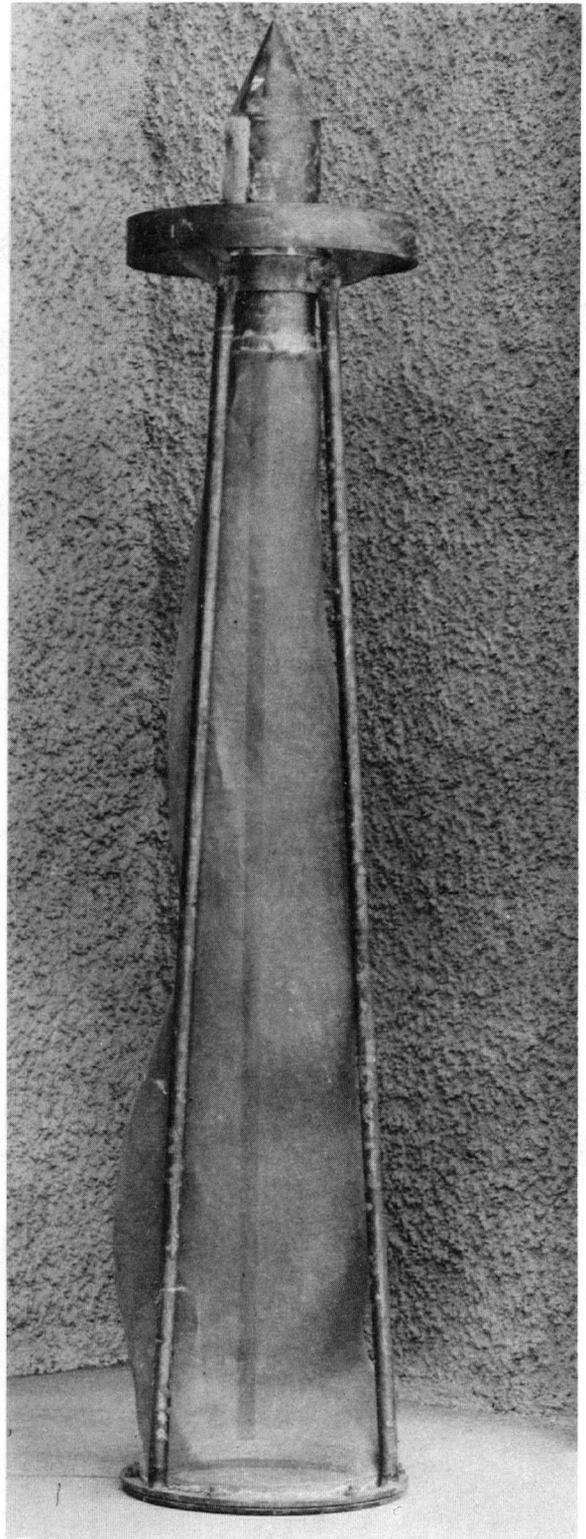


Figure 7b. The filter used in the Catcher

E. bungii. The last group included adolescent and adult specimens of the Euphausacea. Most specimens were adult Euphausia pacifica, ranging from 10 to 20 mm in length.

Every specimen of Euchaeta japonica and every euphausiid contained in the sample was counted, but the numbers of Calanus spp. and Eucalanus bungii were very large and it was necessary to sub-sample and estimate the totals for these.

The subsampling technique was that of Brodskii and Baskakov (1951) (see Appendix 1). In this method the sample is spread evenly over the bottom of a large glass dish and the total number of specimens lying over a known fraction of the total area of the bottom of the dish is counted. The fraction of the bottom of the dish is varied in order that the number of specimens lying in this area is about 100. To this count is added one-half of the number of specimens in any way bisected at the boundaries of the area. This sum is multiplied by the reciprocal of the fraction of the total area to estimate the total number of specimens contained in the dish.

In practice the specimens in at least three different areas were counted from each sample. The mean count was used to calculate the total number of specimens. If these three counts did not agree within 10%, three more counts were made and the results of all six counts meaned. In the majority of samples three counts were sufficient.

The specimens of Eucalanus bungii were too small to be retained quantitatively by the one-metre conical sampler. Therefore only Calanus spp., Euchaeta japonica, and

euphausiids were counted in the collections made with this sampler.

#### Mathematical Procedure:

The data obtained from the collections made during the field trials were subjected to one-way analysis of variance (Steele and Torrie, 1960) to determine whether differences noted between catches made at different speeds were to be considered as real.

The number of specimens collected in each tow was converted to the percentage of the predicted population of each species which it represented by the procedure outlined in the section on the model (pp. 15 to 24). Equation 10 was solved for each of the 24 pairs of values of percentage catch and speed of hauling to yield 24 values of  $X S_e$ . All values of  $X S_e$  for each configuration of sampler and each species were meaned and a fitted curve of percentage catch plotted against speed of hauling was generated from equation 3. Finally, an estimate of the population of each species present in the column of water sampled by each sampler was obtained. This was done by multiplying the number of individuals of that species captured in each sampler by the reciprocal of the percentage of the total which this catch was calculated to represent. A mean estimated population size for each species was computed from the data obtained with each sampler.

A program was written in the Fortran IV language for an I.B.M. 7040 computer which performed all the above calculations.

## RESULTS:

Summaries of data derived from the investigations in the field are presented in Tables 2 to 7. The raw data are reported in terms of mean speeds of hauling ("speed classes"), and mean catches of zooplankton, by species or group, for each speed class. The values reported for the field trials of August, 1965, are means of eight hauls at each speed; the values for the field trials of January, 1966 values are means of three hauls at each speed.

The data have been subjected to one-way analysis of variance (Steel and Torrie, 1960) with speed classes considered as treatments. The calculated values of F, i.e. treatment mean square/error mean square, is reported together with the expected value of F for significance at the 95% level. Although the results of analysis of variance indicate that in some instances the differences between mean catches at different speeds are significant and that in other instances the differences between mean catches at different speeds are not significant, the mean catch increases with increased speed of towing for every sampler, except the 70-cm N.I.O. sampler in both configurations.

Figure 8a shows the results obtained by applying the model to data from collections made with the one-metre conical sampler. The smooth curves of percentage catch plotted against speed of hauling were generated by substituting successively larger values of  $S_0$  in equation 2 (p. 23). No points representing percentage catch as calculated from field data appear on

this plot. The degree of agreement between values of percentage catch given by the fitted curve for the corresponding speed of hauling is shown in Fig. 8b. The two general trends shown by these plots are that the larger animals (euphausiids) are best able to avoid the sampler, and that the selectivity of the sampler is much reduced at the higher speeds of hauling.

The two constants peculiar to each species appear in the table of constants associated with Fig. 8b. The constant,  $X S_e$ , required to generate the fitted curves, is a measure of the ability of a species to escape from the sampler. The value of  $X S_e$  is independent of the size of the population of a species sampled by a sampler. This is not true of the values of  $z$ , the proportionality constant. Values of  $z$  are given because of the check on the validity of the model which they afford. The degree of variation in the values of  $z$  is indicated by the size of the 95% confidence limits upon the mean value of  $z$ . These confidence limits are shown both as absolute values and as percentages of the mean values of  $z$ . It is apparent that the confidence limits, while quite small, increase in size as the number of specimens of a species caught per haul decreases.

Figure 9a shows the results obtained by application of the model to data from field collections made with the one-metre conical sampler in which the flow of water into the mouth was disturbed by the addition of a body (weight) preceding the mouth (Fig. 5b). The products  $X S_e$  for each group are much larger than those obtained with the unmodified sampler (Fig. 8b). These differences indicate that an obvious effect

results from the presence of the body preceding the mouth of the sampler, i.e. the presence of the body allows the animals to detect the sampler at a greater distance than when it is not present.

It is clear (Fig. 9b) that one or more of the assumptions made in the formulation of the model does not hold for euphausiids. Two manifestations of this are that not only is the confidence interval about the mean value of  $z$  large, but that the fit of the points representing field data to the fitted curve is poor.

The results obtained with the 70-cm N.I.O. sampler (Fig. 6a) are shown in Fig. 10. There is little doubt that the assumptions made in the formulation of the model are not valid for this sampler. Therefore no calculations have been performed. Flow meter counts show a slight decrease in the amount of water passing through the sampler, per unit distance towed, with increasing speed. This decrease in the amount of water filtered per haul would not appear great enough to account for the reduction which occurs in the catch. A possible alternative explanation is that for some reason the distance at which zooplanktonic organisms can detect the sampler increases as the speed of hauling increases.

The results shown in Figure 11a were obtained with the 70-cm N.I.O. sampler, modified by the removal of the canvas collar (Fig. 6b). The most important result is the apparent reversal of the trend toward decreased catch at higher speeds of hauling that occurred when the collar was present (Fig. 10).

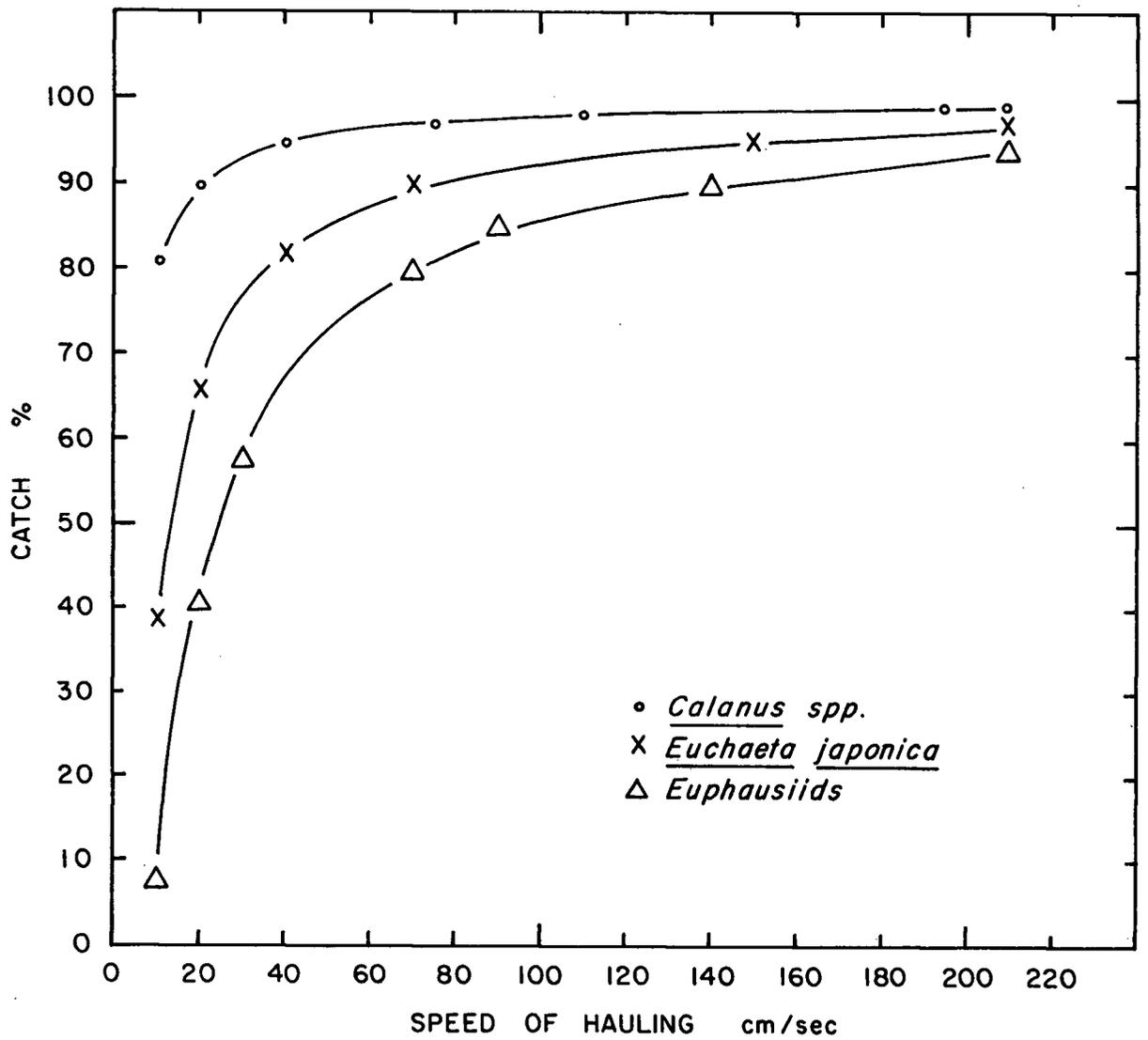
The curves are similar to those obtained with the one-metre conical sampler (Fig. 8a).

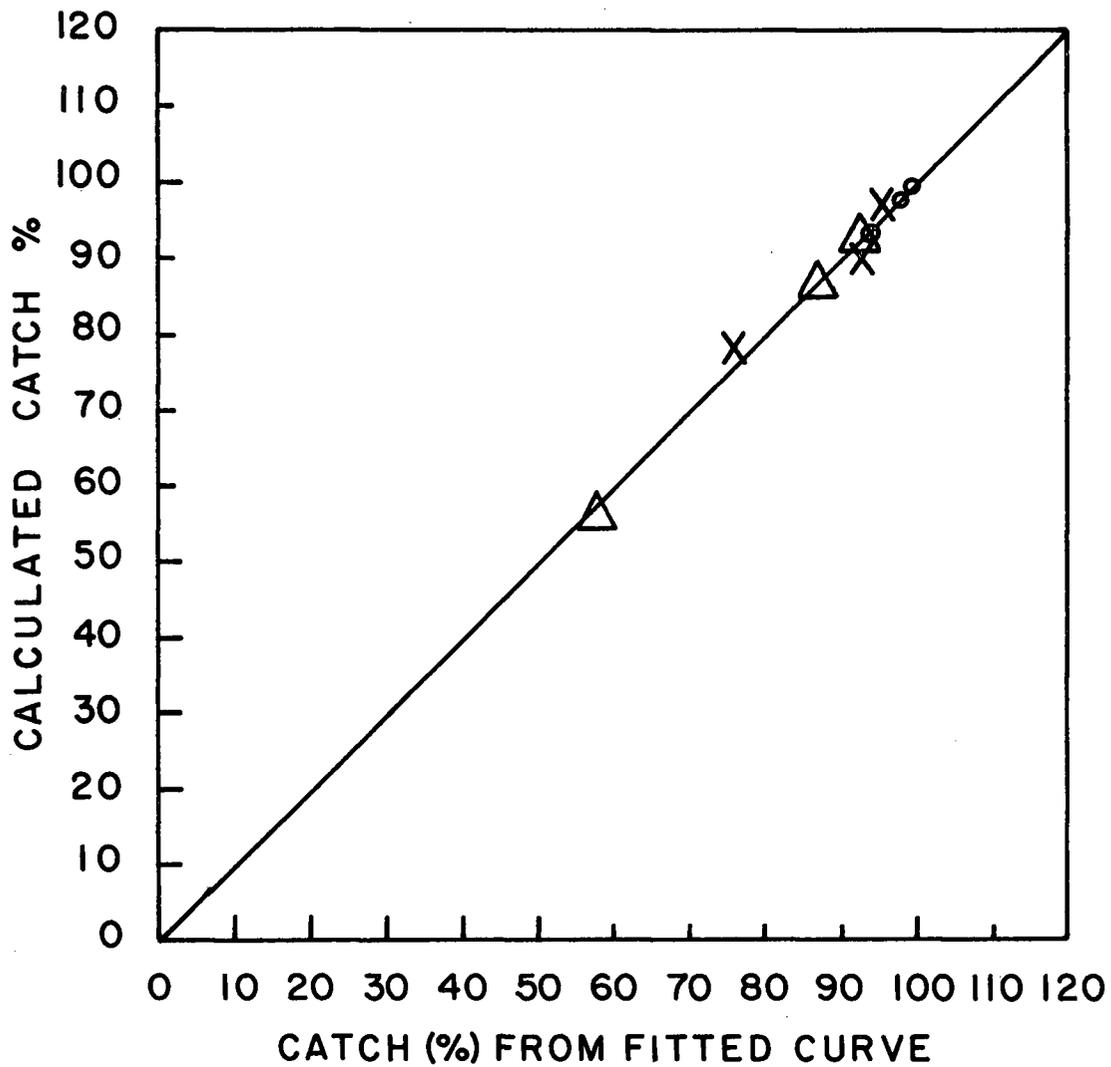
Figure 12a shows the results obtained by application of the model to field data collected with the Catcher. It should be noted that the curves of percentage catch plotted against speed of hauling for Calanus spp. and Eucalanus bungii bungii are superimposed. There is considerable scatter in those points representing percentage catch calculated from the field data (Fig. 12b). This scatter has a consistent pattern. The points representing the high- and low-speed hauls lie above the line of perfect fit, while the points representing the hauls made at intermediate speeds lie below the line of perfect fit.

Figure 13 shows the results obtained by application of the model to unpublished data collected by the Pacific Oceanographic Group, Nanaimo, B. C.\* The data were collected using two similar plankton samplers. One of the plankton samplers was white; the other was dark green. Collections were made with the white sampler under conditions of both daylight and darkness. The results reported herein are for adult euphausiids. They seem to indicate that the visibility of the sampler is an important factor in determining its catching power with respect to euphausiids.

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\*Data courtesy R. LeBrasseur, Pacific Oceanographic Group, Nanaimo, British Columbia, Canada.





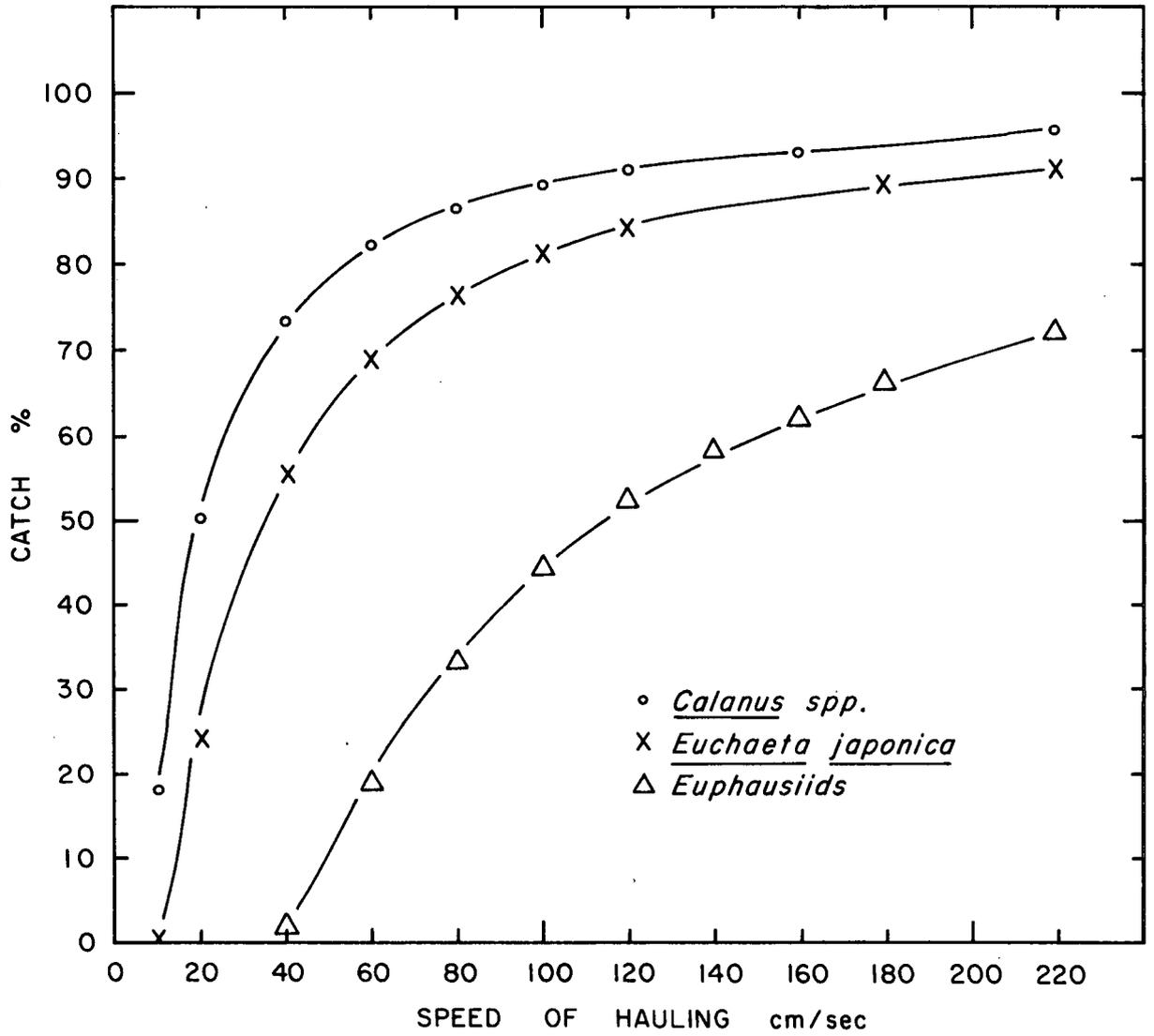
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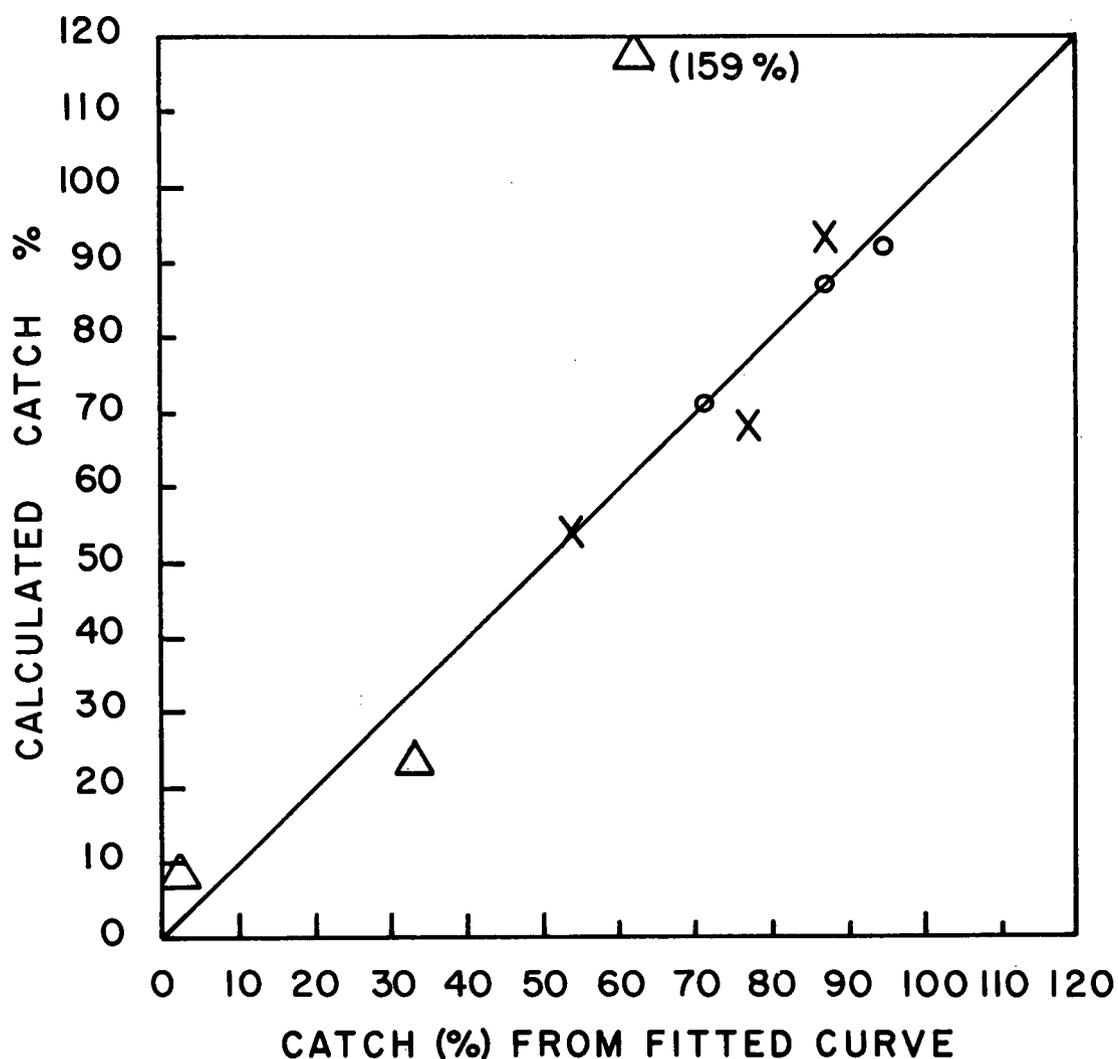
Figure 8a (facing) Percentage catch plotted against speed of hauling for the one-metre conical sampler.

Figure 8b (above) Goodness-of-fit diagram for the results obtained with the one-metre conical sampler. Key is the same as Fig. 8a.

Table of Constants

Species (group)	$X S$ $e$	$z$	95% confidence limits	
<u>Calanus</u> spp.	49.66	0.00011	$\pm .000000017$	(0.15%)
<u>Euchaeta japonica</u>	188.76	0.011	$\pm .000016$	(1.4%)
euphausiids	361.48	0.25	$\pm .000016$	(0.66%)





9b

Figure 9a (facing) Percentage catch plotted against speed of hauling for the modified one-metre conical sampler.

Figure 9b (above) Goodness-of-fit diagram for the results obtained with the modified one-metre conical sampler. Key is the same as Fig. 8a.

Table of Constants

Species (group)	$X S$ $e$	$z$	95% confidence limits
<u>Calanus</u> spp.	290.33	0.000057	$\pm .000000043$ (.0.76%)
<u>Euchaeta japonica</u>	511.164	0.0051	$\pm .000035$ (6.9%)
euphausiids	1585.89	0.0046	$\pm .0018$ (38.8%)

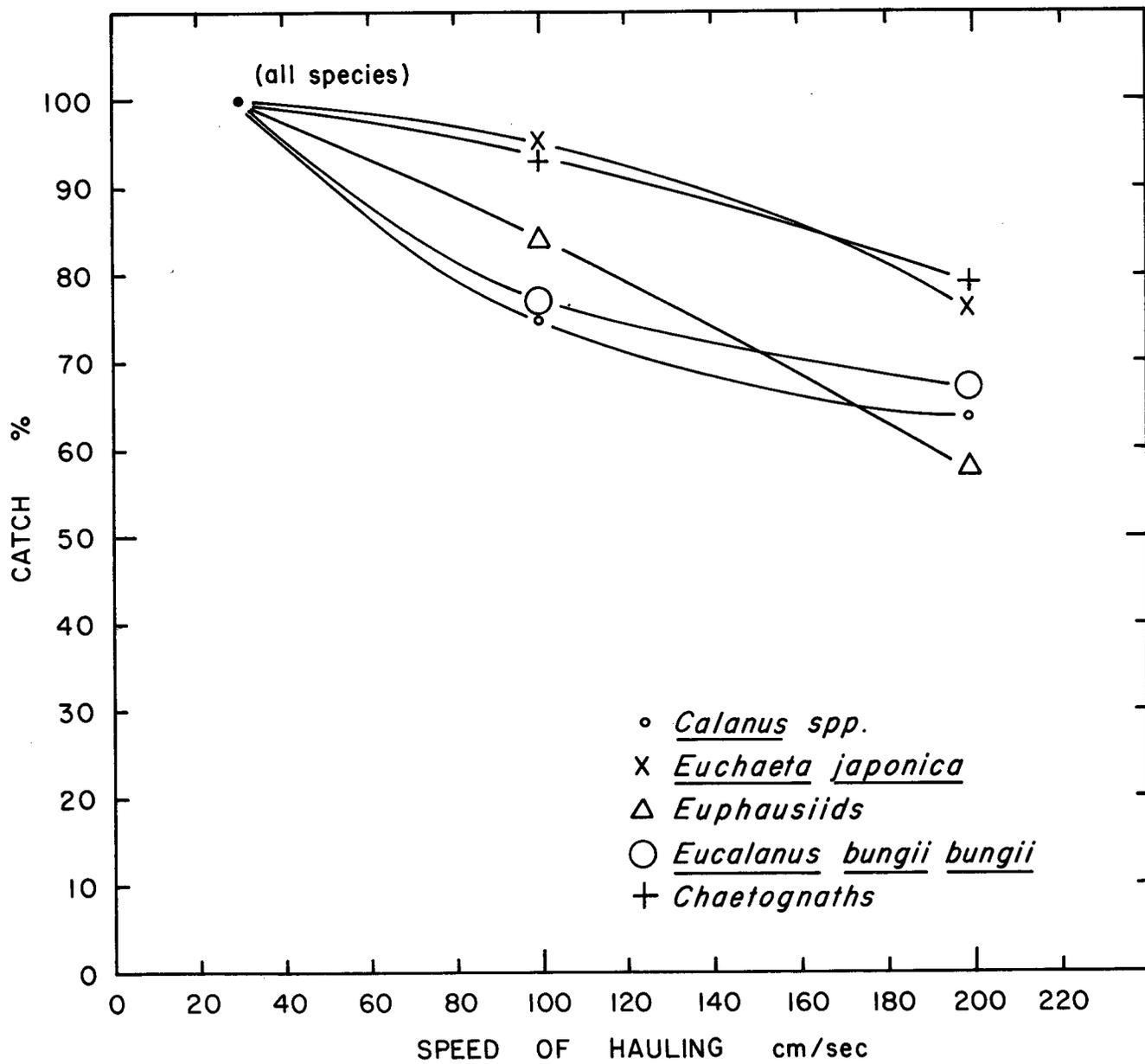
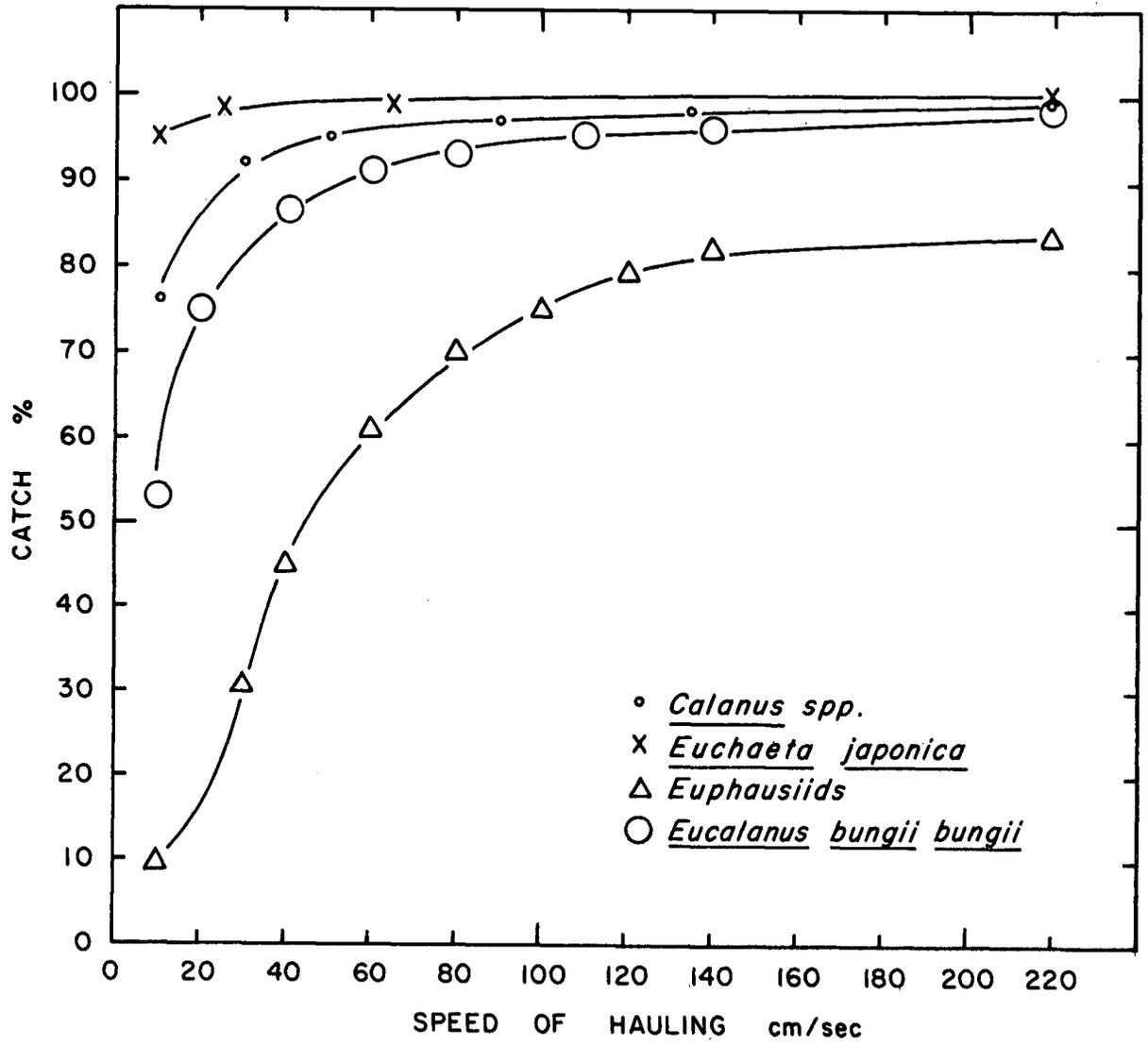
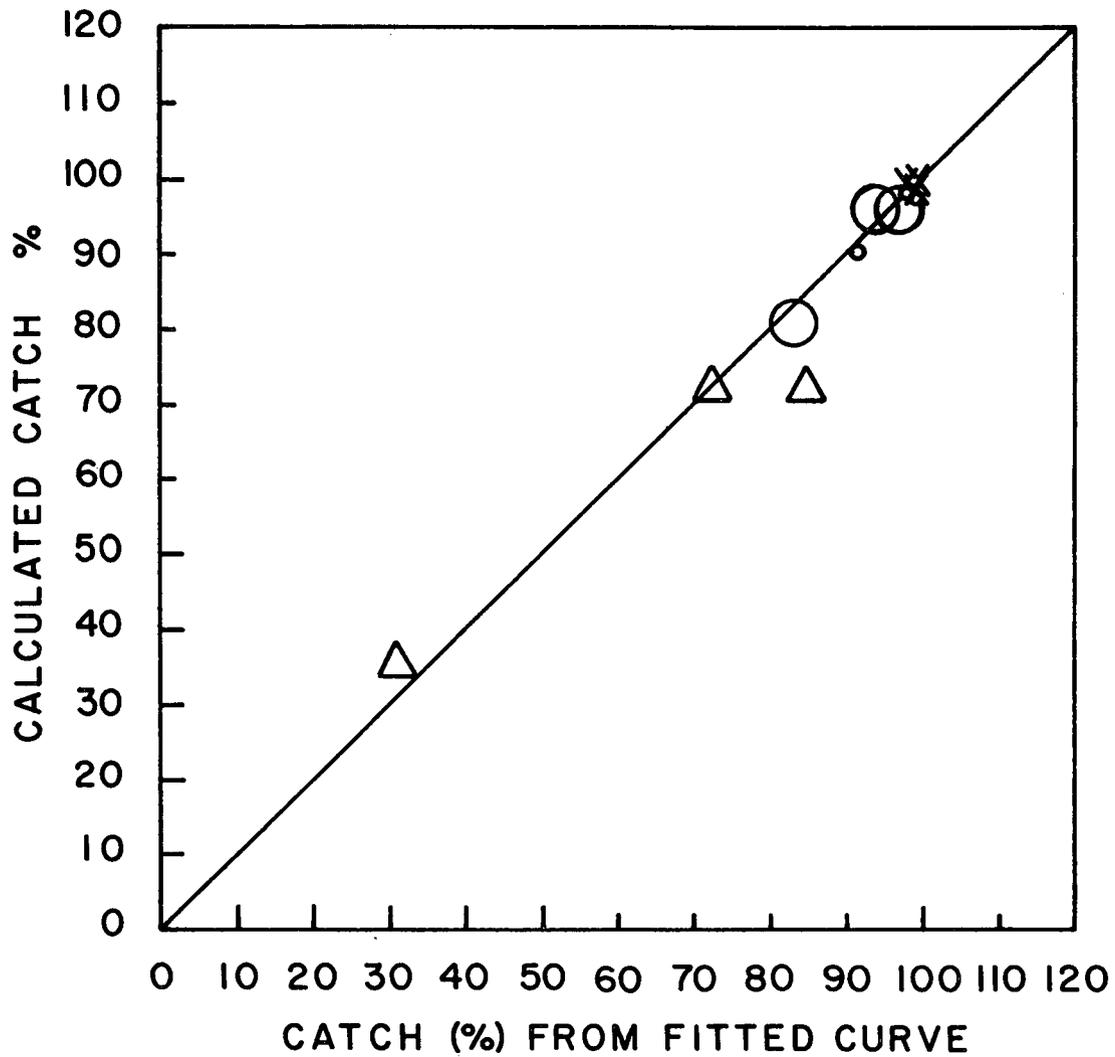


Figure 10 (facing) Results obtained with the N.I.O. 70-cm sampler. Percentage catch is plotted against speed of hauling. Percentage catch has been calculated on the basis of the catch at 30 cm/sec as 100%.



11a



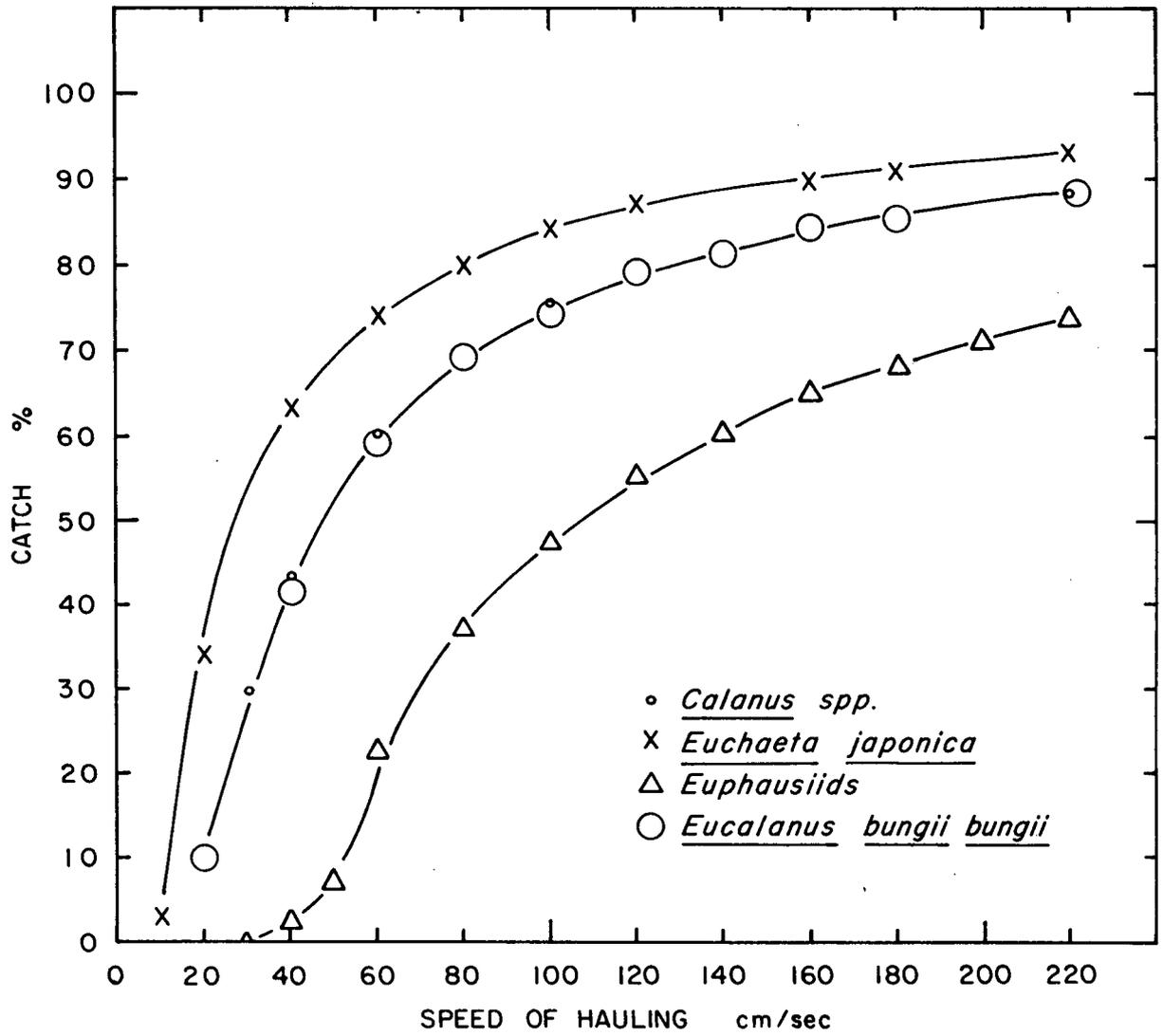
11b

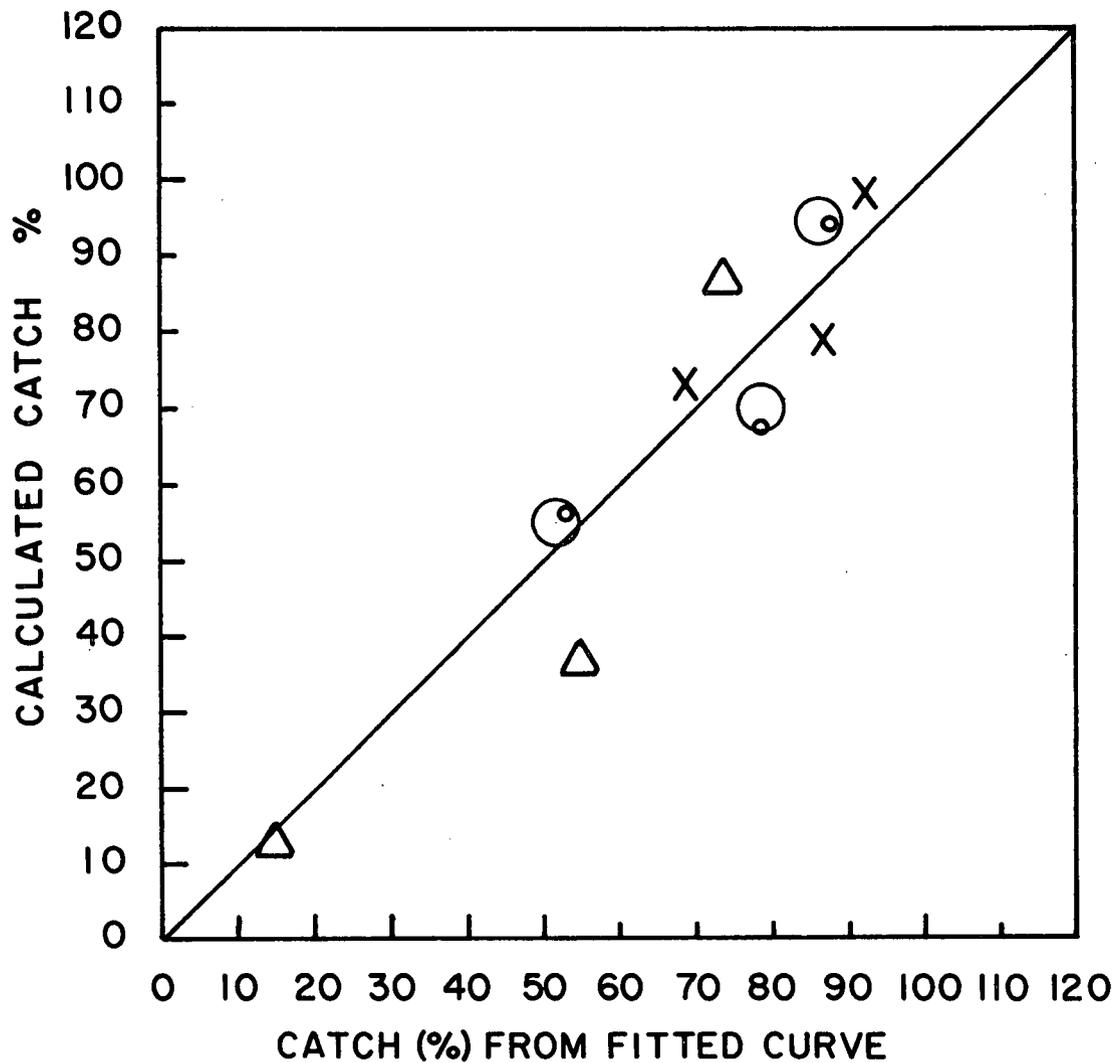
Figure 11a (facing) Percentage catch plotted against speed of hauling for the modified 70-cm N.I.O. sampler.

Figure 11b (above) Goodness-of-fit diagram for the results obtained with the modified 70-cm N.I.O. sampler.

Table of Constants

Species (group)	$\bar{X} S_e$	$z$	95% confidence limits
<u>Calanus</u> spp.	44.34	0.00019	$\pm .00000012$ (0.62%)
<u>Eucalanus</u> b. <u>bungii</u>	95.79	0.00051	$\pm .00000069$ (0.13%)
<u>Euchaeta</u> <u>japonica</u>	8.7234	0.017	$\pm .0000025$ (0.14%)
euphausiids	461.35	0.12	$\pm .028$ (23%)





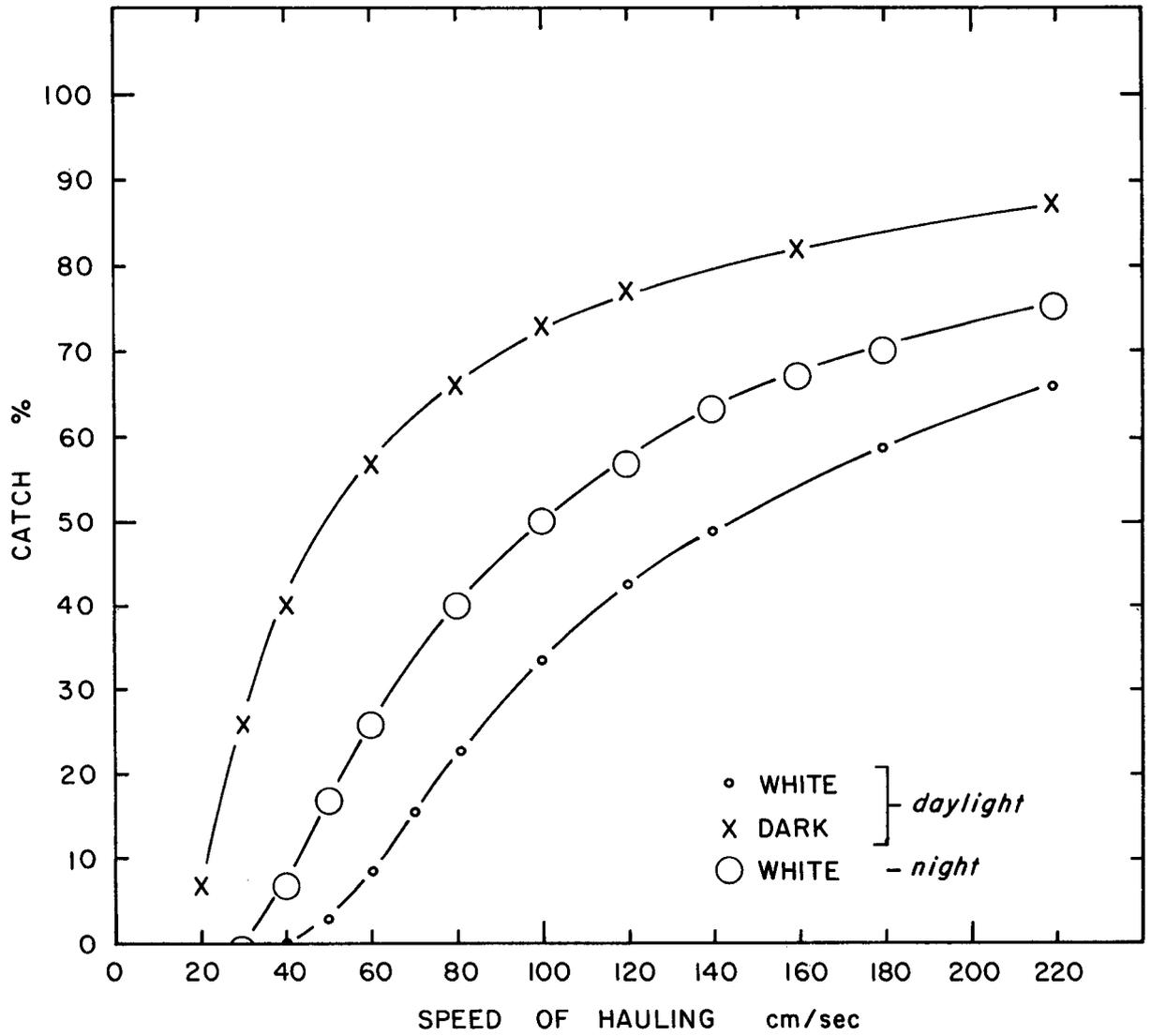
12 b

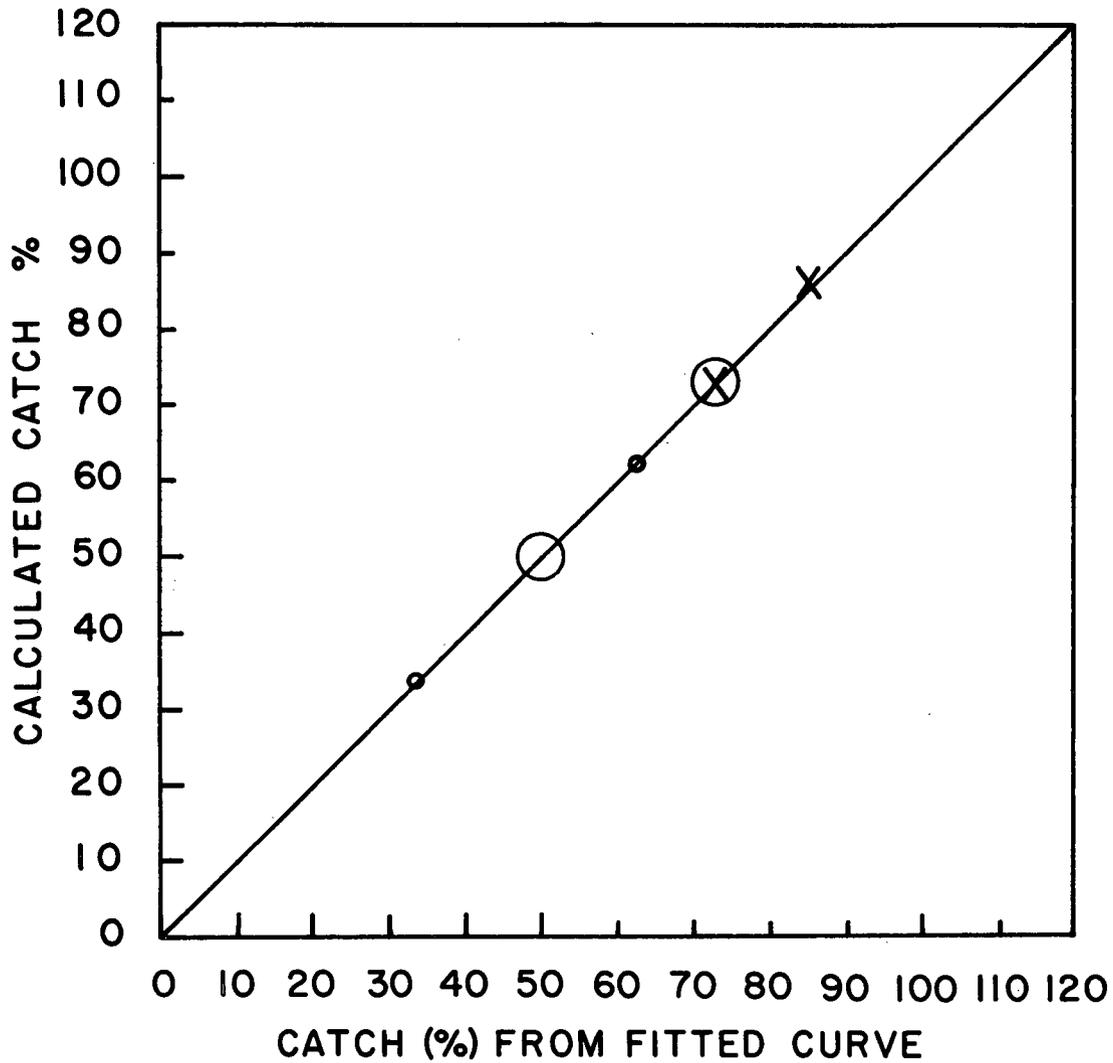
Figure 12a (facing) Percentage catch plotted against speed of hauling for the Catcher.

Figure 12b (above) Goodness of fit diagram for the results obtained with the Catcher. Key is the same as Fig. 12a.

Table of Constants

Species (group)	$\bar{X} S_e$	$z$	95% confidence limits
<u>Calanus spp.</u>	155.94	0.0014	$\pm .000012$ (0.9%)
<u>Eucalanus b. bungii</u>	157.612	0.0054	$\pm .000042$ (7.7%)
<u>Euchaeta Japonica</u>	95.716	0.13	$\pm .00094$ (0.68%)
Euphausiids	358.17	0.98	$\pm .17$ (17%)





13 b

Figure 13a (facing) Percentage catch plotted against speed of hauling for the P.O.G. samplers. All results are for euphausiids.

Figure 13b (above) Goodness-of-fit diagram for the results obtained with the P.O.G. samplers. Because only two speed classes were used all points lie on the line of perfect fit.

Values of  $X S$  for the P.O.G. samplers

e

White sampler-daylight	1189.0
White sampler-dark	831.0
Dark Green sampler-daylight	421.0

Values of  $z$  with confidence limits are not given because only mean catches for each speed class were given.

Table 2  
 Results of Field Trials: August, 1965  
 One-metre Conical Sampler

Speeds of Hauling (cm/sec)	29.39	101.50	206.02
<u>Calanus spp.</u>			
Mean Catch: Specimens/haul	7841	8258	8312
Calculated F = 0.5091	Tabled*	F <sub>.05</sub> = 2.57	(2,21 df)
<u>Euchaeta japonica</u>			
Mean Catch: Specimens/haul	68	78	84
Calculated F = 0.8096	Tabled	F <sub>.05</sub> = 2.57	(2,21 df)
<u>Euphausiids</u>			
Mean Catch: Specimens/haul	22	33	37
Calculated F = 2.8017	Tabled	F <sub>.05</sub> = 2.57	(2,21 df)

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\* Since these are one-tailed F tests, tabled F<sub>.10</sub> is used throughout.

Table 3  
 Results of Field Trials: January, 1966  
 Modified One-metre Conical Sampler

Speeds of Hauling (cm/sec)	37.49	81.48	158.30
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Calanus spp.

Mean Catch: Specimens/haul	12,331	15,170	16,058
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Calculated F = 1.2474	Tabled F <sub>.05</sub> = 3.46 (2,6 df)
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Euchaeta japonica

Mean Catch: Specimens/haul	104	131	177
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Calculated F = 4.1681	Tabled F <sub>.05</sub> = 3.46 (2,6 df)
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Euphausiids

Mean Catch: Specimens/haul	20	52	342
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Calculated F = 30.2068	Tabled F <sub>.05</sub> = 3.46 (2,6 df)
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Table 4

Results of Field Trials: August, 1965

70-cm N.I.O. Sampler

Speeds of Hauling (cm/sec)	30.00	108.0	207.0
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Calanus spp.

Mean Catch: Specimens/haul	6175	4683	3655
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Calculated F = 29.3107	Tabled	$F_{.05} = 2.57$	(2,21 df)
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Eucalanus bungii bungii

Mean Catch: Specimens/haul	1060	834	710
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Calculated F = 15.562	Tabled	$F_{.05} = 2.57$	(2,21 df)
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Euchaeta japonica

Mean Catch: Specimens/haul	40	38	31
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Calculated F = 3.881	Tabled	$F_{.05} = 2.57$	(2,21 df)
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Euphausiids

Mean Catch: Specimens/haul	10	8	5
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Calculated F = 3.58	Tabled	$F_{.05} = 2.57$	(2,21 df)
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Table 5

Results of Field Trials: January, 1966

Modified 70-cm N.I.O. Sampler

Speeds of Hauling (cm/sec)	31.45	92.00	178.53
<u>Calanus spp.</u>			
Mean Catch: Specimens/haul	4715	5081	5025
Calculated F = 0.4770	Tabled $F_{.05} = 3.46$ (2,6 df)		
<u>Eucalanus bungii bungii</u>			
Mean Catch: Specimens/haul	1581	1871	1835
Calculated F = 4.2874	Tabled $F_{.05} = 3.46$ (2,6 df)		
<u>Euchaeta japonica</u>			
Mean Catch: Specimens/haul	54	56	57
Calculated F = 0.074	Tabled $F_{.05} = 3.46$ (2,6 df)		
<u>Euphausiids</u>			
Mean Catch: Specimens/haul	3	8	8
Calculated F = 4.5714	Tabled $F_{.05} = 3.46$ (2,6 df)		

Table 6

## Results of Field Trials: August, 1965

## Catcher

Speeds of Hauling (cm/sec)	50.04	120.36	221.41
<u>Calanus spp.</u>			
Mean Catch: Specimens/haul	391	475	660
Calculated F = 31.893	Tabled $F_{.05} = 2.57$ (2,21 df)		
<u>Eucalanus bungii bungii</u>			
Mean Catch: Specimens/haul	102	127	171
Calculated F = 16.631	Tabled $F_{.05} = 2.57$ (2,21 df)		
<u>Euchaeta japonica</u>			
Mean Catch: Specimens/haul	5.25	5.725	7.00
No F value calculated			
<u>Euphausiids</u>			
Mean Catch: Specimens/haul	.125	.375	.875
No F value calculated			

Table 7

P.O.G. Unpublished Results Obtained in August, 1965\*

Speeds of Hauling (cm/sec)	100	200
White Sampler (daylight)		
Mean Catch: Specimens/haul	1203	2219
White Sampler (dark)		
Mean Catch: Specimens/haul	1971	2867
Dark Green Sampler (daylight)		
Mean Catch: Specimens/haul	2765	3265

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\* All results are for catches of Euphausiids.

## DISCUSSION:

If biological escapement is an important factor in determining the number of zooplanktonic organisms caught by a plankton sampler, then the number caught could be expected to increase as the speed of towing increases because less will escape. The results show, with one exception, that the number of specimens of any species caught did increase as the speed of hauling increased. The question of primary importance is whether these increased catches result from decreased biological escapement. Because of the randomized order in which the hauls were made, the depth from which they were taken, and the continued sampling at one location, it is unlikely that any cyclical phenomena such as diel migrations of the organisms or the effects of the ebb and flow of populations in association with tidal currents could have produced the consistently increased catches at the higher speeds of hauling.

Likewise it is difficult to see how any inhomogeneity in the distribution of the zooplanktonic organisms could selectively increase the catch at the higher speeds of hauling. The null hypothesis that the mean catch did not increase with increased speed of hauling was tested in the statistical analysis of the results. The tests were set up so as to reject the null hypothesis if the probability of its validity was less than 5%. Of the 16 instances analyzed the null hypothesis was rejected in 11 instances and accepted in 5. However, in

the five instances where the null hypothesis had to be accepted the mean catch increased as the speed of hauling increased. Because it is improbable that the action of random chance would cause the mean catch to increase consistently with increased speed of hauling, it may be that the null hypothesis had to be accepted because the increase in catch was small compared to the variation inherent in the field technique.

Another relevant possibility is that the samplers filtered more water at higher speeds of hauling. This is unlikely in view of the results obtained by Bary et al. (1958), Tranter and Heron (1965), and Gilfillan and Pease (in prep) where similar quantities of water were filtered, per unit distance, over a wider range of speeds than was used in the present study. Nor are the increases in catch at high speeds proportionally the same for all animals, with each sampler, as would be expected if the increases were a result of a larger volume of water passing through the sampler at the higher speeds. Therefore it may be assumed that the increased catches at higher speeds of hauling result from more organisms being captured per unit volume of water filtered, i.e. from a decrease in biological escapement at the higher speeds of hauling.

If, as the previous discussion indicates, the increased catches can be assumed to result from decreased biological escapement, the ability of the model to describe the mechanism of biological escapement can be assessed. Three sources of information are available as a check on the validity of the model.

The most powerful of these checks is found in the values of the proportionality factor,  $z$ . A value of  $z$  is calculated for each comparison between two catches of the same species made at different speeds. If the assumptions made in the formulation of the model are valid, these values will be constant for any given sampler and species as long as the size of the population sampled does not change. The values of  $z$  obtained from the data collected in the course of this study, with two exceptions, are nearly constant. This is shown by the relatively small 95% confidence intervals around the mean values of  $z$  (Tables associated with Figs. 8b, 9b, 11b, 12b). There is a persistent trend toward larger confidence limits on the mean values of  $z$  as the number of specimens of a particular species in the sample decreases. Because this occurs in every instance it almost certainly results from the fact that, in the formulation of the model, the assumptions are statistical. That is, the model deals with the escape reactions of a large population of zooplanktonic organisms; it is incapable of dealing with the escape reactions of a single organism. As the number of specimens of a species decreases below approximately 10 to 50, the ability of the model to predict their escape reactions is reduced. This effect shows most clearly in the instance of the Catcher where the total number of euphausiids caught over 24 tows was only 11 individuals. Here the confidence limits on the mean value of  $z$  for euphausiids are large. For the one-metre conical sampler modified by the presence of the weight the numbers of

euphausiids caught were large enough for statistical accuracy, but the values of  $z$  are not constant. This implies that one or more of the assumptions made in the formulation of the model is not valid for these organisms, unlike the results obtained with the same sampler for copepods (Fig. 9a) which conform to those obtained with the unmodified sampler (Fig. 8a).

Estimates of the size of the populations, after removing the effects of biological escapement by means of the model, of the same species given by different samplers are another check on the validity of the model. This is provided that it can be assumed that the same population was sampled by the several samplers.

It is possible to make three comparisons of estimates of the sizes of the same populations of zooplanktonic organisms (Table 8). A comparison of the estimates of the sizes of the Calanus spp., Euchaeta japonica, and euphausiid populations given by the one-metre conical sampler and the Catcher as calculated from data collected in August, 1965 shows that for Calanus spp. the estimates differ by 20%, but that for E. japonica and euphausiids the estimates differ by 100%. However, because the latter two groups were represented by so few individuals in each sample collected by the Catcher, it is probable that only the estimate of the population size for Calanus spp. is valid.

The assumption that the same populations of zooplanktonic organisms were sampled by both samplers may not be strictly true, for the trials of August, 1965, spread over a

Table 8

Comparison of Population Estimates in Numbers/m<sup>3</sup> of  
Water Filtered.\*

August 1965

	1-Meter Conical Sampler	Catcher
<u>Calanus</u> spp.	53.48	42.58
<u>Euchaeta japonica</u>	.28	.42
euphausiids	.13	.062

January 1966

	Modified 1-m Sampler	Modified 70 cm N.I.O. Sampler
<u>Calanus</u> spp.	55.33	43.61
<u>Euchaeta japonica</u>	.61	.56
euphausiids	.68	.55

P.O.G. Data (results for euphausiids only)

White Sampler (daylight)	92.58
Dark Green Sampler (daylight)	99.45
White Sampler (dark)	102.68

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\*Samplers assumed to filter 100% of water presented to them.

two week period. But, because of the closeness of the estimates of the size of the Calanus spp. population, it is reasonable to assume that large changes did not occur in the sizes of the populations of other species. Even if the data from August, 1965 trials is questionable, other evidence is available from the trials of January, 1966, and from the data collected by P.O.G. for comparison. It is much less likely that there were any significant changes in the sizes of the zooplanktonic populations sampled during the two days required to complete the January, 1966 trials.

The results from the January, 1966 trials allow a comparison to be drawn between the estimates of the sizes of the Calanus spp., Euchaeta japonica, and euphausiid populations given by the modified one-metre conical sampler and the modified 70-cm N.I.O. sampler. For Calanus spp., the size of the population estimated from the collections made with the two samplers agree within 20%; for Euchaeta japonica agreement is within 10%; and for euphausiids within 20%.

A further comparison of the results of the P.O.G. trials using white and green samplers by day and by night is possible. Here the estimates of the size of the euphausiid population given by the three samplers of the same basic design agree within 10% after the effects of biological escapement have been removed by means of the model. The estimates of the size of euphausiid population given by the raw data collected at a speed of hauling of 100 cm/sec (the standard used) are in the ratio 1:1.67:2.1.

These comparisons appear to indicate that the results obtained by application of the model to data collected with different samplers are comparable. That is, if sampler A, which is calculated to be 25% efficient with respect to a given species at speed x, catches 25 specimens, and sampler B, which is calculated to be 50% efficient with respect to the same species at speed y, catches 50 specimens, the population of that species was 100 specimens per unit volume in both instances. That it is possible to make such estimates, even though they may be only approximate, is a great advantage when it is desired to compare the collections made with different samplers at different times and places.

A third source of evidence concerning the accuracy with which the model describes the processes of biological escape-ment lies in the agreement between the values of percentage catch calculated from the field data, and percentage catch taken from the fitted curve of percentage catch plotted against speed of hauling for equivalent speeds of hauling. Because the values of percentage catch calculated from the raw data are used to generate this curve the comparison can be expected to show only gross anomalies in the raw data. This is so because the points used to generate the curve will fall on it only if the assumptions made in the formulation of the model are justified.

The degree of agreement between points representing percentage catch, as calculated from raw data, and percentage catch shown the fitted curves is illustrated in Figs. 8b

to 13b. For the most part agreement is very good. The points calculated from the raw data for the Catcher fit the computed curve reasonably well, but with a consistent pattern in their dispersion. The points representing the catches at 50 cm/sec and 200 cm/sec are high and those representing the catches at 100 cm/sec are low. A possible explanation for this may be that the hydrodynamic characteristics of the Catcher change between 100 cm/sec and 200 cm/sec. It is believed that the Catcher accepts about 10% more water per unit distance at speeds of towing above about 200 cm/sec (4 kt) (Bary, pers. comm.). This increase in the amount of water filtered is thought to result from a venturi effect at the after end of the sampler at the higher speeds of towing.

Another example, in which there is a gross departure from the fitted curve, is that of the results obtained for euphausiids when towing with the one-metre conical sampler preceded by the weight. Here, a great increase in the number of euphausiids captured occurs in the collections made at 200 cm/sec over those made at 100 cm/sec. An increase in the amount of water filtered does not appear to be responsible because the catches of Calanus spp. and Euchaeta japonica show no such sudden increase. No satisfactory explanation appears possible other than assuming that for some reason, probably associated with the hydrodynamic characteristics of the weight, the euphausiids were either much less able to detect the sampler which does not seem reasonable, or that they were much less able to escape from

the sampler. All other samplers show good agreement between points calculated from the field data and the curves generated by the model.

The small confidence limits on the mean values of  $z$  and the closeness of the fit of the points calculated from field data to the fitted curve demonstrate the consistency of the description of biological escapement given by the model for any one sampler. The question of the absolute accuracy of the estimates of percentage catch is answered by the comparison of estimates of the size of the same population of zooplanktonic organisms given by different samplers. There is some evidence that samplers with smaller mouth openings tend to underestimate the size of the population of zooplanktonic organisms sampled (Table 7). This underestimation may result from the organisms avoiding a zone of turbulent water which develops when the long towing wire is drawn vertically through the water. For any one speed and length of wire this zone of turbulence would be the same diameter whichever sampler was being towed. Therefore, the flow into those samplers with smaller mouth openings would be relatively more affected than samplers with larger mouth openings. If organisms avoid the turbulent area, the result would be to underestimate the size of the population of zooplankton sampled. This effect would become greater as the area of the mouth of the sampler decreased. Because of the many unknown factors it is not possible to calculate the exact dimensions of this turbulent boundary layer. However, rough calculations

(LeBlond, pers. comm.)\* indicate that it could occupy as much as 30% of the area of the mouth of the 70-cm N.I.O. sampler. The area of the mouth of this sampler is approximately one-half that of the one-metre conical sampler, so the expected discrepancy in the estimates of the size of the same zooplanktonic population would be 15%. This is about the magnitude of the discrepancy that appears to exist between the estimates of the size of the same populations of various zooplanktonic species given by these two samplers.

Further analysis of Flemminger and Clutter's (1965) data (Clutter, pers. comm.) indicates that they may have been affected by a region devoid of zooplankton surrounding the towing wire. However, this in no way invalidates their original conclusions concerning the existence of a peripheral zone from which zooplankton escape.

The four quantities accounted for by the model may not be the only ones involved in the processes of biological escapement. However, the evidence indicates clearly that as long as the assumptions made in the formulation of the model are justified, these four quantities appear to be the ones of major importance in determining the catching power of any given plankton sampler.

Now that the results given by the application of the model data from field collections have been shown to be consistent not only for results obtained from any one sampler, but also among samplers, it is possible to discuss the results obtained with the individual samplers.

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### One-Metre Conical Sampler:

One of the noteworthy features of the results from the trials was the high efficiency of the one-metre conical sampler. It appears that the only estimate of the efficiency of a conical sampler is that of Hansen and Anderson (1962). These authors estimated the efficiency of a 50-cm conical sampler by comparing the catches it made with simultaneous catches made using an eight-litre water bottle. Thus their estimate of 18% efficiency for the 50-cm conical sampler is with respect to the total zooplankton present, inclusive of the smallest organisms. Therefore, their estimate includes organisms lost through the meshes of the filter as well as organisms lost as a result of biological escapement. Because most of the zooplankton in the area sampled were very small, e.g. copepod nauplii, it is probable that Hansen and Anderson's estimate of the efficiency of the conical sampler with respect to the total zooplankton present, as shown by the water bottle, has no real relation to the efficiency of the conical sampler with respect to zooplankton large enough to be retained completely by the filter. The results obtained in the present study strongly suggest that the one-metre conical sampler used in this study is very efficient at collecting zooplankton.

### 70-cm N.I.O. Sampler:

Interpretation of the results of the field trials of the present study indicate that, over the range of speeds

used, the 70-cm N.I.O. sampler is not as desirable a plankton sampler as the one-metre conical sampler, primarily because there is little possibility of improving its performance by increasing the speed at which it is hauled. The cause of the slight reduction in flow through the sampler at speeds of hauling in excess of 30 cm/sec is obscure. Whatever the cause, the effects of the reduction probably are analogous to what occurs when clogging of the meshes of the filter takes place. In such conditions, the reduction in flow can cause a large increase in the magnitude and extent of the acceleration fronts preceding the mouth of the sampler (Smith, pers. comm.). The result of this effect is to enable the zooplankton to detect the sampler at a greater distance. This may be the immediate cause of the reduction in catch at higher speeds of hauling.

The more successful results of the field trials with the 70-cm N.I.O. sampler, modified by removal of the canvas collar, indicate that the distance at which zooplanktonic organisms can detect the sampler may not change with speed when the canvas collar is not present. Whether the small reduction in catch at 200 cm/sec over that at 100 cm/sec (Table 4) is real or an artifact of field or laboratory technique is not clear. The curves of percentage catch plotted against speed of hauling for the modified 70-cm N.I.O. sampler have been calculated on the basis that this reduction in catch is not real. However it must be borne in mind that the canvas collar may not be the entire cause of

the reduction in catch in the standard sampler. It may be that any impervious collar ahead of the mouth of the sampler may cause a reduction in flow through the sampler. If this is so, some effect resulting from the presence of the 30.5 cm metal cylinder which remained in place on the modified sampler could be expected. The evidence at hand does not appear conclusive regarding any hypothesis. In any event, the 70-cm N.I.O. sampler modified by the removal of the canvas cylinder from in front of the mouth appears to be more efficient than the standard 70-cm N.I.O. sampler.

#### Catcher:

The results based on collections made with the Catcher for Calanus spp. and Eucalanus bungii bungii are probably accurate because the number of specimens of each species which were caught are relatively large. Other results must be regarded with caution; too few specimens of Euchaeta japonica and euphausiids were collected to give a reliable estimate of its catching power with respect to these groups. The results indicate that, for the range of speeds of hauling used in the field trials, the Catcher is less able to collect zooplankton than the one-metre conical sampler. Extrapolation of the curves for percentage catch plotted against speed of hauling indicates that at speeds of hauling greater than 300 cm/sec (6kt) the Catcher may be an efficient sampling device. The low catching power of the Catcher at the low speeds of hauling may result from the turbulent zone created by up to 400 m of

wire preceding the relatively small mouth of the sampler; additionally because the mouth opening of the sampler is smaller it may be easier for zooplanktonic organisms to avoid being caught. When the Catcher is towed horizontally, as it is designed to be towed, the mouth of the sampler is completely unobstructed. Therefore the catching power can be expected to increase somewhat in conditions of horizontal towing. At the same time the results indicate that without any increase in catching power the Catcher should be efficient at the speeds at which it is usually towed (6 kt or more).

#### Experimental Samplers:

The trials with the modified one-metre conical sampler, modified by the presence of a weight preceding the mouth, were undertaken to obtain an indication of the distance at which zooplanktonic organisms are able to detect the presence of the sampler. It was assumed that by suspending a body (lead weight) some distance (80 cm) in front of its mouth, the distance at which the organisms could detect the approaching sampler might be increased. If any of the selected species are able to detect the unmodified sampler at a distance in excess of 80 cm, then by adding the weight, little or no change in the sampler's catching power could be expected because the organisms already would have been alerted before the weight would have reached them. However if the organisms are not able to detect the sampler at a distance of 80 cm the presence of the weight could be expected to decrease its catching power by

increasing the distance,  $X$  (Fig. 3), at which the organisms can detect the presence of the sampler. Such an increase in  $X$  would effect an increase in the product  $X S_e$  (equation 10, p. 24).

The products  $X S_e$  increased, on the average, by a factor of 4.4, which, because in all other ways the sampler was not changed, is attributable to the presence of the weight. It is not possible to evaluate this result because of the unknown distance at which the organisms were able to detect the presence of the weight, but it seems reasonable to assume that organisms are not able to detect the sampler (unmodified) at a distance much in excess of 80 cm. Thus it appears that Barkeley's (1964) estimate of 250 cm for the distance at which zooplanktonic organisms are able to detect the sampler may be excessive.

The object of the trials with the modified 70-cm N.I.O. sampler was to determine whether the decrease in flow through the sampler, at higher speeds of hauling, with the concomitant decrease in the catching power of the sampler resulted from increased resistance to flow through the filter, or whether it resulted from some property of the canvas sleeve preceding the filter. The results suggest strongly that at least some of the undesirable properties of the 70-cm N.I.O. sampler at high speeds can be attributed to the presence of the canvas collar. Without the canvas collar the efficiency of the 70-cm N.I.O. sampler approaches that of the one-metre conical sampler as is shown by Fig. 11a. However, a slight reduction

in catch does occur between 100 and 200 cm/sec. It is difficult to say whether this reduction in catch is real, or whether it is an artifact of either the field or lab technique. The plots of percentage catch against speed of hauling for the modified 70-cm N.I.O. sampler are calculated on the basis that no real reduction in catch occurs at the higher speeds of hauling. Therefore they must be regarded with a certain amount of caution until there is sufficient evidence to show whether the reduction in catch is, in fact, real, or an artifact.

#### One-Square-Metre P.O.G. Samplers:

The results of the P.O.G. trials in which white and dark green, modified, Hensen-type samplers were towed in conditions of both daylight and darkness permit the assessment of the effect of the visibility of the sampler on its catching power with respect to euphausiids (animals possessing compound eyes). The samplers used had a mouth area equal to one square metre.

In daylight the ratio of the product  $X S_e$  for the white sampler to that of the dark green sampler is 2.82:1. In darkness the ratio is 1.42:1. These results appear to indicate that the colour may be contributing to the effectiveness, in terms of catching power, even at night. That the catching power of the white sampler in daylight should be relatively low seems obvious from the results. Probably this is attributable to its being readily seen, but why the colour should

continue to be effective at night is not clear. Perhaps in darkness bioluminescence from organisms would cause a white sampler to be more visible than a dark green one. However, it might be expected that most of the bioluminescence would be generated when the bioluminescent organisms strike the filter, in which case it is difficult to see why the colour of the sampler should make any difference.

A comparison between the plot of percentage catch against speed of hauling with respect to euphausiids for the dark green P.O.G. sampler, and the same plot for the one-metre conical sampler, indicates that the P.O.G. sampler is less able to capture euphausiids than the one-metre sampler. It indicates also that the Hensen-type configuration is probably not as good a design for plankton samplers as is the simple conical sampler.

#### Plankton Sampler Design:

Barkeley's (1964) computations suggest that plankton samplers should be made much larger than they are at present if the collections are to be representative of even the larger zooplanktonic organisms. His computations are based on the assumption that zooplanktonic organisms are able to detect a sampler one metre in diameter at a distance of 250 cm. Because the results of the present study indicate that zooplanktonic organisms are probably not able to detect the presence of a plankton sampler one metre in diameter at a distance of more than 80 cm, Barkeley's recommendations need to be re-evaluated. A decrease in the distance at which

zooplanktonic organisms are able to detect the sampler should make it possible to decrease the size of the optimal sampler and yet keep it an effective tool.

The results of this study show that, for the range of sizes of organisms studied, plankton samplers with mouth diameters of 70 to 100 cm are probably adequate to collect representative samples from zooplanktonic communities provided that they are hauled somewhat faster than usual, i.e. 150 to 200 cm/sec as opposed to the more usual 100 cm/sec. By an extension of this reasoning, the possible penalty paid by reducing the diameter of the mouth opening of a plankton sampler may be recompensed by the increase in the number of organisms collected by towing at higher speeds. This has been part of the reasoning underlying the design of the high speed samplers, but the present study appears to be the first attempt to justify this reasoning quantitatively. Certainly the 23-cm mouth of the Catcher appears to be useful, but most other high speed samplers (Gulf I, Arnold, 1952; Gulf V, Arnold, 1959; Jet Net, Clarke, 1964) have mouth diameters less than 10 cm. Further work is required to determine the extent to which the diameter of the mouth opening may be reduced and still be compensated for by increasing the speed of towing.

From the above brief discussion concerning plankton sampler design it appears that: firstly, every effort be made to facilitate the flow of water through the sampler; secondly, the plankton sampler should be made as difficult to detect as possible, not only by means of colouring, but by

streamlining and making as small as possible all parts which must precede the mouth of the sampler. Finally, no modifications should be made in the design of any plankton sampler without thorough trials to determine what effect these modifications may have on the catching power of the sampler.

#### The Use and Utility of the Model:

Perhaps the greatest utility of the model is to the zooplankton ecologist who desires to obtain data concerning the size and species composition of the zooplanktonic community which is quantitative. For the purpose of this discussion the zooplanktonic community is defined as those members of the marine community which are pelagic animals between the size-limits of 0.5 mm to a few centimetres in length. Pelagic animals larger than these size-limits are considered to comprise the nekton.

To say that data are quantitative implies that the number of species and their relative abundance in the sample are the same as in the community sampled and that the volume of water which has been filtered is accurately known. The problems involved in determining the volume of water filtered by the plankton sampler have been discussed elsewhere (pp. 8-11) Likewise the possible errors introduced into data as a result of the selectivity of the sampler (p. 5) and extrusion of animals through the meshes of the filter (p. 3) have been discussed above.

Presuming that the previous arguments and calculations are valid, the value of the model to the zooplankton ecologist is that once a sampler has been calibrated with respect to the species to be investigated selectivity of the sampler is no longer a problem for species which the sampler is able to capture at all. Thus the zooplankton ecologist need only select a sampling device which will capture a few specimens of all the species to be studied and calibrate it with respect to those species to obtain data relatively free from errors introduced by biological escapement. The model will also be useful when it is desired to compare catches made with different samplers at different times. This is especially valuable when one sampler cannot be used to sample all the species to be studied. Such a situation might arise when both very small and very large species were to be studied.

However, the calibration of the sampler requires the greatest care if any benefit is to accrue from its use. It must be certain that the same population is sampled by each haul, and that the volume of water filtered during each haul is accurately known, of the same. Also, enough specimens of each species must be captured by each haul to ensure accuracy in the calculations. The lower limit on the number of specimens captured by each haul is probably from 10-50.

Another important application of the model is in the testing of experimental samplers. Here the use of the model should enable comparisons to be made on an absolute basis between different samplers. Again every precaution must be taken to ensure that the data collected fulfil the requirements of the model.

## GENERAL CONCLUSIONS:

1. Biological escapement can cause difficulties in obtaining a representative sample from zooplanktonic communities, not only in the form of low estimates of population densities for single species, but as errors in estimates of the species composition of the community.
2. Four quantities, the radius of the sampler, the speed at which it is towed, the effective speed which the organisms can attain in escaping from the sampler, and the distance at which the organisms can detect the sampler, are considered in the model. These are probably the factors of prime importance in describing the process of biological escapement.
3. The results given by the application of the model to data from collections made in the field are not only consistent for data collected with any one sampler, but also for data collected with different samplers.
4. For the organisms studied, samplers having mouth diameters of 70 to 100 cm are probably adequate for collecting a representative sample, provided that they are towed at 150 to 200 cm/sec or more.

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## APPENDIX I

## The Subsampling Technique:

The subsampling technique of Brodskii and Baskakov (1951) consists of counting the number of specimens of a species or group which lie within a known fraction of the area of the bottom of a dish. This method depends upon an even distribution of the specimens in the bottom of the dish. A distribution which appears even to the eye is adequate. Also the diameter of the (circular) area to be counted should be several (3-5) times the length of the specimens which are to be subsampled. If these criteria are met the method can provide accurate and precise data.

A source of systematic error in the subsampling technique arises from the interaction between the animals which are to be subsampled and the walls of the dish. There tends to be a zone at the junction of the walls and bottom of the dish in which animals are not found. Thus the area in which the animals are evenly distributed is slightly smaller than the area of the bottom of the dish. The area in which the animals are evenly distributed can be termed the effective area of the bottom of the dish. A further source of systematic error arises from errors in delimiting the area to be counted. Therefore it is best to subsample a known number of specimens to determine the exact fraction of the effective area of the bottom of the dish which each subsampling area represents. This is done by making 10-20 counts and

obtaining the mean number of specimens per subsampling area.

In practice it is desirable to redistribute the specimens before each count of the number within the subsampling area. Also one-half of the number of animals which lie across the boundaries of the area should be added to the number of animals lying completely within the boundaries of the subsampling area.

Table 9 gives a summary of the results of 15 counts made with a subsampling area nominally equal to 1/20th of the area of the bottom of the dish. The dish contained 1343 euphausiids. If the subsampling area had been precisely 1/20th of the area of the bottom of the dish, each subsampling area should have contained 67.15 euphausiids. However, the mean number of euphausiids per subsampling area was 63.8. This indicates that the subsampling area is actually 1/21st of the effective area of the bottom of the dish.

The goodness of fit of the predicted and actual numbers of euphausiids in the dish was determined by calculating a value for Chi-Square. Calculation of Chi-Square on the basis of the subsampling area being 1/20th of the area of the bottom of the dish gave a value of 4.66. This indicates very good agreement between the predicted and actual number of specimens in the dish.

Table 9

Results of Fifteen Successive Counts of the Number of Euphausiids Lying Within 1/20th of the Area of the Bottom of a Dish Containing 1343 Euphausiids

Counted	Counted	Counted
59	68	64
61	68	66
63	62	65
62	65	59
60	66	69

Total = 957

Mean = 63.8

Expected number within subsampling area = 67.15

Chi-Square = 4.66

Probability of a larger Chi-Square (14 df) = .99