

Use of the *Pisces IV* Submersible for Zooplankton Studies in Coastal Waters of British Columbia

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This study evaluates the usefulness of a small submersible for observations of the plankton. A method for calculating plankton densities from estimates of mean interanimal distances is described. Estimates made by this method were compared with estimates based on net sampling and were found to be in fair general agreement with them. Fragile gelatinous forms were better counted from the submersible, small organisms by netting. Some delicate species, known to be abundant from submersible observations, were never recognized in net samples. Submersible observations also gave important insights into vertical distribution of the plankton. Several species were found to exist within unexpectedly narrow and sharply defined layers, often at densities greatly surpassing density estimates based on net samples. In Saanich Inlet, B.C., plankton distribution was studied in relation to the seasonal formation and dispersion of the oxygen-deficient basin water. Other data deal with behavior, color change, bioluminescence, and vertical migration of planktonic organisms. We conclude that submersible observations are potentially valuable in plankton research, and we make recommendations regarding instrumentation and observer training as an aid in planning future dives.

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Le but de la présente étude est d'évaluer l'utilité d'un submersible de petite taille pour observer le plancton. On y décrit une méthode de calcul des densités du plancton à partir d'estimations de distances moyennes entre animaux. Nous comparons les estimations obtenues par cette méthode avec celles d'échantillonnages au filet et trouvons assez bonne concordance entre les deux. Il est plus facile de dénombrer les formes gélatineuses fragiles depuis le submersible, alors que les petits organismes le sont plus facilement par échantillonnage au filet. C'est ainsi que certaines espèces délicates, que des observations par submersible prouvent abondantes, ne sont jamais identifiées dans les échantillons des filets. En outre, les observations par submersible donnent une très bonne idée de la distribution verticale du plancton. On constate que plusieurs espèces vivent dans des couches inopinément étroites et nettement définies, souvent à des densités dépassant de beaucoup les estimations fondées sur les échantillons prélevés au filet. Dans l'inlet Saanich (C.-B.), nous avons étudié la distribution du plancton en relation avec sa formation saisonnière et la dispersion de l'eau du bassin, pauvre en oxygène. Les autres données portent sur le comportement, le changement de coloration, la bioluminescence et la migration verticale des organismes planctoniques. Nous concluons que les observations par submersible offrent beaucoup de possibilités comme outils de recherche sur le plancton, et faisons certaines recommandations relatives aux appareils et à la formation d'observateurs, dans le but d'aider à la planification des plongées futures.

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DEEP submersible research vessels have been used for marine biological investigations since about 1953, mainly for work on the benthos, as in the explorations by *Alvin* in the Galápagos rifts (Corliss et al. 1979). Observations on planktonic organisms have occasionally been reported, but typically, these deal with rare and interesting animals seen in the

course of dives made for other purposes. The discovery and capture of rhodaliid siphonophores ("dandelions") by *Alvin* (Corliss et al. 1979; Clark 1979) is one example, others being the observation and collection of a new scyphozoan medusa by *Deepstar* (Russell 1967), of a new ctenophore by *Alvin* (Madin and Harbison 1978), of pelagic holothurians by *Turtle* and *Sea Cliff* (Barnes et al. 1976), and of giant larvacean houses by *Deepstar* (Barham 1979).

Observations on unusual aggregations of siphonophores (Rogers et al. 1978), on feeding mechanisms (Youngbluth 1982), and on the composition of the deep-scattering layers (e.g. Barham 1963, 1966; Milliman and Manheim 1968) represent contributions to plankton ecology in a more general sense. However, to find submersibles being used for systematic reporting of the overall distribution of a wide range of zooplankton species in the water column, we must go back to the pioneering studies of Bernard (1955) and Trégouboff (1956, 1958, 1961, 1962), both of whom used the Piccard submersible *F.N.R.S. III*, predecessor to the *Trieste*. A complete bibliography of the work of *F.N.R.S. III* up to 1957 is given by Fage (1958). A contribution by Franqueville (1970) follows in the same tradition.

The Canadian *Pisces* submersibles (MacDonald 1975) have been used quite extensively for studies of the marine benthos, the most recent example being Tunnicliffe (1981). The few reports covering the plankton are brief and are restricted to generalities (e.g. Herlinveaux 1970; Levings and McDaniel 1973).

The present series of studies using *Pisces IV* had as its objectives (1) the further pursuit of Herlinveaux's (1970) goal of assessing the potential of *Pisces* submersibles for biological oceanography, (2) the development of more quantitative approaches to visual reporting of plankton composition, and (3) the use of these methods to examine certain specific aspects of plankton biology in British Columbia coastal waters.

Dive Sites

Locations of the dives are shown in Fig. 1.

Saanich Inlet — A total of 25 dives by one or both authors in company with other observers were carried out between August 1980 and April 1981. Saanich Inlet, on the southeast side of Vancouver Island, is 24 km long and 7.2 km wide at its widest part and about 200 m deep in the central region for most of its length. There is a sill at the mouth, where the depth is 75 m (Herlinveaux 1962; Deuser 1975). The deep water inside the sill is isolated for much of the year and undergoes progressive oxygen depletion, along with reduction of nitrates, nitrites, and sulphate and production of hydrogen sulphide. Upwelling off the open coast leads indirectly to an annual influx of dense water, which may cross the sill and enter Saanich Inlet, displacing between 18 and 46% of the water in the basin (Anderson and Devol 1973). Oxygen data for 1980–1981 are given by Tunnicliffe (1981). This flushing is usually restricted to the months of August and September. The new water descends to the bottom of the basin or to an equilibrium point near the bottom. After flushing, oxygen depletion commences. Conditions of low oxygen concentration, plus the presence of hydrogen sulphide in this zone, make it generally inhospitable to animal life, though the benthic community has been shown to exhibit a remarkable tolerance to periodic low-oxygen conditions (Tunnicliffe 1981).

Stuart Channel — Lying directly north of Saanich Inlet, but lacking a sill and open at both ends, Stuart Channel was chosen as a dive site for comparison with Saanich Inlet. It is well oxygenated to the bottom. Dives were conducted between March 30 and April 13, 1981.

Jervis Inlet — Data were collected in dives on May 21, 1980, September 29, 1980, and February 22–23, 1981. Jervis Inlet is characterized by low runoff. There is no glacial silt in the water. Seasonal cycles in temperature, salinity, and oxygen are minor below the top 10 m (Pickard and Stanton 1980).

Knight Inlet — The data included here were obtained by Dr V. J. Tunnicliffe during dives concerned mainly with observation of epilithic faunal assemblages. Knight Inlet carries a high glacial sediment load. Despite the greater amount of freshwater entering Knight than Jervis, there is little difference in temperature, salinity, and oxygen content between the two inlets below 10 m (Pickard and Stanton 1980). A sill at Hoeya Head rises to 63 m from the surface. The plankton observed above and below the sill appeared similar, and the data have been combined for the present account.

Howe Sound — The data reported here were collected by Dr V. J. Tunnicliffe during dives in March 1981. Howe Sound has a 40-m sill in Montagu Channel, which partially isolated the 275-m-deep inner basin from the rest of the inlet. The outer water is similar to water from the Strait of Georgia. Basin water undergoes severe oxygen depletion at certain times (Bell 1973, 1974), but at the time of the present dives, mixing was evidently in progress or had recently occurred, as the water contained in excess of $1 \text{ mL} \cdot \text{L}^{-1}$ throughout the water column. The distribution of the plankton appeared similar in the inner basin and outer channel, and the sightings have been combined in the present report.

Methods

DESCRIPTION OF *PISCES IV* SUBMERSIBLE

Constructed in 1972 by International Hydrodynamics of North Vancouver, *Pisces IV* is owned by the Department of Fisheries and Oceans (Canada) and is based at the Institute of Ocean Sciences, Sidney, B.C.

The cabin of the submersible measures approximately 2 m in diameter, which allows spaces for a pilot and two observers. It can operate to depths of 2000 m. Depending on the power drain, dives of 4–8 h are regularly undertaken. The life support system can operate for 216 person-hours. Observations are made through three ports (15 cm inside diameter, 36 cm outside diameter). Two 1000-W lights are mounted outside the observer's ports, and two 500-W lights are mounted above the pilot's port. Adjustment of the angle of these lights is essential for accurate observation of the plankton.

A hydraulic manipulator arm is mounted ahead of the pilot port, along with other instrumentation. Water samples can be taken through a valve in the hull during dives.

The *Pisces IV* has a variable buoyancy system that includes both a hard ballast system, in which small buoyancy adjustments are made by pumping water in and out of ballast chambers, and a soft ballast system, operating on compressed air. This versatile system allows for rapid, small adjustments in the vessel's buoyancy and fine control of the rate of ascent and descent, the need for which has been noted by users of some other submersibles, where such adjustments were not so convenient.

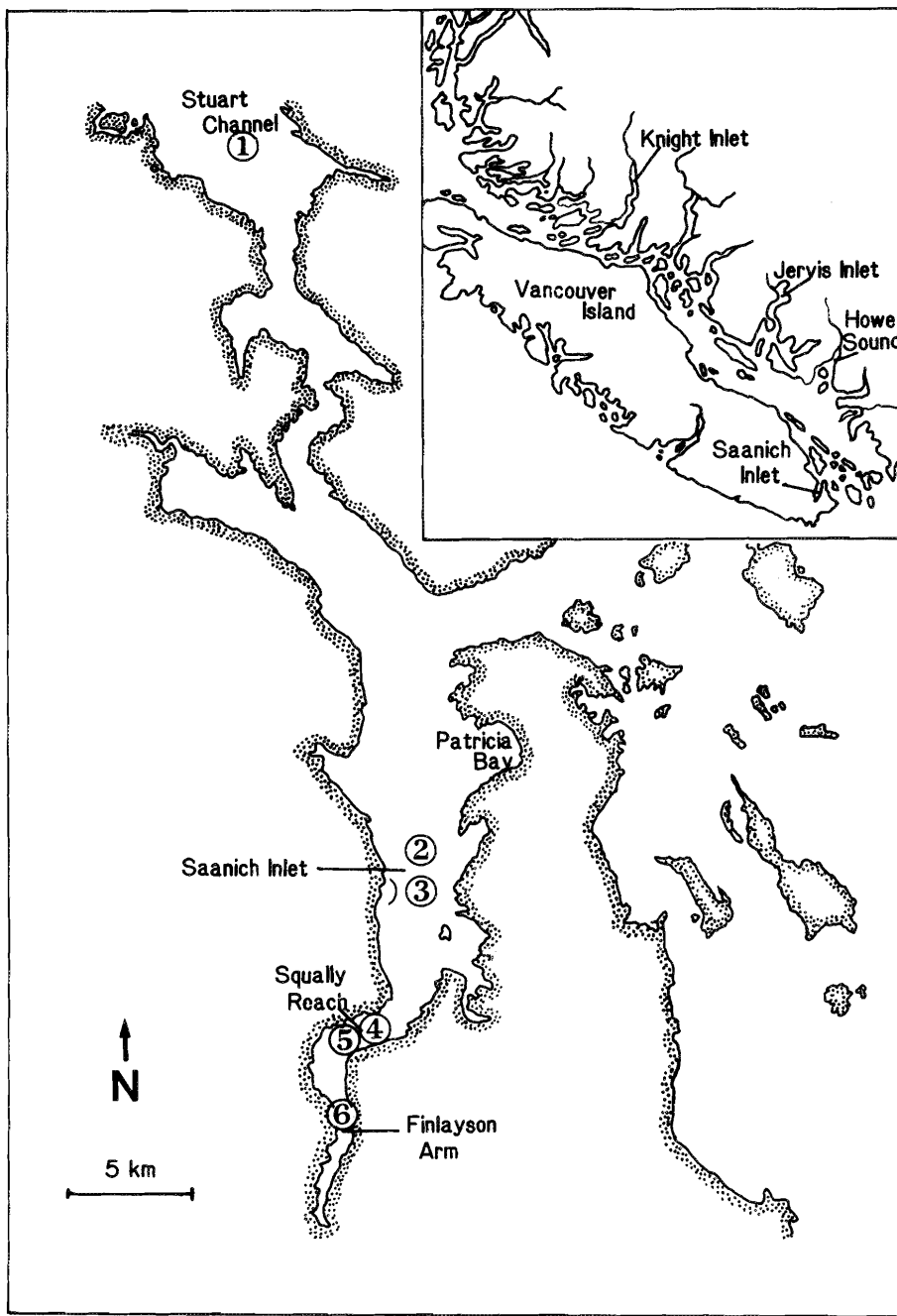


FIG. 1. Sites on the coast of British Columbia where dives were made. Station 1 (209-m depth) lies equidistant between Crofton and Vesuvius Bay; station 2 (200–210 m) lies off Yarrow Point; station 3 (210 m) lies off Tozier Rock; station 4 (220 m) lies off McCurdy Point; station 5 (215 m) lies off Elbow Point; station 6 (200 m) is in the middle of Finlayson Arm.

COLLECTION, IDENTIFICATION, AND COUNTING OF PLANKTON

On two occasions, plankton samples were taken at the dive site using a 75-cm-diameter closing net with 333- μ m mesh. Vertical hauls were made over known depth ranges, and the

density and composition of the plankton was determined for comparison with estimates made by direct observation from *Piscis*. Water samples taken during dives were analyzed for oxygen content by the Winckler procedure.

Visual observations made from the submersible during

TABLE 1. Density of organisms estimated from observed average center-to-center distances between organisms. Number per cubic metre is calculated from the formula: number of organisms/volume (m^3) = $1.41/\text{distance} (m^3)$ and assumes that closest packing of spheres with an organism at the center of each sphere is an appropriate model for the distribution of these organisms.

Observed average center-to-center distance between organisms	Calculated No. $\cdot m^{-3}$
1 cm	1 410 000
2 cm	176 250
3 cm	52 222
4 cm	22 031
5 cm	11 280
10 cm	1 410
15 cm	418
20 cm	176
30 cm	52
40 cm	22
50 cm	11
1 m	1.41
1.5 m	0.42
2 m	0.18

dives were recorded verbally on tape recorders. Photography of plankton through the ports was attempted using the external strobe light, but the photographs lacked sufficient clarity to be useful for purposes of quantification and identification.

Sources for identification of species included Fulton (1968), Shih et al. (1971), and Kozloff (1974). Identification of medusae was aided by reference to Arai and Brinkmann-Voss (1980). For pelagic polychaetes, reference was made to Tebble (1962) and Ushakov (1974), and for decapod larvae, Hart (1971) was referred to.

In preliminary trials, three observers were assigned to report independently on plankton distribution and density at the same site on successive days. The observers were familiar with the local plankton but only one of them had previous submersible experience. From these trials, methods were selected for counting the plankton and displaying the results graphically. In most dives, a tubular plastic frame delineating a space of known cubic dimensions was mounted in front of each observer port, and the observers counted or estimated the numbers of the organisms in this space.

In the data for Saanich Inlet, densities are shown graphically by spots. The density of spots gives a rough indication of the density of the organism at a particular depth in relation to its density, and that of other species, at other depths and times, but these data are not to be interpreted in terms of absolute values. Where densities could not be systematically estimated (data from Jervis, Howe, and Knight inlets) only the range is given.

In later dives, densities were calculated from estimates of the average center-to-center distance between organisms. Numbers of organisms per unit volume can be calculated on a model of closest packing of equal spheres, assuming each animal to be at the center of a sphere. In either hexagonal or face-centered closest packing of spheres, the spheres occupy 74% of the total volume (Van Vlack 1964). Thus, the number of spheres (N) times the volume of a sphere equals 74% of the total volume:

$$(N)(\frac{4}{3}\pi r^3) = (0.74)(\text{volume}).$$

TABLE 2. Principal species referred to in the text.

Hydromedusae
<i>Aequorea victoria</i>
<i>Phialidium gregarium</i>
<i>Euphysa japonica</i>
<i>Proboscoidactyla flavicirrata</i>
<i>Aegina citrea</i>
<i>Aglantha digitale</i>
Siphonophora
<i>Muggiaea atlantica</i>
<i>Dimophyes arctica</i>
<i>Nanomia cara</i>
Ctenophora
<i>Pleurobrachia bachei</i>
<i>Pleurobrachia</i> species B (determination pending)
<i>Bolinopsis infundibulum</i> (determination pending)
<i>Beroe abyssicola</i>
Pteropoda
<i>Cione limacina</i>
Polychaeta
<i>Tomopteris pacifica</i>
<i>Tomopteris septentrionalis</i>
Copepoda
<i>Aetideus divergens</i>
<i>Calanus</i> spp.
<i>Euchaeta elongata</i>
<i>Metridia pacificus</i>
Amphipoda
<i>Cyphocaris challengeri</i>
<i>Parathemisto pacifica</i>
<i>Orchomenella affinis</i> (= <i>O. obtusa</i>)
Euphausiacea
<i>Euphausia pacifica</i>
Decapoda
<i>Munida quadrispina</i>
Chaetognatha
<i>Sagitta elegans</i>
Appendicularia
<i>Oikopleura dioica</i>
<i>Oikopleura labradoriensis</i>

Therefore, for N organisms:

$$N/\text{volume} = 0.74/\frac{4}{3}\pi r^3.$$

Thus

$$N/\text{volume} = 1.41/d^3$$

will yield densities of planktonic animals based on d , the observed average distance between animals (in centimetres or metres, corresponding to volume in litres or cubic metres, respectively).*

A set of distances and equivalent densities covering the range encountered in the *Pisces* work is provided in Table 1.

*NOTE ADDED IN PROOF: Hamner and Carleton (1979) provide a formula relating average nearest neighbor distance to density based on the assumption of isahedronic packing.

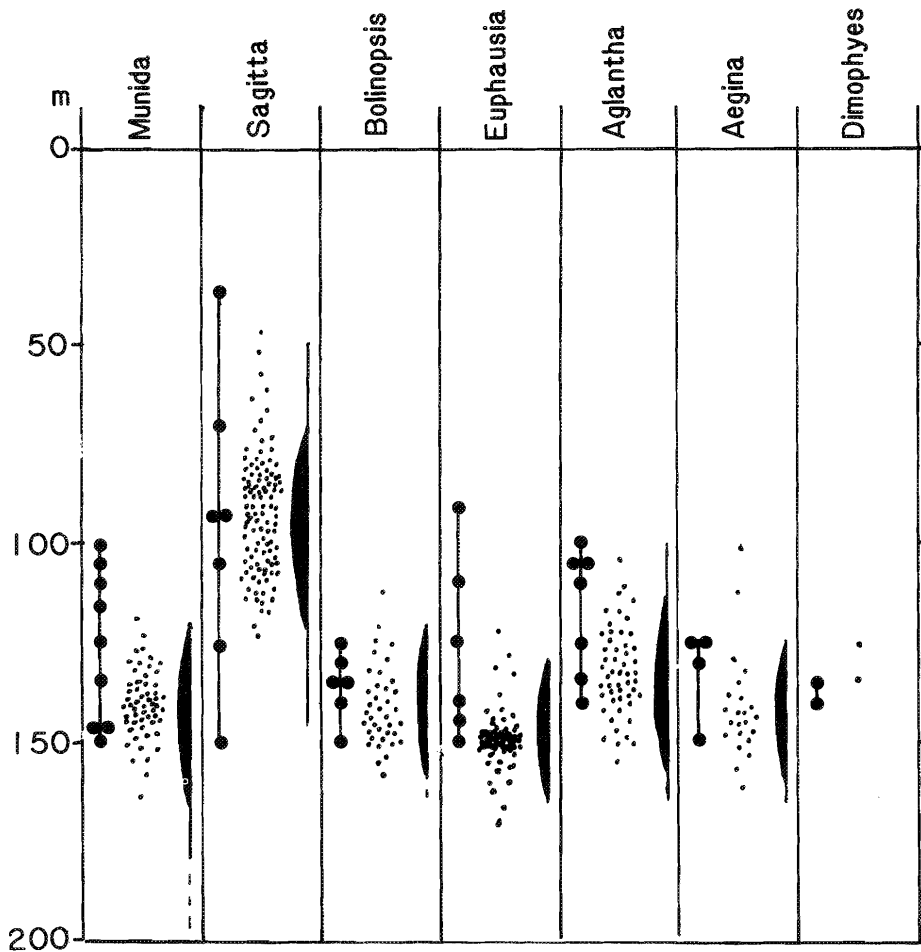


FIG. 2. Agreement among observers. Distributions of selected species were plotted independently by three naïve observers. The dives were conducted during the early afternoon during the period between August 18 and August 20, 1980, at station 3, Saanich Inlet.

During dives, a graduated scale was placed outside each observer port as an aid in judging distances.

The reliability of this method of estimating densities was tested in experiments conducted in laboratory tanks using known concentrations of suspended objects (plankton, fish eggs, etc.). The most convenient test objects proved to be "model medusae": fish liver oil capsules fixed in formalin to render the gelatin insoluble, washed, and suspended in tap water to which ethanol was added to make the capsules neutrally buoyant. Capsules were added arbitrarily to produce different densities, which were then estimated by four observers using the interanimal center-to-center distance formula. Afterwards, the actual numbers of capsules were determined and their densities per cubic metre calculated directly. The water in the tank was kept in gentle irregular motion during the counts.

Results

The principal species observed during the study are listed in Table 2.

OBSERVER AGREEMENT IN *PISCES* OBSERVATIONS

Results from trials conducted at the beginning of the study are shown in Fig. 2. Observer 1 recorded plankton sightings as single spots, chiefly with a view to establishing range, indicating regions of high abundance by a double spot. Observer 2 indicated abundance by spot density, as described under Methods. Observer 3 showed abundance in another manner. It will be apparent that there was fairly good agreement between the sightings. The differences may, in part, represent true differences in plankton distribution on the three occasions when the dives were made.

A possible source of confusion in some dives is that, in descending or moving forwards through the water column, the submersible carries a body of water with it containing trapped organisms. In addition to such passive displacements, some organisms such as euphausiids, which are strong swimmers and are positively phototactic, cluster around the lights and follow the submersible downward during slow descents. Observer 1 (Fig. 2) disregarded sightings of *Munida*, *Euphausia*, etc. below about 150 m, believing that

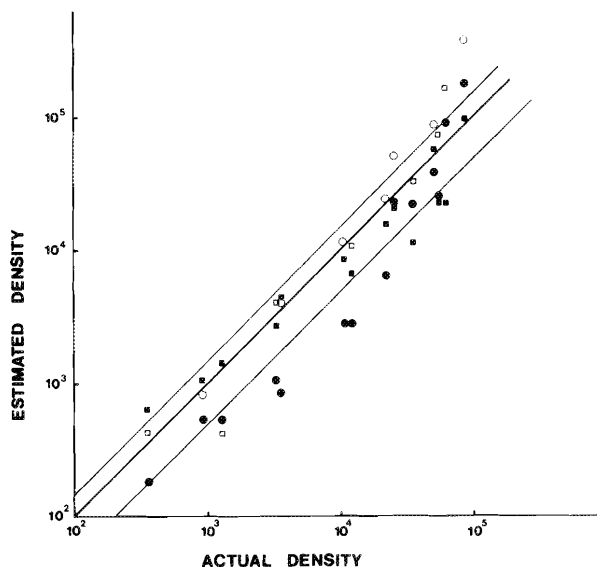


FIG. 3. Density estimates by four observers in model medusa experiment. Density units are numbers of animals per cubic metre. Correct estimates would fall along the center line (50% error limits are shown on either side). Solid circles and squares are estimates by the two authors.

their presence there was due to movement of the submersible or its lights. This was later shown to occur on a number of occasions. In later dives, when we were attempting to establish precise limits to the zonation, we made a point of coming up from below as well as going down into areas we were interested in and of keeping the lights off during ascents and descents, except when counts were to be made. It was sometimes found advantageous to maintain slow forward movement with the thrusters while ascending or descending. The submersible thus enters new water all the time, and forms that are attracted or repelled by light do not have sufficient time to move toward or away from the advancing lights. Trimming the submersible with the bow up minimizes the forward trapping effect.

LABORATORY TESTS ON RELIABILITY OF FIELD DENSITY ESTIMATES

Actual densities and estimates by four observers are compared in Fig. 3. The agreement of observers' estimates with actual densities, and the agreement between observers, was evaluated by correlation using the Pearson product-moment correlation coefficient, which ranges from 0 (no relationship) to 1.0 (perfect relationship). Over the set of 14 test densities our estimates correlated 0.86 and 0.87 with actual values and 0.88 with each other. While a few estimates differed from actual values by over 100%, the overall mean percentage error was 53%. The greatest inaccuracies were noted at the highest actual density values ($>60\,000 \cdot \text{m}^{-3}$). Considering only the estimates of densities below this value, mean percentage error was 37%.

COMPARISON OF NET HAULS AND *PISCES* OBSERVATIONS

On November 4, 1980, and March 30, 1981, plankton tows were carried out in Saanich Inlet for comparison with submersible counts made concurrently. Fair agreement between the two data sets was found on both occasions. Table 3 lists the data for hydromedusae, siphonophores, and ctenophores from the November 4 counts.

As also noted by Franqueville (1970), net sampling is clearly more effective in the case of small transparent objects like eudoxids, which could not be accurately counted from the submersible but were scored as "few" or "common" (the same would apply to copepods and crustacean microplankton). However, observations from the *Piscès* revealed a considerably higher density of ctenophores than did the net counts, and one common species (*Pleurobrachia* species B) was not recognizable at all in the net samples, presumably because of disintegration under the stress of capture. The submersible showed higher numbers for *Aegina* probably for the same reason. The November data were obtained at a time when the plankton was dispersed over a much greater vertical range than during most of the year, when anoxic water limits distribution in the lower levels. In March, submersible observations showed several species to be present in high concentrations in narrow bands over the anoxic zone. The data for *Aglantha* are shown in Fig. 4 compared with data from plankton hauls. Similarly, in August 1981, *Bolinopsis* reached densities of $20 \cdot \text{m}^{-3}$ within a narrow layer at 145–150 m. Because the net integrates the densities from all the levels it traverses, it fails to reveal the sharp discontinuities and very high local concentrations seen by observers in the submersible. With prior knowledge, or good luck, net samples might be taken at just the right depths to reveal the stratification precisely, but the fact remains that in none of the present series of net hauls and in none of the previous reports is there any adequate indication of the precision of the layering or the high densities achieved within these narrow bands. The advantages of the submersible are quite clear in this regard.

SUBMERSIBLE OBSERVATIONS FROM SAANICH INLET, STUART CHANNEL AND MAINLAND FJORDS

The observations from Saanich Inlet and Stuart Channel have been taken from the more comprehensive study of Mills (1982) and are intended to serve as examples illustrating the usefulness of submersible observations.

Figure 5 shows plankton distribution as observed from the submersible for three periods, during two of which the water below a certain depth was seriously deficient in oxygen. On the other occasion, mixing had occurred. The plankton was limited to water containing more than $0.2 \text{ mL O}_2 \cdot \text{L}^{-1}$ with the exception of an amphipod, *Orchomenella affinis*, already shown by Hoos (1970) to be tolerant of anoxia.

During periods when the water column was adequately oxygenated to the bottom, most species were also distributed all the way to the bottom, but some, notably *Euphausia pacifica*, continued to show a concentration at an intermediate depth.

It was very obvious from the submersible observations that

TABLE 3. Comparison of plankton densities estimated from net samples (two at each depth) and counted by eye from the submersible in Saanich Inlet, Nov. 4, 1980.

Species	Plankton tows		Visual counts	
	Depth (m)	No. · m ⁻³	Depth (m)	No. · m ⁻³
Hydromedusae				
<i>Aegina citrea</i>	75–130	0.04, 0	100–185	0.2–0.5
	130–180	0.09, 0		
<i>Aglantha digitule</i>	0–25	0, 0.09	80–185	2–10
	25–50	0, 0.09		
	75–130	2.60, 2.15		
	130–180	2.27, 1.86		
<i>Phalidium gregarium</i>	0–25	0.09, 0.09	Surface only	<0.5
<i>Proboscoidactyla</i>	0–25	0, 0.27	0–75	<0.2
<i>flavicirrata</i>	25–50	0.18, 0.09		
	50–75	0.27, 0		
Siphonophora				
<i>Dimophyes arctica</i>	50–75	0.36, 0.18	60–100	<0.2
(polygastric)	75–130	0.12, 0.17		
<i>Dimophyes arctica</i>	50–75	0.09, 0.18	140–170	Few
(eudoxids)	75–130	0.29, 0.29		
	130–180	0.18, 0.28		
<i>Muggiaea atlantica</i>	0–25	1.09, 0.91	15–34	0.5
(polygastric)	25–50	2.00, 3.45	35–47	5.0
	50–75	2.73, 5.82	48–70	0.5
	130–180	0.05, 0		
<i>Muggiaea atlantica</i>	0–25	5.54, 5.46	30–60	Common
(eudoxids)	25–50	9.00, 14.63		
	50–75	2.73, 5.82		
	130–180	0.05, 0		
<i>Nanomia cara</i>	50–75	0.09, 0	165–180	Only two seen
Ctenophora				
<i>Bolinopsis</i>	50–75	0, 0.09	20–185	0.2–0.5
<i>infundibulum</i>	130–180	0, 0.05		
<i>Pleurobrachia</i>	0–25	0.09, 0	0–75	<0.2
<i>bachei</i>	25–50	0.09, 0		
<i>Pleurobrachia</i>	None recognizable		100–154	0.2–0.5
species B			155–165	5
			166–185	0.2–0.5

the zone just above the anoxic layer, whether this fell at 160 or 100 m, contained a high concentration of plankton.

In general, the plankton distribution at the two ends of Saanich Inlet was closely similar during the period in question (Fig. 6), but marked differences were observed between Saanich Inlet and Stuart Channel.

Oikopleura dioica was undergoing an intense bloom at the time in question, reaching densities of 10 000 · m⁻³, as recorded on another occasion by Seki (1973). Its distribution was similar at all three sites. *Aglantha* and *Euphausia* were located in narrow layers around the 100-m mark. The concentrations of these forms were much higher in Saanich Inlet than in Stuart Channel. *Oikopleura labradoriensis*, *Sagitta*, *Bolinopsis*, and the two species of *Pleurobrachia* all showed a greater downward range in Stuart Channel than in Saanich Inlet, which must be partly attributed to the absence of an oxygen-deficient zone in Stuart Channel, supporting similar findings by Hoos (1970). The greater upward dispersion of several species in Stuart Channel suggests that certain weakly swimming forms are less able to maintain a "preferred" depth in a water mass subject to tidal mixing.

Night dives were successfully conducted on two occasions, making it possible to compare night and daytime distributions within a single 24-h period (Fig. 7).

The results confirm that *Euphausia* and *Sagitta* migrate toward the surface at night, as previously shown by net sampling (e.g. Arai and Fulton 1973) and as also shown for euphausiids and chaetognaths in the Mediterranean (Franqueville 1970) and in Norwegian fjords (Hopkins and Gulliksen 1977). It was also noted that *Munida* is a migrator. *Aglantha* migrated on one occasion, but not on the other. This is interesting in view of the existence of conflicting reports (reviewed by Mackie 1980) from various parts of the world as to whether *Aglantha* migrates or not, and in which direction.

Oikopleura labradoriensis may be a migrator, but the redistribution was not as obvious as in the other cases mentioned. There are indications in our records that both species of *Pleurobrachia* may be migrators, but numbers were too small for this to be established with certainty. Some of the amphipods and copepods definitely migrate, but because of difficulties with identification, these results are omitted.

Diel changes in the depth of components of the sound

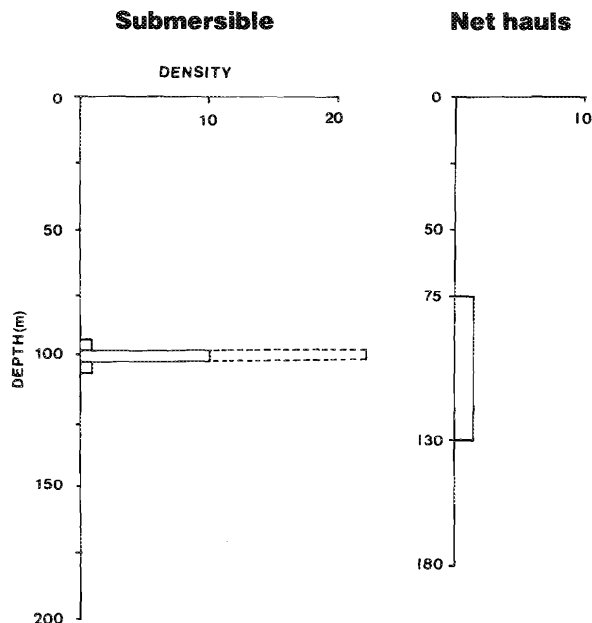


FIG. 4. Distribution of the medusa *Aglantha digitale* at station 2, Saanich Inlet, March 30, 1981. Comparison of visual density estimates from the submersible and density estimates obtained by plankton tows. Density units are numbers of animals per cubic metre; depth units are metres.

scattering layers in Saanich Inlet have generally been interpreted in terms of the movement of fishes (e.g. Herlinveaux 1962; Bary 1967), but the presence of invertebrate plankton, particularly euphausiids, in very high concentrations just above the oxycline at certain times suggests that they alone may be sufficient to produce the scattering even with relatively low-frequency sounders (see calculations by Hersey and Backus 1962). There seems to be little doubt that euphausiids produce a midwater scattering layer as detected by high-frequency echo sounding in Saanich Inlet (Bary and Pieper 1970) and in other areas (Pieper 1979).

The most striking feature observed during the *Pisces* dives in Saanich Inlet was the extraordinarily high concentrations of euphausiids just over the oxycline (see Fig. 5). The highest previous estimates for Saanich Inlet are $280 \cdot \text{m}^{-3}$ (Bary 1966) and $250 \cdot \text{m}^{-3}$ (Boden and Kampa 1965). We have found local concentrations of euphausiids in bands of 2–3 m thickness reaching densities as high as $10\,000 \cdot \text{m}^{-3}$, equivalent to a center-to-center spacing of approximately 5 cm. Net sampling can easily miss such concentrations as in the case of *Aglantha* (Fig. 4). Care was taken in these observations to distinguish natural aggregations from concentrations induced by the submersible's lights. Table 4 gives data from various dives. Usually, there was a single high-density band, but on one occasion, two bands were seen. Euphausiid densities of this order of magnitude have previously been reported only in surface swarms (Terazaki 1980).

Some indication of the precision of the banding can be given by quoting from detailed notes made after a daytime dive at station 2 on March 30 (Mills 1982):

"Above 99 m, only isolated individuals were seen; at 99 m, density was approximately $10 \cdot \text{m}^{-3}$, and an observer could look down from the submersible into a cloud of *Euphausia* that began rather abruptly at 100 m, where, within a meter, the density increased from about $100 \cdot \text{m}^{-3}$ to $10,000 \cdot \text{m}^{-3}$. Density began declining below 102 or 103 m, so that only 100–400 m^{-3} were present by 108 m. At 112 m, the density was less than $10 \cdot \text{m}^{-3}$, and by 115 m only a few scattered *Euphausia* were left."

Opportunities to dive in Jervis Inlet, one of the mainland fjords, were too limited to allow more than a bare cataloguing of the more obvious planktonic species. Similarly, the sightings for Howe Sound and Knight Inlet are of a preliminary nature, but they serve to show that, in many respects, the spring plankton in the three inlets is similar. Exceptions exist; for instance, the absence of *Munida* larvae in Knight Inlet. Adult *Munida* are rare here, possibly because of the high sediment load. Figure 8 shows the ranges of selected species. Squid and fish are omitted, as the focus here is on the plankton community in the narrower sense.

The distributions of the species observed in Jervis Inlet may be considered under four general categories:

Group 1 (epipelagic) — Examples are *Muggiaea*, rarely seen below 100 m, and *Phialidium*. In the September 1980 dive, *Muggiaea* showed an upper distribution limit at 35 m, probably the bottom of the halocline. However, *Probosciodactyla* and *Aequorea* were present above the halocline, and *Pleurobrachia bachei* was distributed on both sides of it down to 40 m.

Group 2 (upper mesopelagic "narrow band" forms) — *Aglantha*, *Munida*, and *Euphausia* fall within this group, showing distributions similar to those of their conspecifics in Saanich Inlet.

Group 3 (mesopelagic "broad band" forms) — These include all except one of the remaining forms shown in Fig. 8. Of these, *Nanomia* and *Euphysa* showed a deeper distribution as adults than as young. *Aegina* young, by contrast, occurred deeper than the adults. A second species of *Tomopteris*, presumed to be *T. septentrionalis*, and *Dimophyes artica* also belong in group 3, along with two unidentified ctenophores, a colorless beroid, and a large elongate cydippid. Finally, a *Lensia*-like diphyid and a small agalmid siphonophore, about half the size of a mature *Nanomia*, colorless and deep living, were quite conspicuous in the lower group 3 range.

Group 4 (bathypelagic) — The only representative of the Jervis plankton that can be assigned to this class is *Beroe abyssicola*, which appears to be confined to the aphotic zone, and shows the dark red coloration typical of such forms.

GENERAL OBSERVATIONS

The opportunity to observe midwater animals feeding, swimming, and interacting in their natural habitat is one of the great attractions of submersible operations. The presence of a motionless submersible is unlikely to affect the behavior of

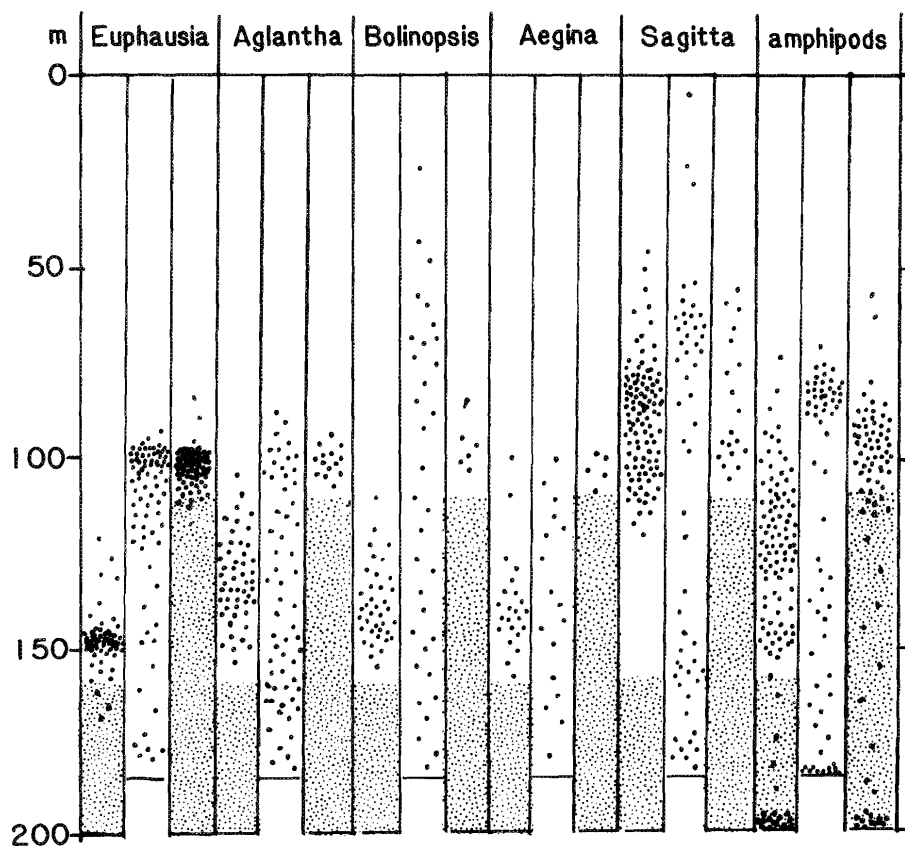


FIG. 5. Distribution of selected species in relation to the oxycline, Saanich Inlet, station 2. The three columns under each species give data for August 20–22, November 5–7, 1980, and March 30–April 3, 1981, respectively. Stippling shows oxygen-deficient zone ($<0.2 \text{ mL O}_2 \cdot \text{L}^{-1}$).

most planktonic species, except insofar as the lights may produce responses. Mackie (1974) questioned some of Barham's observations of siphonophore behavior on these grounds, but we can now confirm the validity of Barham's report on the behavior of *Nanomia*, having observed the same activities under conditions where the lights could not have been responsible. Barham (1970) suggested that some marine organisms are sensitive to electric signals produced by submersibles, but this possibility has yet to be systematically explored.

Many members of the zooplankton are normally in a state of restless activity, and this applies not only to crustacean microplankton but to some larger, gelatinous forms as well. Eudoxids and polygastric stages of *Muggiaea* and medusae such as *Aglantha* have been seen performing the rhythmic feeding cycles associated with food collection seen in the laboratory. *Aglantha* also perform the rapid escape type of swimming (Donaldson et al. 1980) in conditions that suggest that escape from potentially damaging contact with other organisms is frequently called for and effectively executed. *Aegina* are seen swimming with the tentacles clustered "teepee" fashion above the bell, very much as illustrated for *Aeginopsis* by Pérès (1959). *Bolinopsis* usually hang vertically, with their oral lobes down, beating their combs

enough to maintain this position. Occasionally, the ctenophore contracts its lobes suddenly and swims off rapidly to one side. *Pleurobrachia* species *B* can cruise slowly with tentacles outstretched or more rapidly (approximately $2 \text{ cm} \cdot \text{s}^{-1}$) with them contracted. *Tomopteris* appear to swim continuously. *Sagitta* make spasmodic darting movements. *Munida* larvae hang with chelae held vertically over their heads. *Oikopleura* beat their tails in a slow rhythm while in their houses but swim in rapid bursts when outside.

According to Franqueville (1970), the zooplankton is in perpetual movement, ascending and descending, except during a short period around the middle of the day. This observation was not verified in the present study, but alternating ascents and descents were observed in *Aglantha*.

Munida larvae are white during the day at their midwater depth, but on rising to the surface at night, they are red, doubtlessly due to chromatophore expansion. The photoprotective advantage attributed to such changes in copepods (Hairston 1980) can hardly apply here. It is of interest that another pelagic galatheid, *Pleuroncodes*, also performs vertical migrations (Boyd 1967) and shows diel changes in coloration (C. M. Boyd, Dalhousie University, personal communication).

Previous submersible users in British Columbia waters

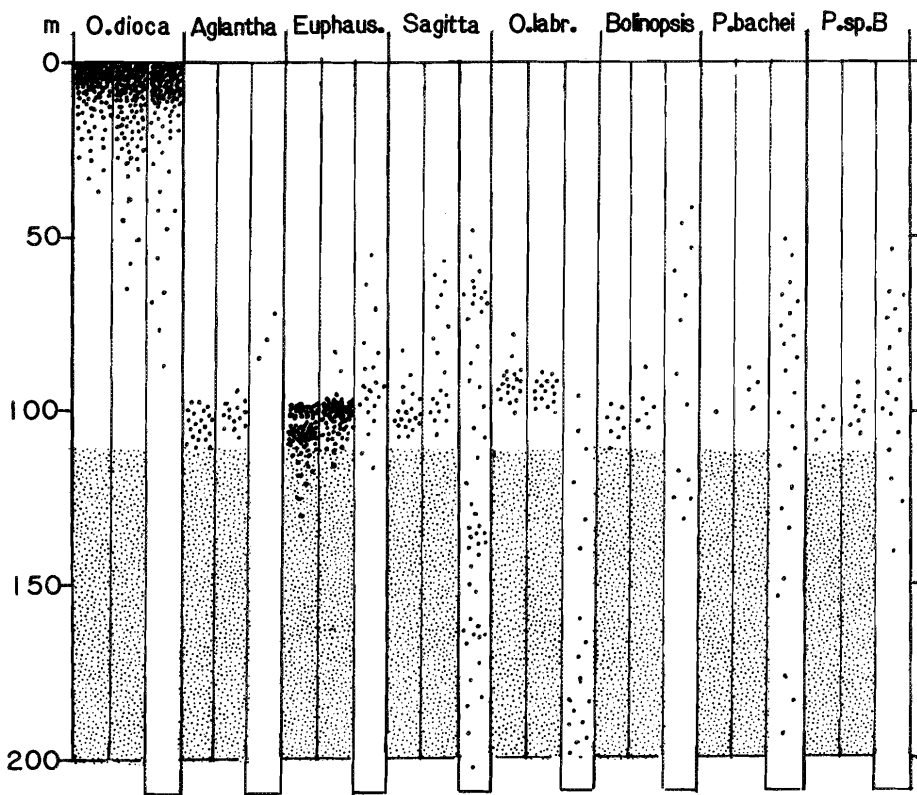


FIG. 6. Distribution of selected species in Saanich Inlet compared with Stuart Channel, March 30–April 3, 1981. Under each species, the three columns represent, respectively, stations 4, 5, and 6, stations 2 and 3, and station 1. Stippling shows dysaerobic zone of Saanich Inlet.

have commented on the abundance of "mucus" in the water. Herlinveaux (1970) suggested that some such objects were decomposing ctenophores. Levings and McDaniel (1973) regarded them as clusters of dead phytoplankton. The material in question occurs in the form of sheets up to 10 cm wide, filaments, and medusiform "parachutes" and presumably corresponds to the "marine snow" of some authors (e.g. Silver et al. 1978; Caron et al. 1982). The aggregates were most frequently observed just above the oxycline in Saanich Inlet, where they achieved densities as high as $500 \cdot \text{m}^{-3}$. They were present in lower concentrations in the anoxic layer. Aggregates seen in the upper water were usually small and may correspond to the microbial clumps reported by Seki (1971). Zonation of such aggregates has been described in waters off Toulon (Pérès and Piccard 1956) and St. Tropez (Franqueville 1970).

Very fine particles were conspicuous in the basin water of Saanich Inlet, forming milky clouds toward the top of the oxygen-depleted water. Elemental sulphur is reported to occur in the anoxic water (R. H. Herlinveaux, Institute of Ocean Sciences, Sidney, B.C., personal communication), but manganese oxide and associated bacteria may also be present at the oxycline (Emerson et al. 1979).

Finally, crustacean exoskeletons and abandoned *Oikopleura* houses were frequently seen from the submersible.

Considering the abundance of euphausiids in the inlet and the fact that they molt throughout life, there must be a substantial fallout of exoskeletal debris entering the anoxic layer.

Light emission from *Oikopleura* was very striking near the surface at night, when these forms were abundant. The empty houses as well as inhabited ones luminesce, as noted by Galt (1978). Flashes due to hydromedusae such as *Phialidium gregarium* and to euphausiids were of common occurrence but were not systematically studied.

During a dive in March 1981 it was noted that large, filamentous "parachutes" were strongly luminescent when the water was perturbed by the motion of the submersible. This was observed only down to 108 cm, the top of the oxycline. Below that point the aggregates did not emit light. Marine snow is known to provide a habitat for very large numbers of bacteria (Caron et al. 1982), and the luminescence may therefore be of bacterial origin and hence oxygen dependent.

The *Pisces* can be set to move slowly forward at 0.5 knots ($25 \text{ cm} \cdot \text{s}^{-1}$), which allows the observers to note variations in plankton composition and density at any given depth. Patchiness was apparent in Saanich Inlet. In one dive, density of *Euphausia pacifica* at 104 m varied in a single transect from 1000 to $10\,000 \cdot \text{m}^{-3}$. *Aglantha digitale* varied from 2 to $25 \cdot \text{m}^{-3}$ at 100 m. Accurate plotting of patches should be feasible in a manoeuvrable submersible such as *Pisces*.

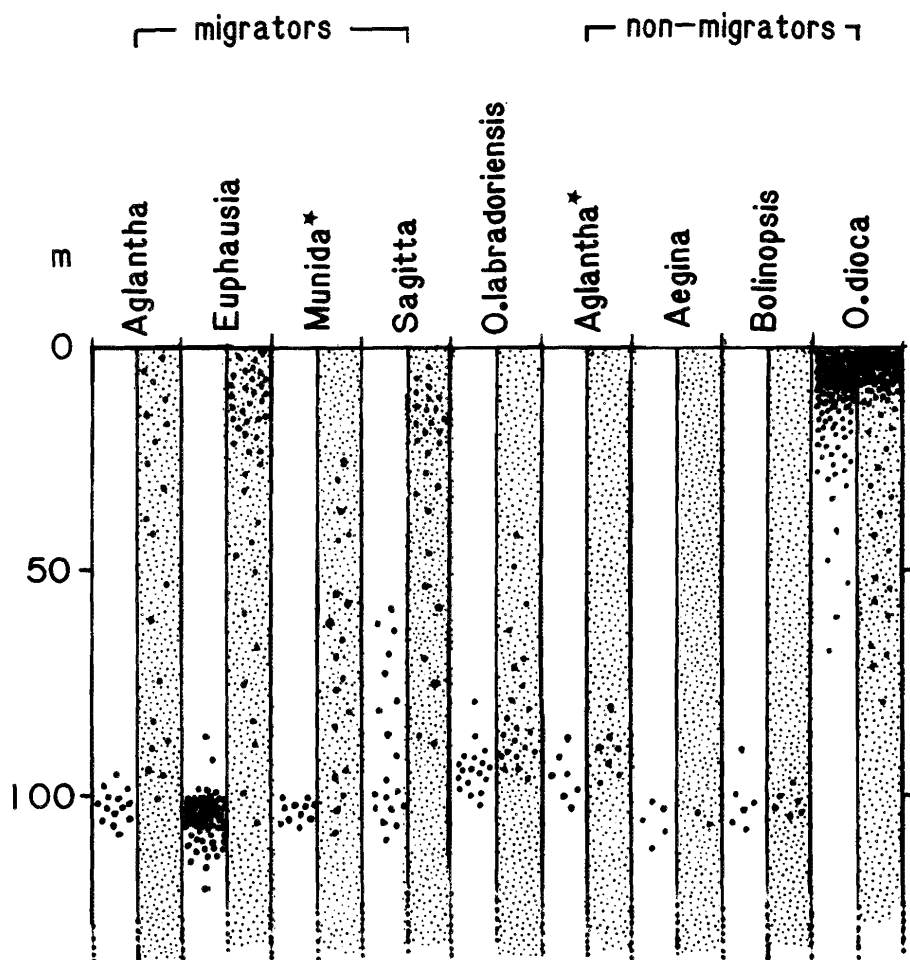


FIG. 7. Distribution of selected species as observed in consecutive day-night dives, station 2, Saanich Inlet, illustrating vertical migration. The day dive (empty columns) took place at 13:30–16:30 h, March 30, 1981, and the night dive (stippled column) took place at 21:00–23:00 h, March 30, 1981, except in the cases of *Munida** and *Aglantha**, which were observed during an earlier pair of dives on March 11, 1981.

TABLE 4. Stratification of *Euphausia pacifica*, Saanich Inlet, Aug. 1980–March 1981.

Data	Time	Station	Depth range (m)	Concentration depth (m)	Concentration density (No. \cdot m $^{-3}$)
Aug. 19–22	Day	C, D, E	120–170	147–150	1500
Nov. 4–7	Day	B, C	94–180	97–102	100–500
Mar. 11–12	Day	C	70–120	98–103	1000
	Night	C	10–105	10–40	500
Mar. 30–Apr. 3	Day	E, F	85–120	99–112	1000–10 000
Mar. 30	Night	E	0–105	10–15	50

Discussion

BIOLOGICAL INSIGHTS

The current series of dives has allowed us to gain a better appreciation of the composition of the macroplankton com-

munities along the coast of British Columbia. This applies especially to gelatinous forms (which were the main focus of the study) and most of all for those ctenophores poorly preserved in net hauls.

Data from net sampling (Hoos 1970), echo sounding (Bary 1967), and respiration measurements (Devol 1981)

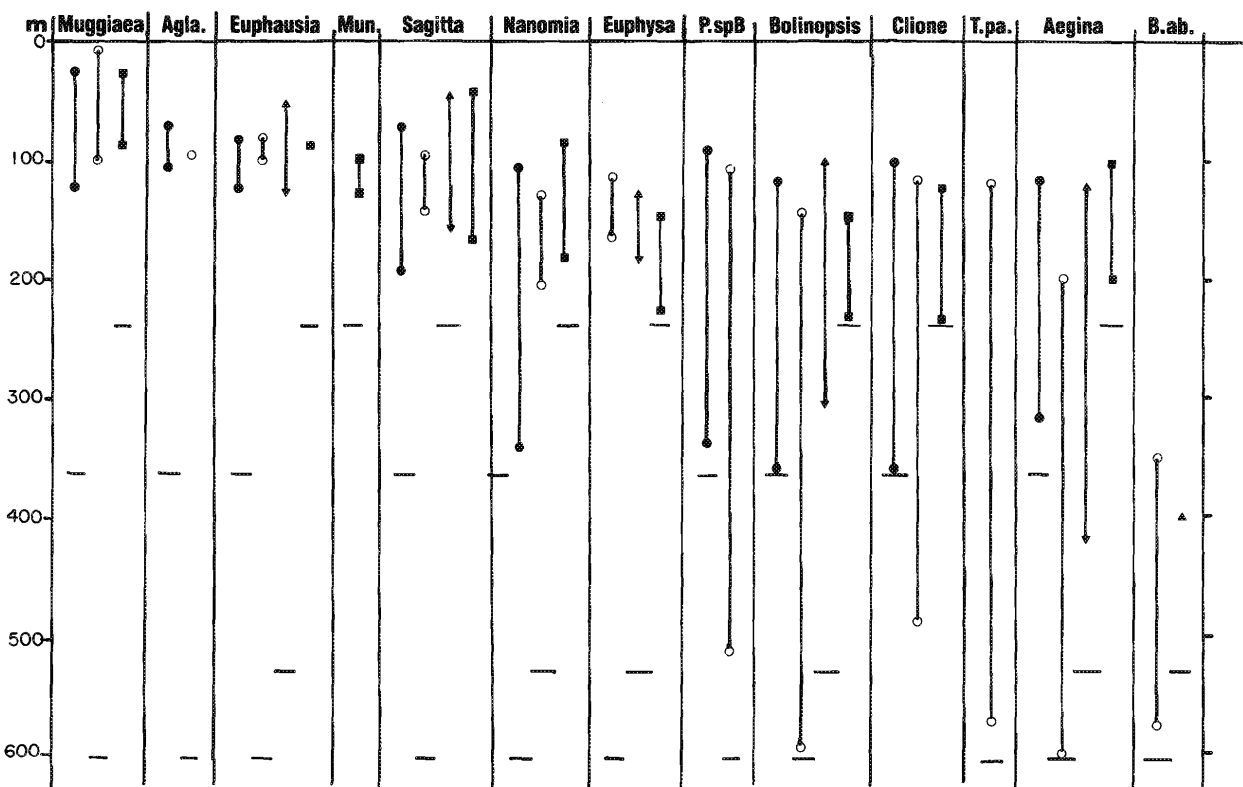


FIG. 8. Vertical distribution of selected species in Jervis Inlet, Knight Inlet, and Howe Sound, spring 1980 and 1981. Horizontal lines indicate depth to which submersible descended. ●, Jervis Inlet, May 21, 1981; ○, Jervis Inlet, February 22–23, 1981; ▲, Knight Inlet, February 12–19, 1981; ■, Howe Sound, March 17–20, 1981.

all indicate elevated concentrations of plankton over the oxycline, but the observations from *Pisces* show that several species (e.g. *Agathia* and *Euphausia*) occur in much higher numbers and within much narrower bands than hitherto suspected. Waters containing less than about $0.2 \text{ mL O}_2 \cdot \text{L}^{-1}$ are known to be inhospitable to most zooplankton (Longhurst 1967) although where oxygen minimum layers show sufficient long-term stability some species may adapt toward a more anaerobic existence (Childress 1975), as *Orchomenella affinis* appears to have done in Saanich Inlet. The accumulation of plankton above the oxycline in Saanich Inlet may simply be due to a barrier or false-bottom effect upon diurnally migrating species (Devol 1981). The possibility that the abundance of zooplankton here is due in part to increased food availability is an attractive one, because microorganisms are known to thrive at oxic–anoxic interface regions in other areas (Karl et al. 1977). Bacteria catalyzing oxidation of manganese, iron, and sulphur could represent an important food source. The recent work of Devol (1981) shows no evidence of increase in microzooplankton respiration at the oxycline, but Emerson et al. (1979) estimate that 80% (by weight) of the particles in this zone are bacteria, and the issue cannot yet be regarded as settled.

Whether or not the high densities of euphausiids over the oxycline are partly due to their ability to exploit a chemoautotrophic carbon production, it is well demonstrated that

they migrate to the surface at night and presumably ingest food derived from photosynthetic production. Several other crustaceans and *Sagitta* follow a similar migration path in Saanich Inlet. Information on copepods and other smaller crustacean zooplankters is scanty. These forms are difficult to observe from submersibles, but this drawback can be offset by better training of observers. Recently, we have found it possible to distinguish six copepod species from the observer ports of the *Pisces*.

We have verified that the dysaerobic zone of Saanich Inlet is inhospitable to all plankton, except the amphipod *Orchomenella affinis*. While Saanich is certainly a "rather weird" inlet (Pieper, in discussion following Bary and Pieper 1970), it has received a great deal of attention over the years since 1927 (Herlinveaux 1962) and is currently of interest in providing a possible model for the chemical–microbiological processes believed to be occurring in hydrothermal vent regions of the ocean floor.

POTENTIAL OF *PISCES IV* FOR PLANKTON WORK

The basic vehicle is one of the most manoeuvrable small submersibles and is therefore well suited to delicate operations in the pelagic as well as in the benthic realms. The submersible can reveal important facts about both the composition and the distribution of the plankton and of the activ-

ities and interactions of the organisms composing it, adding to the data obtained by other means. There are, however, still some ways in which its usefulness could be improved, and some of these points may be applicable to other submersibles.

- 1) Training of observers: the ability of observers to distinguish as many organisms as possible down to the species level is a factor of the first importance and justifies extensive pre-dive preparation.
- 2) Continuous automatic monitoring during dives of water conductivity, temperature, and depth, as well as oxygen content would be of considerable benefit in terms of the efficient use of observer time.
- 3) Light penetration: interpretation of plankton movements in the epi- and meso-pelagic realms obviously calls for exact information on light penetration.
- 4) For many applications, it would seem desirable to make dives concurrently with echo sounding at various frequencies. The observers in the submersible can directly report on the composition of the scattering layers.
- 5) Of great value is the regular checking of submersible sightings against data obtained by net sampling. Observers in the submersible can see many things missed by net sampling and vice versa. It would be of considerable interest to conduct submersible observations in conjunction with surveys made with a sophisticated closing net system such as Bioness (Sameoto et al. 1980).
- 6) Of proven value in the hands of submersible users elsewhere have been devices for capturing and transporting specimens undamaged to the surface and for obtaining seawater samples containing particles or other suspended objects under the direct control of observers within the submersible. Such devices should be developed for use with *Piscès*.

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