

Midwater macroplankton of British Columbia studied by submersible *PISCES IV*

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Abstract. Data are reported from 30 dives during winter and spring 1980–83 at sites in the Strait of Georgia and inlets running off it, and in inlets on the west coast of Vancouver Island. Observations were made from the surface to the bottom (maximum 733 m) but most attention was given to the midwater plankton community. The vertical distribution and abundance of hydromedusae, siphonophores, ctenophores, euphausiids, pelagic worms and molluscs were recorded systematically, along with data for one copepod species (*Neocalanus plumchrus*). The midwater environment was found to be stable in terms of species composition and depth ranges, which permitted the data for several years and many locations to be pooled. Four categories of plankton are recognized: (a) epipelagic (concentrated in the top 50 m); (b) mesopelagic (50–175 m); (c) bathypelagic (below 175 m); and (d) meso-bathypelagic (forms living in both meso- and bathypelagic zones). Species in this last category behave like mesopelagic forms at the upper end of their ranges, migrating to the surface at night. Deeper-lying members of the same species do not migrate. For six such species, the cut-off point between migratory and non-migratory components was found to lie at a mean depth of 175 m. This depth is therefore taken as the demarcation point between the meso- and bathypelagic zones. Taking account of published data on light penetration, it is estimated that, for the whole region, daytime light intensity at 175 m, and hence the effective limit for phototaxis of the species in question, lies in the range 10^{-8} – 10^{-9} $\mu\text{W cm}^{-2}$.

Introduction

The use of manned submersibles for plankton studies has obvious attractions. Behaviour can be observed directly *in situ* and the distribution of fragile gelatinous plankton species which are poorly preserved in net samples can be recorded. On the other hand, observations for submersibles are difficult to quantitate and, unless devices are available for capturing specimens seen during dives, identification may pose a problem. A discussion of these topics by a group of food-chain workers (Mauchline, 1977) led to the general conclusion that 'this anecdotal information is of tremendous value in understanding many aspects of the biology of midwater organisms'.

It was with the object of making submersible observations less anecdotal and more quantitative that Mackie and Mills (1983) carried out a preliminary series of dives with the submersible *PISCES IV*. They were concerned primarily with methodology. A similar study by Russian workers using *ARGUS* came out at about the same time (Vinogradov and Shushkina, 1982).

In the present report observations from *PISCES* are presented in detail. The focus is on the gelatinous macroplankton as the component most readily observed from the submersible and least well known from net sampling studies. Information was also obtained on crustaceans, chaetognaths and larvaceans, but most of these forms have been intensively studied by conventional sampling techniques (reviewed by Harrison *et al.*, 1983) and, with the exception of one copepod and one euphausiid, are ignored in the present account. Fishes and squid are also omitted. Observations on these forms are hard to interpret because they are acutely photosensitive and are capable of rapidly escaping from the vicinity of the submersible or of aggregating near it, in either case

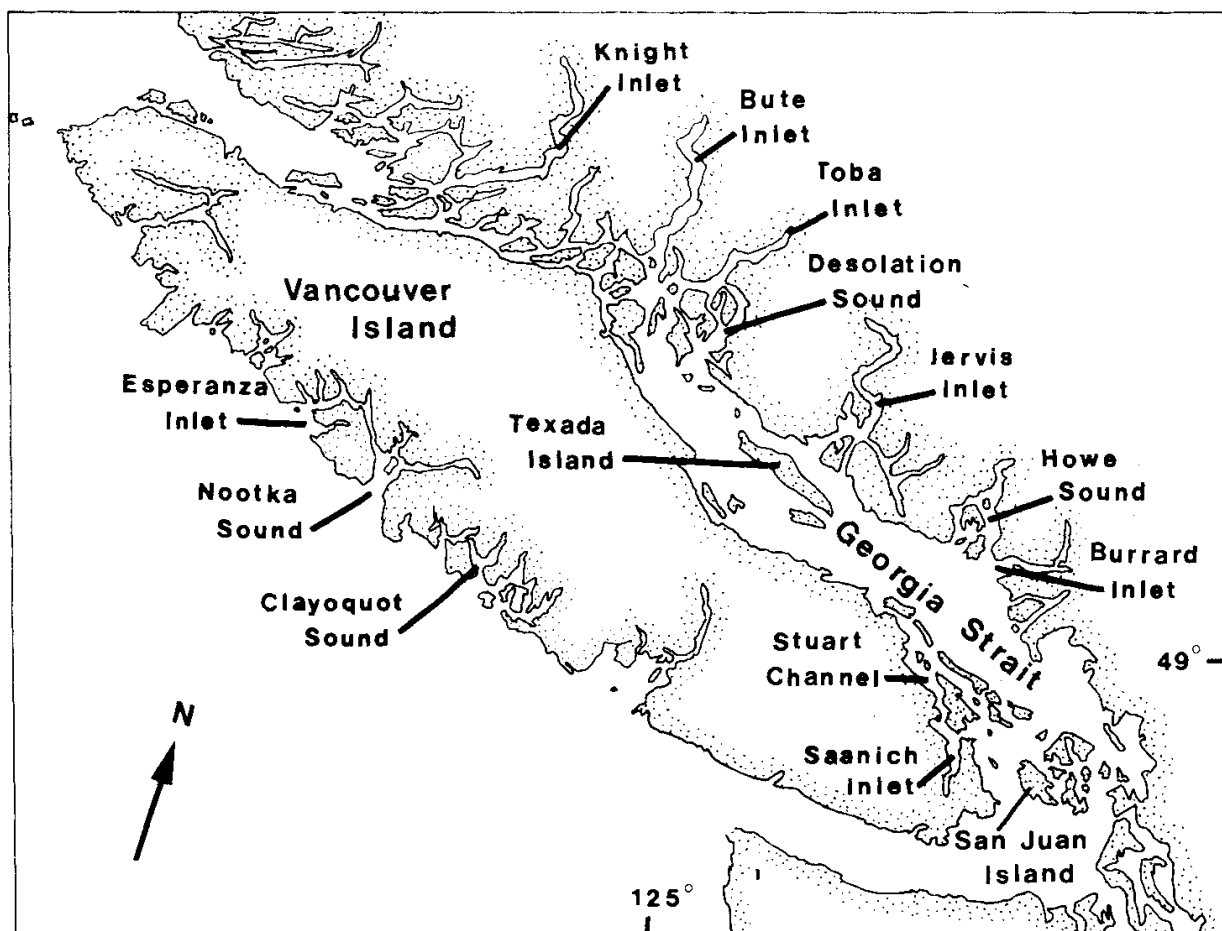


Fig. 1. Map of the study area.

presenting a distorted picture of the normal distribution.

Observations of the plankton presented here are restricted to what may be termed the midwater community (i.e., forms showing daytime distributions from ~50 m down to the bottom). Epipelagic species (living in the top 50 m) are hard to study from the submersible because of difficulties associated with manoeuvring near the surface and because the diffuse scattering of daylight makes it impossible to achieve dark-field illumination using the submersible's lights, which is a necessary condition for accurate sighting.

The sites chosen for dives are shown in Figure 1. Harrison *et al.* (1983) recognize six well-developed inlet systems associated with the Strait of Georgia. We were able to dive in four of these: Jarvis Inlet, Howe Sound, Desolation Sound and Saanich Inlet. The last named differs from typical coastal inlets in having an anoxic basin for a large part of the year which drastically alters the midwater plankton distribution. Data from dives in Saanich Inlet will be presented separately (C.E.Mills, in preparation). For comparison with the four inlet systems, we have dived in two locations in the open straits, one just south of Texada Island, close to Gardner's (1977) Geo 1748 sampling station and to the main sampling station of Arai and Mason (1982), the other in Stuart Channel. Some observations by V.J.Tunncliffe from Knight Inlet are also included.

For comparison with all of the above 'inner' sites, we have dived in the relatively shallow 'outer' inlets of the Nootka-Esperanza system and Clayoquot Sound on the west side of Vancouver Island. Plans to dive in deep water off the continental shelf

Table I. Summary of dive sites.

Area	Dive site	Acronym
Jervis Inlet	Foley Head	JF
	Saumarez Bluff, Prince of Wales Reach	JS
	Point Patrick, Princess Royal Reach	JP
Howe Sound	Point Artaban, Gambier Island	HG
	Inner Basin	HI
Central Georgia Strait	Stuart Channel	ST
	Point Upwood, Texada Island	TE
Northern Georgia Strait (Desolation Sound)	Toba Inlet	TO
	Homfray Channel	HO
	Waddington Channel	WA
	Pendrell Sound	PE
Knight Inlet	Over the sill	KS
	Sail Cone	KC
	Tomakstum Island	KT
	Naena Point	KN
	Tsukola Point	KK
	Rubble Point	KR
West side of Vancouver Island	Tlupana Inlet, off Nootka Sound	TL
	Tahsis Inlet, off Nootka Sound	TA
	Hecate Channel, off Esperanza Inlet	HE
	Shelter Inlet, off Clayoquot Sound	SH

were abandoned owing to weather conditions. Thus, the dives reported here fall into six regional categories, as listed in Table I.

Water characteristics for the area are described by Pickard (1961, 1963). While surface temperatures and salinities vary considerably and in complex ways, these variations have little effect on conditions in deeper water at the dive sites. There is no evidence that the distribution of the midwater plankton is significantly affected by temperature or salinity discontinuities. No such barriers were detected below ~ 30 m at any time. Oxygen becomes a limiting factor when its concentration falls below ~ 0.2 ml/l $^{-1}$ as in Saanich Inlet, but the waters surveyed in the present study were not so affected.

This study represents a first attempt to make a quantitative determination by direct observation of the distribution of the many interesting and poorly known midwater gelatinous plankton species in a region of deep coastal fjords. Information of this sort is essential for even the most preliminary assessment of the significance of the species in question as members of midwater food chains.

Methods

The characteristics of *PISCES IV* and details of our methods of observation and enumeration of the plankton have been fully described elsewhere (Mackie and Mills, 1983). For the 1983 dives, plankton trapping devices which could be operated under visual control from the submersible were constructed. These proved useful for capturing midwater organisms and bringing them to the surface in pristine condition.

In Figures 2–9, each spot represents a depth at which one or more members of the

species in question were sighted during a single slow descent through the water column. If specimens were sighted during subsequent ascents or descents during the same dive, they were not included. An exception was made for sightings which substantially extended the vertical range as determined initially. Where the density of a species could be estimated with confidence, a number representing numbers of animals m^{-3} takes the place of a spot. Absence of numbers does not necessarily mean that only one specimen was seen. The observers were often too busy recording the overall distributional picture to estimate densities of individual species.

Two observers as well as the pilot were present in all dives but in the interests of consistency only one set of sightings (those of the author) have been included in the figures, except where the second observer's sightings substantially extended the observed depth range or filled in anomalous gaps in the author's records. However, all the observations reported for the dive carried out in Jervis Inlet on the morning of 24 May 1983 were made by C.E.Mills and J.Fulton. The Knight Inlet data were extracted from dive transcripts made available by V.J.Tunncliffe.

For each species a summary distribution curve was made by dividing the vertical range up into 20-m sections and counting the total number of sightings within each section. This number was then expressed as a percentage of an arbitrarily selected 'maximum', the number of dives passing through the section in question multiplied by three (which was the largest number of sightings ever recorded for any species in a single 20-m section). The points so obtained were plotted and a curve fitted to them (Figures 11, 12). Points are included for *Dimophyes arctica* (Figure 11) but have been omitted elsewhere for simplicity. Night-dive data were included in the counts only for species which did not show a nocturnal redistribution pattern. Where a number takes the place of a spot, this was counted as a single sighting regardless of magnitude. A broken line at the lower end of a curve indicates that the plot in this region is an extrapolation from the upper, reliable part of the curve into a lower depth region where animals were present but which was visited on too few occasions for a curve to be drawn with normal confidence.

The purpose of the summary curves is to show the typical vertical range of each species and the relative sighting frequency at different depths. All the dives were lumped together to provide the data base for calculation of these distribution curves. The mid-water environment appears to be fairly homogeneous and most species show similar distributions throughout the study area, with only minor regional and seasonal variations. Some exceptions are noted in the sections dealing with individual species which follow.

Siphonophora

Calycophora

Dimophyes arctica (Figure 2A). Commonly seen between 30 and 160 m, this species may reach concentrations as high as 10 m^{-3} . There is no evidence of seasonal or diurnal changes in distribution. *D. arctica* has been reported abundant at much greater depths in other areas (Angel *et al.*, 1982). Some of the deeper sightings of '*Muggiaea atlantica*' reported by Mackie and Mills (1983) were probably *D. arctica*. Subsequent observations and study of net samples suggest that *M. atlantica* is an epipelagic species rarely

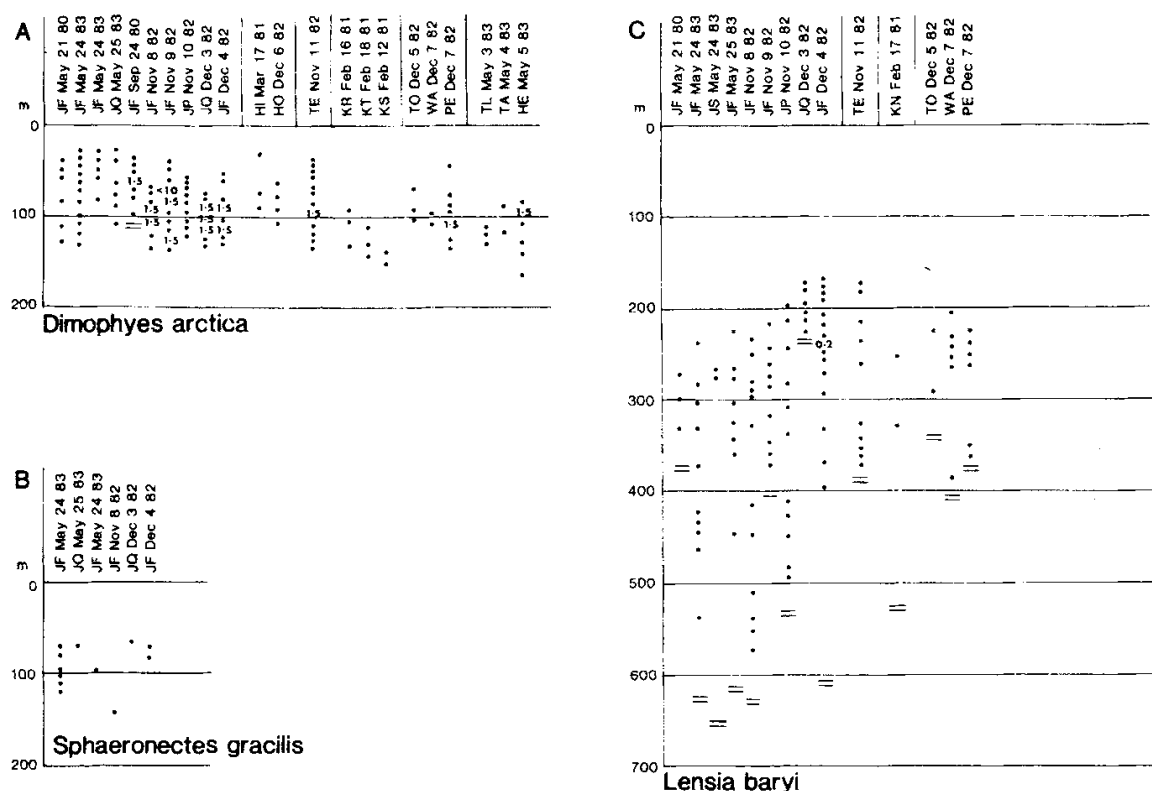


Fig. 2. Sightings of the calycophoran siphonophores: (A) *Dimophyes arctica*, (B) *Sphaeronectes gracilis* and (C) *Lensia baryi*. Double horizontal lines represent the greatest depth reached in the dive, which was usually the bottom.

occurring below ~50 m, and thus not a member of the midwater community.

Sphaeronectes gracilis (Figure 2B). Observed only in Jervis Inlet, where it was seen in both winter and spring months at 70–140 m, the small (3-cm long) transparent species may have escaped detection or have been mistaken for a larval siphonophore or eudoxid on other occasions. Even so, it is doubtful if *Sphaeronectes* ever constitutes a numerically important component of the regional plankton. There appear to be no records for this area, though *S. gracilis* is known from California (Bigelow and Leslie, 1930).

Lensia baryi (Figure 2C). The existence of a species of *Lensia* in Jervis Inlet was noted briefly by Mackie and Mills (1983) but the identification was unclear at the time, and there may have been some confusion with *D. arctica* in the region where the two overlap. Specimens of both species have since been captured alive from the submersible and their identifications verified. The first description of this species (Totton, 1965) was based on specimens from Burke Inlet, British Columbia. *L. baryi* was present at most inner dive sites, but was absent from the outer coastal inlets.

Physonectae

Nanomia cara (Figure 3A). Reports of *Nanomia* in coastal waters of British Columbia sometimes refer to *N. bijuga*, sometimes to *N. cara*. Mackie (1964) gave reasons for assigning all specimens to *N. cara*. Specimens captured from *PISCES IV* have been examined by P.R. Pugh who reports that the distinction between the two species is still unclear, but that our species conforms most closely to *N. cara*.

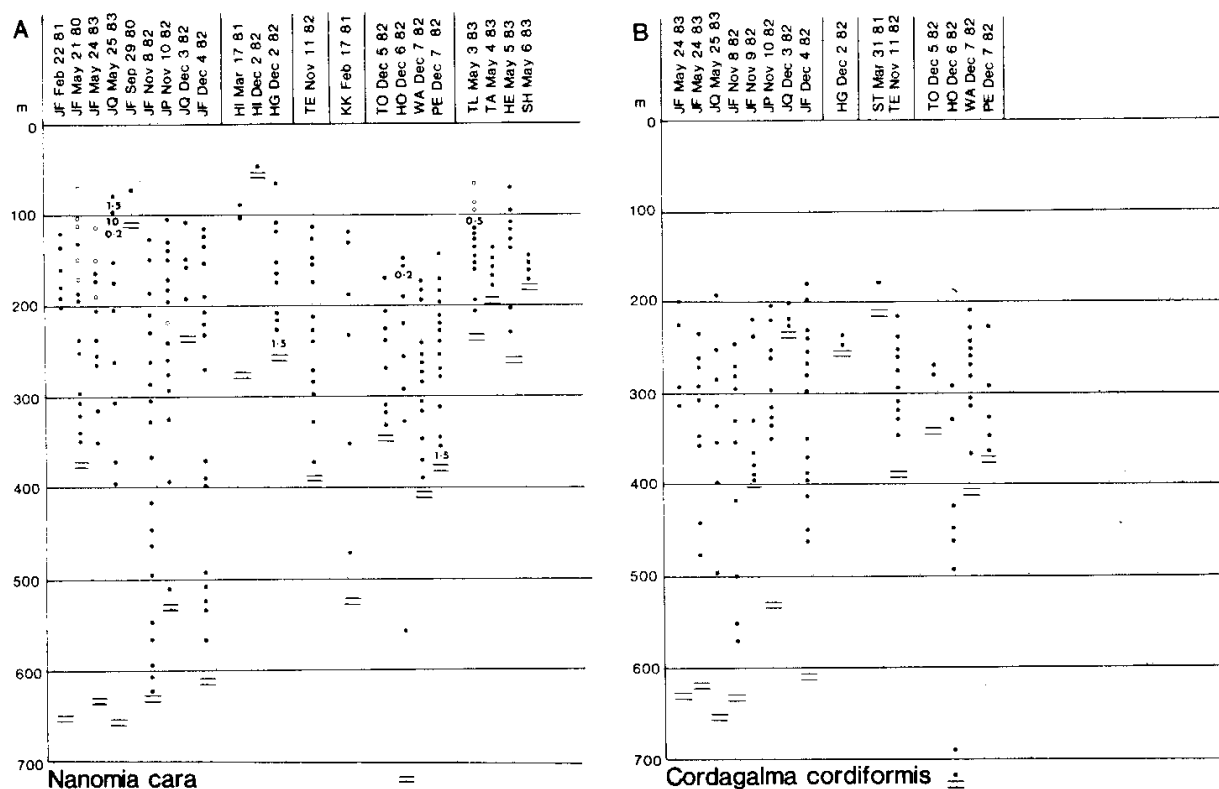


Fig. 3. Sightings of physonectid siphonophores: (A) *Nanomia cara* and (B) *Cordagalma cordiformis*. Open circles in A represent sightings of immature specimens.

Nanomia was seen in nearly all dives and at depths ranging from 70 to 620 m. It thus shows one of the greatest daytime vertical ranges of any of our species. An upper portion of the population migrates to the surface at night (Figure 13).

In Jervis Inlet, small specimens were seen in the upper part of the vertical range during May, and the population as a whole did not appear to extend below 400 m, but in November and December, specimens were often seen below 400 m. There is a similar, deep sighting for Homfray Channel. These observations suggest a seasonal progression starting with a spring crop of early post-larval stages at ~70–190 m, these individuals growing and penetrating deeper waters as the season advances.

Cordagalma cordiformis (Figure 3B). A small, colourless, deep-living agalmid was seen by Mackie and Mills (1983) in Jervis Inlet, but could not be identified. Specimens have since been caught from the submersible in a manipulator-held plankton trap, and nectophores have been retrieved from plankton samples in the same location. Our specimens conform perfectly to Carré's (1968) description of *C. cordiformis*.

Cordagalma shows a distribution almost identical to that of *L. baryi*. It is probably the most fragile of all physonectid siphonophores, which may explain the infrequency with which it has been reported from net samples. Slight swirling caused by a touch on the submersible's thrusters can cause it to break up into segments 10–50 mm long. Many such stem fragments were seen during dives under conditions where fragmentation could not have been due to the submersible. It would appear that fragmentation is a normal form of autotomy presumably serving to distribute the sexual products.

Cordagalma swims very slowly and, unlike *Nanomia*, is incapable of reverse locomotion.

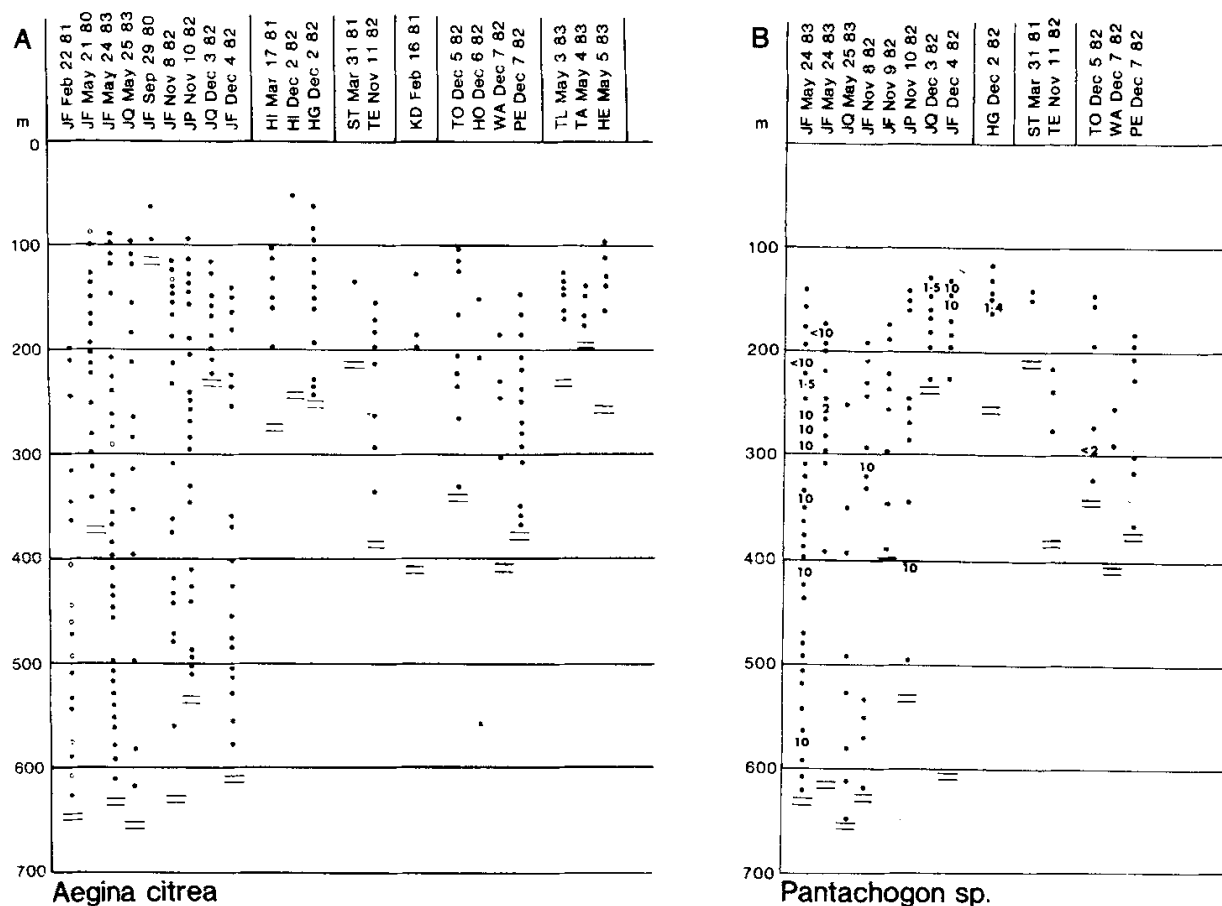


Fig. 4. Sightings of hydromedusae: (A) *Aegina citrea* and (B) *Pantachogon haeckeli*.

tion. Despite the minute size of the float, it is neutrally buoyant owing to the abundant gelatinous bracts and gonophores.

Hydromedusae

Narcomedusae

Aegina citrea (Figure 4A). Seen in nearly all dives, *Aegina* has an extensive vertical range and occurs at densities up to 10 m^{-3} . Few specimens were seen above 100 m during the day, confirming Arai and Mason (1982) but contradicting Gardner (1977) who found none below 200 m. *Aegina* may occur in very deep water as summarized by Arai and Mason (1982). A portion of the population above 200 m migrated to the surface at night in Jervis Inlet (Figure 13).

Small specimens of *Aegina* have been observed both in spring and autumn. Some extremely small specimens were seen in November at 450 m and data from several dives suggests that the young stages lie in deep water. Arai and Mason (1982) found small specimens most abundant at 200 m in April, 150 m in May.

Aegina is preyed upon by the large orange amphipod *Hyperia medusarum*. Specimens in all stages of destruction were seen from the submersible.

Trachymedusae

Pantachogon sp. (Figure 4B). The species in question very closely resembles *P. scotti*

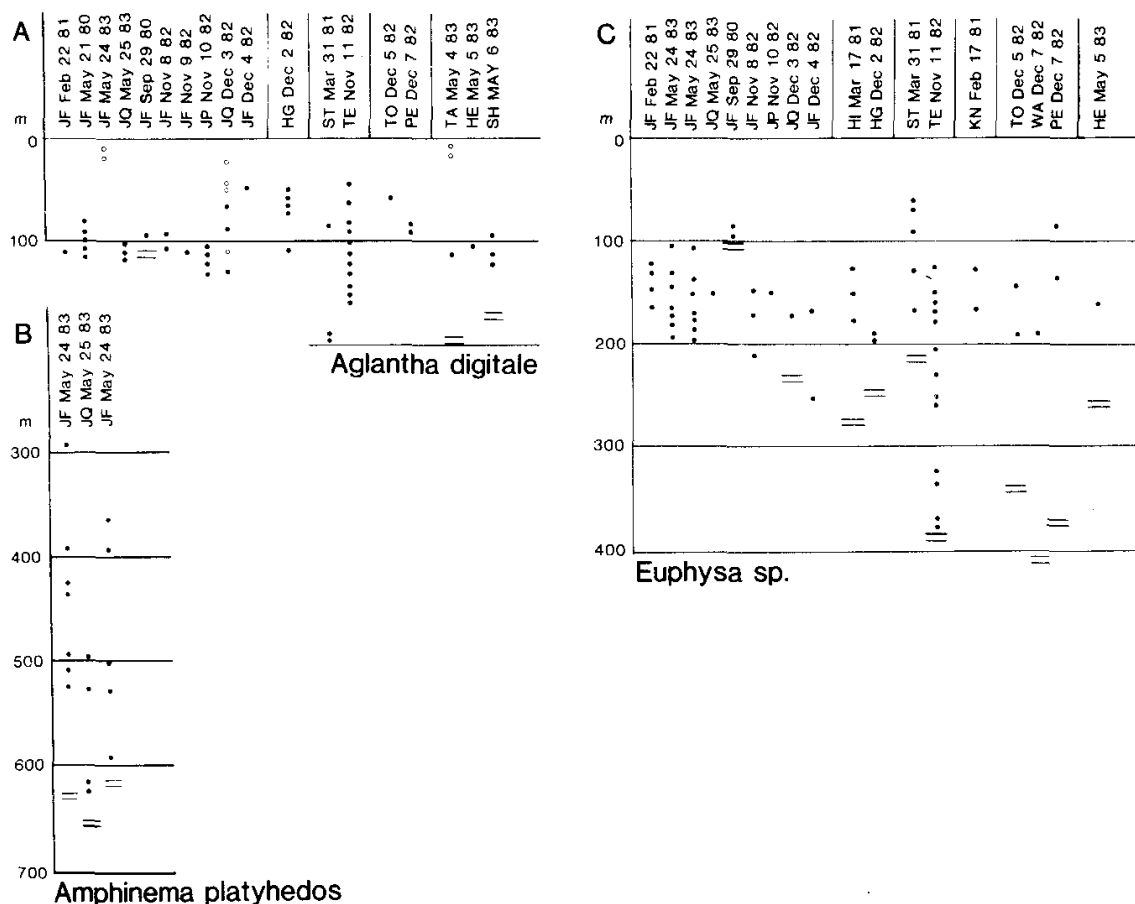


Fig. 5. Sightings of hydromedusae: (A) *Aglantha digitale*, (B) *Amphinema platyhedos* (?) and (C) *Euphysa* sp.

(Browne) but as the latter has not previously been recorded for the North Pacific, the determination will be left indefinite here pending study by a specialist. This tiny medusa was seen from 130 m to the bottom in most inner coastal locations, at densities up to 10 m^{-3} . In life, it holds its numerous fine tentacles stretched out symmetrically around it in the horizontal plane, like a halo. Periods of quiescence alternate with periods of frantic activity. Swimming contraction frequencies in the order of 5 Hz are exhibited in short bursts of frenzied locomotion.

Aglantha digitale (Figure 5A). Both in the protected inlets on the west side of Vancouver Island and those off Georgia Strait, *Aglantha* lay at 50–130 m during the day, but in open strait sites specimens were distributed more deeply, down to 200 m. Possibly this reflects greater mixing at the open sites. Arai and Brinkmann Voss (1980) review the extensive literature on this species. During our night dives in Jervis Inlet specimens were not abundant enough for a diel migration pattern to be apparent, and previous evidence is equivocal on this point (Mackie and Mills, 1983). Very small specimens were seen near the surface in May, confirming Zelickmann (1972) and Arai and Fulton (1973).

Ptychogastria polaris. This medusa, identified by M.N.Arai and A.Brinkmann-Voss from a single specimen captured from *PISCES* below 300 m in Jervis Inlet, was frequently seen attached to rock faces, to which it clings with its adhesive organs. We have only twice seen specimens swimming freely, always near the bottom. *Ptychogastria*

should be classified as an epibenthic form, capable of brief pelagic excursions. As deduced by Browne (1903) from its muscle structure, *Ptychogastria* is a vigorous swimmer. In the inlets off the Strait of Georgia, *Ptychogastria* has been seen between 200 and 580 m. Additional records from inlets further north, and from Cobb and Brown Bear Seamounts, mostly fall within the same depth range (V.J. Tunnicliffe, unpublished data).

Anthomedusae

Amphinema platyhedos (Figure 5B). Sixteen specimens were seen in three dives in Jervis Inlet. Specimens could not be captured for identification but the resemblance to Arai and Brinkmann-Voss' (1983) description of *A. platyhedos* is compelling. The data are insufficient to allow inclusion of this species in the summary distribution figures, but the depth range observed in Jervis Inlet corresponds to that described by Arai and Brinkmann Voss (1983) for other sites, and the species is evidently one of the deepest of all the truly pelagic species in the area, peaking between 450 and 500 m. The two perradial tentacles were usually held out almost horizontally on either side of the bell, extending as far as 15 cm on either side. Most specimens were inactive, but swimming was occasionally seen.

Euphysa sp. (Figure 5C). Doubt persists about the correct species designation of the common, midwater *Euphysa* of the Strait of Georgia (Arai and Mason, 1982). We earlier (Mackie and Mills, 1983) assigned it to *E. japonica*, following Kramp (1982). Arai and Mason found *Euphysa* in depths >150 m in the central strait. Our observations show peak abundance at about this depth. Density is never high. There is evidence for nocturnal redistribution (Figure 13).

Leptomedusae

Ptychogena lactea. Apart from one sighting at 450 m in Jervis Inlet, our only observations of this species were in the Nootka-Esperanza inlet complex, where they were seen between 50 and 220 m. All sightings were in November and December. In the Strait of Georgia (Arai and Mason, 1982) and San Juan Islands (Mills, 1981) *Ptychogena* disappears from the plankton in July.

Foersteria purpurea. Seen in only three dives (JF, 8 Nov 1982; ST, 31 Mar 1982; TL, 3 May 1983), this species usually lies immediately over the bottom, where it may be quite abundant. It should be considered a suprabenthic rather than a pelagic species. Specimens captured for identification differed slightly from preserved *F. purpurea* in minor points of tentacle number and gonad morphology, so the identification is tentative (M.N. Arai, personal communication).

Ctenophora

Lobata

Bolinopsis sp. (Figure 6A). Uncertainty regarding the species designations of this ubiquitous lobate, referred to as *Bolinopsis infundibulum* by Mackie and Mills (1983), persists. Several lobates seem to be present in the area. Both in spring and winter, specimens of a small lobate were frequently seen in the top 80 m. These are included

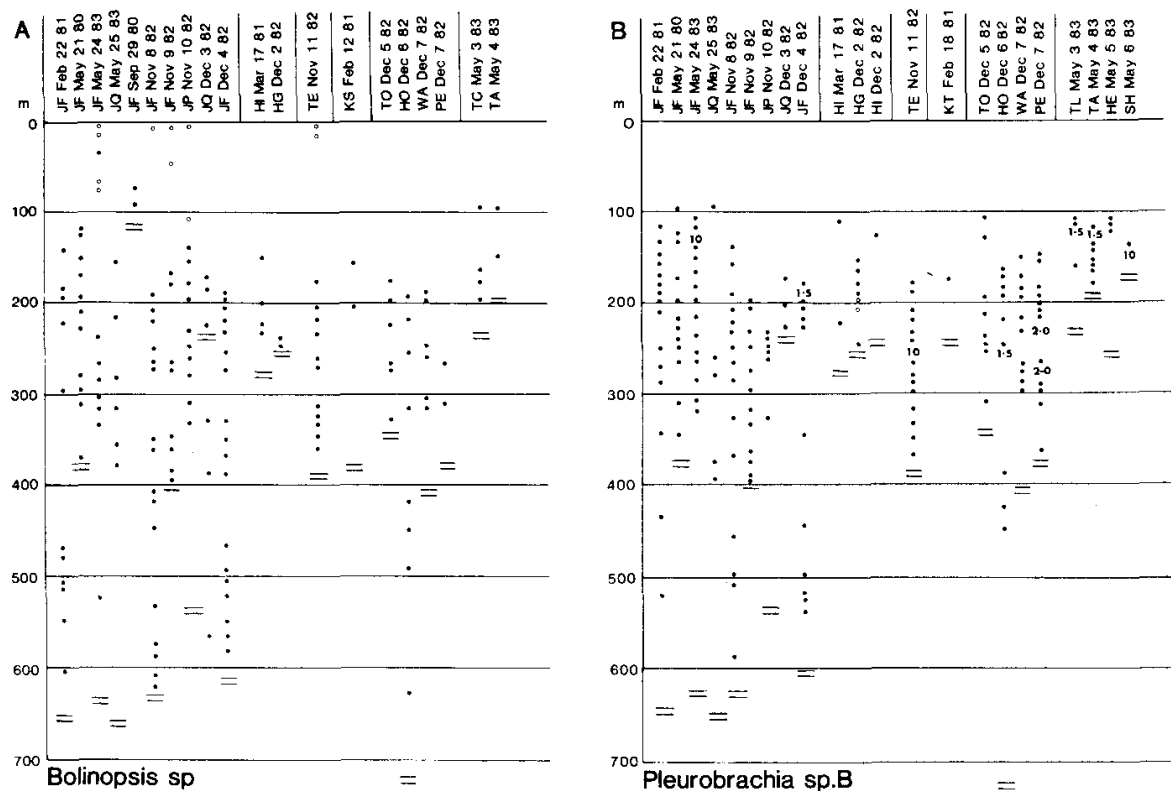


Fig. 6. Sightings of ctenophores: (A) *Bolinopsis* sp. and (B) *Pleurobrachia* sp. B. Open circles in A represent small lobates which may have been young *Bolinopsis* sp. but whose identity was not established.

in Figure 6A as open circles. It is possible that they were young specimens of the species of *Bolinopsis* that constitutes the main population but this requires confirmation. Because of uncertainty on this point, the small lobates are omitted from the *Bolinopsis* distribution curve (Figure 12A).

The zone of peak abundance for the main population lies at 250 m, with numbers falling off slowly with depth. Though individuals are usually spaced widely apart (> 3 m) the large size of these ctenophores (< 15 cm length) suggests that they have an important impact on the midwater crustacean plankton.

Cydippida

Pleurobrachia sp. (Figure 6B). The species referred to here is probably the same form occasionally seen at Friday Harbor, San Juan Islands which has widely spaced tentillae that contract into tight coils, as in *P. helicoides* (Ralph, 1950). Mackie and Mills (1983) called it *Pleurobrachia* sp. B to distinguish it from the common, surface living *P. bachei*. Larger specimens often have a whitish, opaque appearance. Attempts to preserve specimens caught in the plankton trap failed. Despite considerable care, they disintegrated completely on contact with the fixative. Because of its delicacy, the species is hard to recognize in fresh plankton, impossible after fixation. The only report of netted specimens which may belong to this species is Mortensen's (1927) mention of three specimens of a 'faintly whitish' cydippid from 400 m in the central Strait of Georgia. The specimens, which he called *Tinerfe* sp., could not be preserved. While there is undoubtedly a general resemblance to published drawings of *Tinerfe*, I am advised by S.Y. Chiu (Xiamen University, Fugien, China) that the position of the tentacle sheath

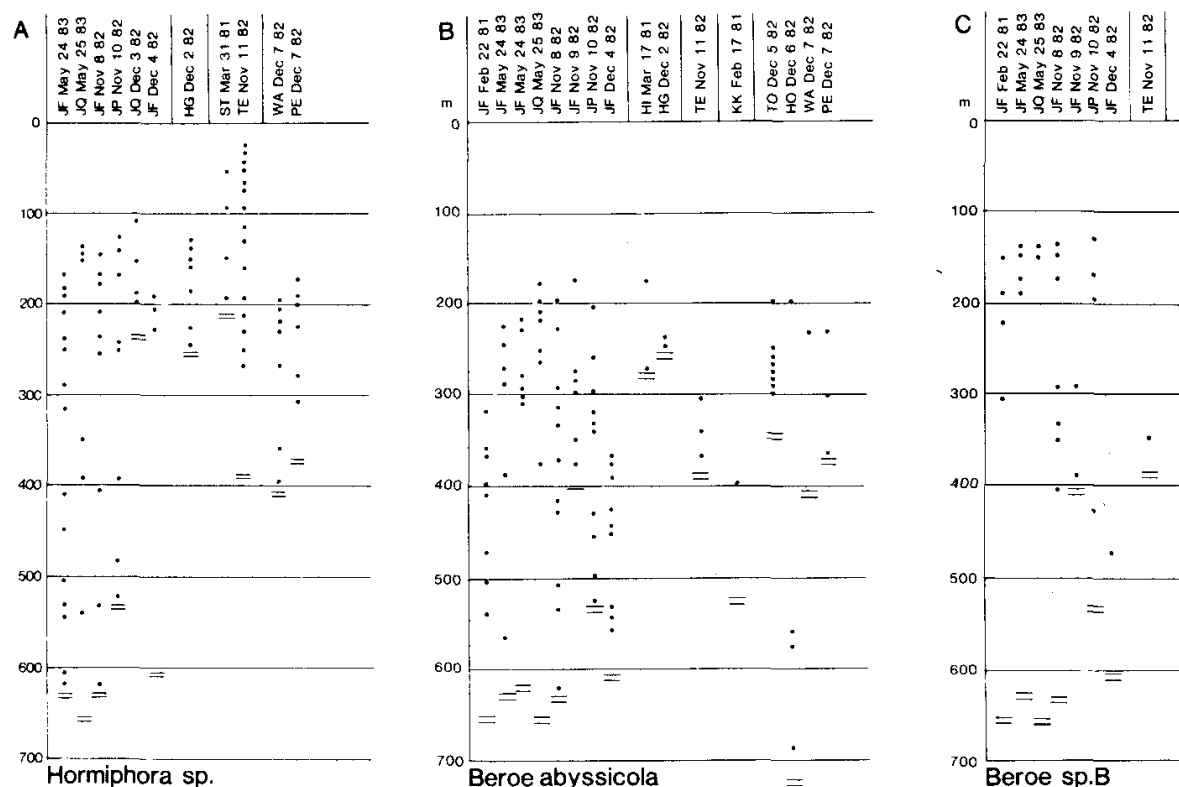


Fig. 7. Sightings of ctenophores: (A) *Hormiphora* sp., (B) *Beroe abyssicola* and (C) *Beroe* sp.B.

openings makes *Pleurobrachia* preferable, pending positive identification.

The zone of peak abundance lies near 250 m. Numbers fall off sharply with depth. The upper daytime limit lies at ~ 100 m. The species can swim backwards by reversing the power stroke in the comb plates, or hang motionless with the cilia arrested. Normal (forwards) swimming is very rapid and the animal tends to corkscrew as it swims. *Pleurobrachia* sp. B is the most abundant ctenophore in the study area. Densities reach 10 m^{-3} , and it was seen at all dive sites.

Hormiphora sp. (Figure 7A). Preserved specimens of this cydippid caught from the submersible were identified to *Hormiphora* sp. by G.R.Harbison (personal communication). *H. cucumis* and possibly other species occur in the San Juan Islands (Mills, 1981).

Peak abundance lies near 200 m. Specimens were seen above 100 m only in open strait sites, which seem to be better mixed than the inlets. Specimens were seen all the way to the bottom in Jervis Inlet. Though sightings were few, there are strong indications that *Hormiphora* is a vertical migrator (Figure 13).

Beroida

Beroe abyssicola (Figure 7B). The zone of peak abundance as observed from *PISCES IV* lies at 310 m with sightings declining slowly down to 690 m. Few specimens were seen above 200 m. M.N.Arai (personal communication) reports maximum density at 200–350 m in the central strait. The species is usually recognizable from the 'deep claret colour' (Mortensen, 1927) of the pharynx wall, but some specimens were paler.

Beroe sp. B (Figure 7C). Consistently seen in Jervis Inlet in both winter and spring, this colourless beroid was only once observed at another dive site. The observed depth

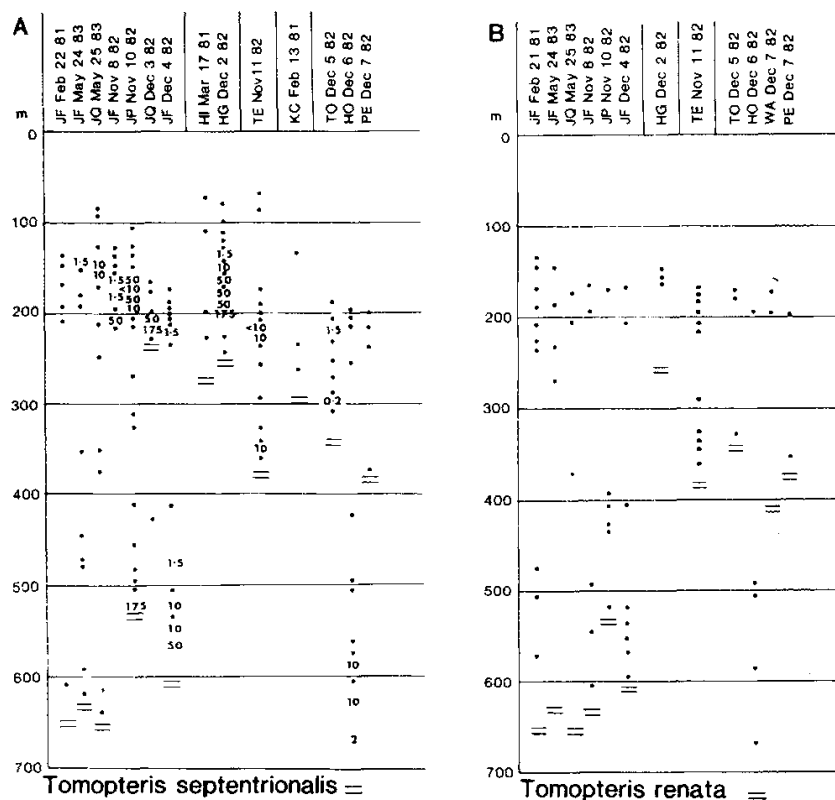


Fig. 8. Sightings of pelagic polychaetes: (A) *Tomopteris septentrionalis* and (B) *Tomopteris renata*.

range was 130–470 m. Numbers were always small. These observations are in accord with Fulton's (1968) capsule description of *B. cucumis* ('deep; rare, all year'), but specimens were not captured and the species cannot be determined with certainty.

Polychaeta

Tomopteris septentrionalis (Figure 8A). This predatory species has previously been found in densities up to 50 m^{-3} in vertical hauls from 400 m (Stephens *et al.*, 1969). In our dives, the daytime density peak lay at 210 m. This is consistent with Gardner (1977) and with recent *BIONESS* data from the central Strait of Georgia where J.D.Fulton (unpublished data) found 60% of the population of *Tomopteris* spp. (which would include *T. renata*) at 180 m in the morning (April 1983). Our data show *T. septentrionalis* present all the way to the bottom. Densities as high as 10 m^{-3} have been observed at 620 m. There is some indication of bimodality in the distribution, with a substantial part of the population concentrated between 500 and 600 m, but this requires confirmation. The species is often abundant close to the bottom, reaching densities as high as 175 m^{-3} , regardless of the depth. Migration to the surface occurs at night (Figure 13).

Tomopteris renata (Figure 8B). This large species, referred to earlier as *T. pacifica* (Mackie and Mills, 1983), though never as abundant as *T. septentrionalis*, like the latter was often abundant close to the bottom and migrated to the surface at night (Figure 13). Neither species of *Tomopteris* was observed in the inlets on the west side of Vancouver Island.

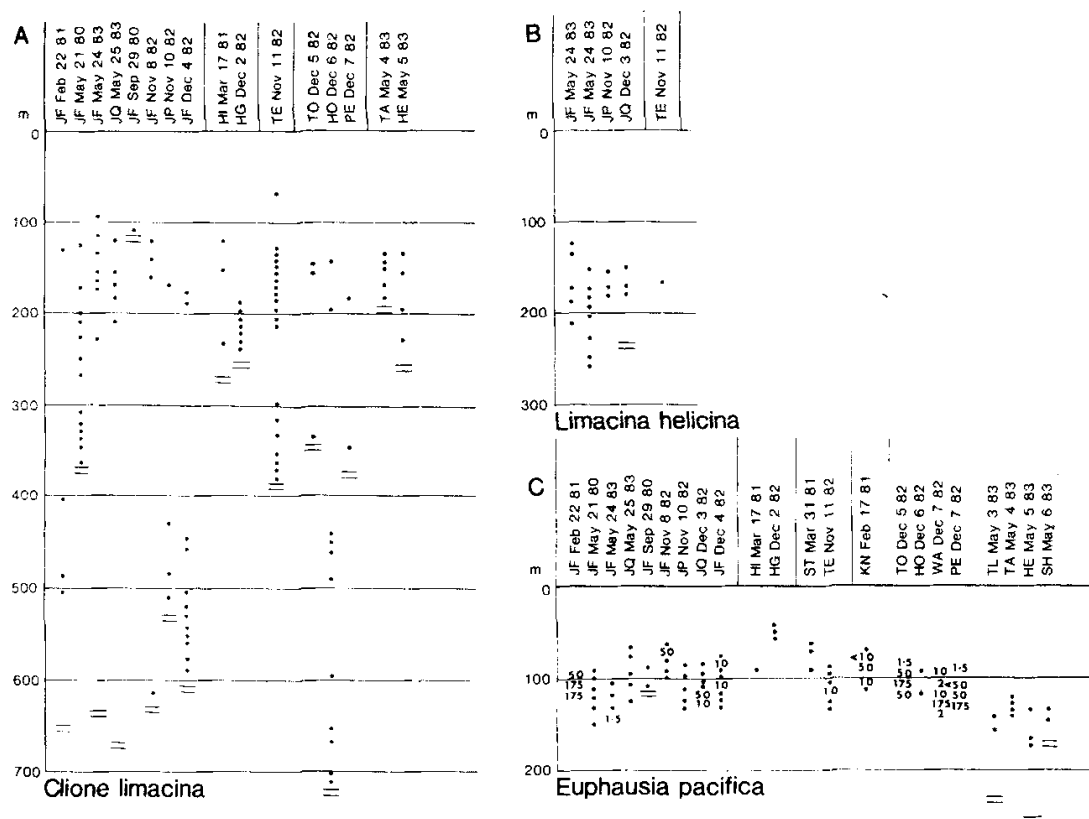


Fig. 9. Sightings of (A) *Clione limacina*, (B) *Limacina helicina* and (C) *Euphausia pacifica*.

Other polychaetes. *Typhloscolex mülleri* an obligate predator on chaetognaths, was sighted below 235 m (JF, 24 May 1983) by J.D. Fulton. The pelagic alciopid polychaete *Rhynchonerella angelini* was seen on many dives in inner coastal waters and is probably the midwater 'nereid' mentioned in V.J. Tunncliffe's notes from Knight Inlet. Sightings were mostly of single individuals scattered fairly evenly from 1 to 600 m.

Pteropoda

Clione limacina (Figure 9A). Most daytime sightings were below 100 m. Peak abundance lay at ~180 m in May, but there were indications of a substantial population in deeper water in November and December. Gardner (1977), however, still found 69% of the population above 200 m in early winter. A few sightings made in November in Jervis Inlet suggest that *Clione* migrates to the surface at night but a reverse migration pattern has been reported for this species in the Bay of Fundy (Newman and Corey, 1984). Mating pairs were seen from the submersible at 136–150 m on 25 May 1983 in Jervis Inlet by Ilde Szabo (personal communication).

Limacina helicina (Figure 9B). As prey of *Clione*, *Limacina* would be expected to determine the distribution of the latter, as reported in other areas (e.g., Newman and Corey, 1984). Lalli (1970) compares the incidence of the two and finds that in almost every case, *Limacina* is more abundant than *Clione*. In our PISCES dives, *Limacina* was sighted in only six dives, five of them in Jervis Inlet. Sightings were of single individuals except on one occasion when a density of 10 m^{-3} was recovered. No specimens were seen below 260 m. A sighting near the surface at 2100 hours (JF, 9 Nov 1983) is con-

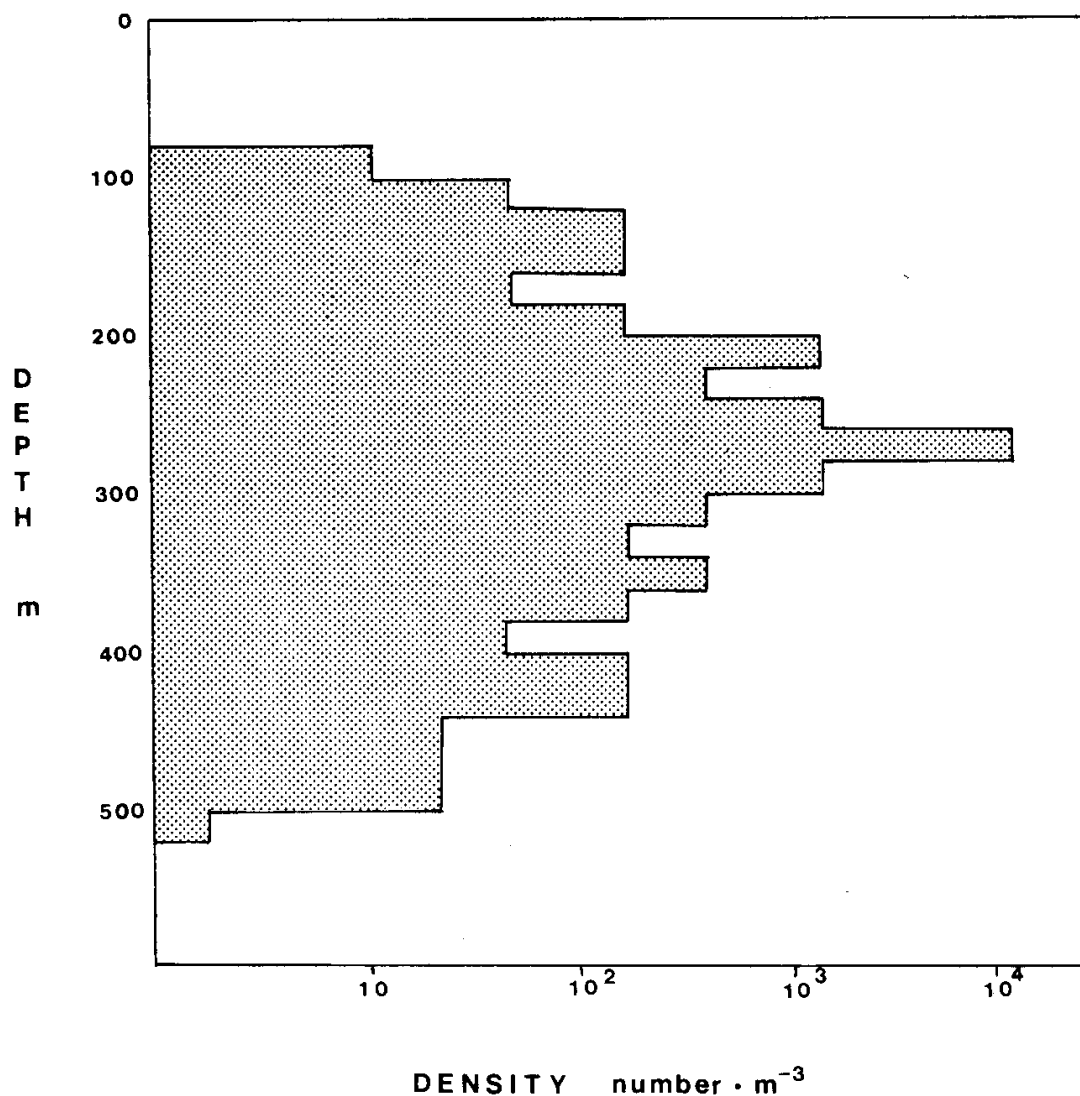


Fig. 10. Vertical distribution and abundance of *Neocalanus plumchrus*, Jervis Inlet, Nov-Dec 1983.

sistent with other evidence that *Limacina* species migrate to the surface at night (e.g., Solis and von Westernhagen, 1979).

Crustacea

Euphausia pacifica (Figure 9C). This species was observed in most daytime dives in a 'narrow band' distribution centered around the 100-m line. Densities rarely exceeded 50 m^{-3} in contrast to findings in Saanich Inlet (Mackie and Mills, 1983) where *Euphausia* reaches concentrations as high as $10\,000 \text{ m}^{-3}$ immediately over the oxycline. Euphausiid distribution around the coasts of British Columbia is covered comprehensively by Fulton *et al.* (1982).

Neocalanus plumchrus (Figure 10). Copepod sightings were recorded in all dives, but most of these observations lack precision for several reasons: many species are present, they are hard to distinguish from the submersible, and both species composition and density can change quite abruptly as one descends through the water column. Thus, unless dives are made with the specific purpose of plotting copepod distributions, useful data are unlikely to accrue. We have obtained useful data for only one species, *Neocalanus plumchrus*.

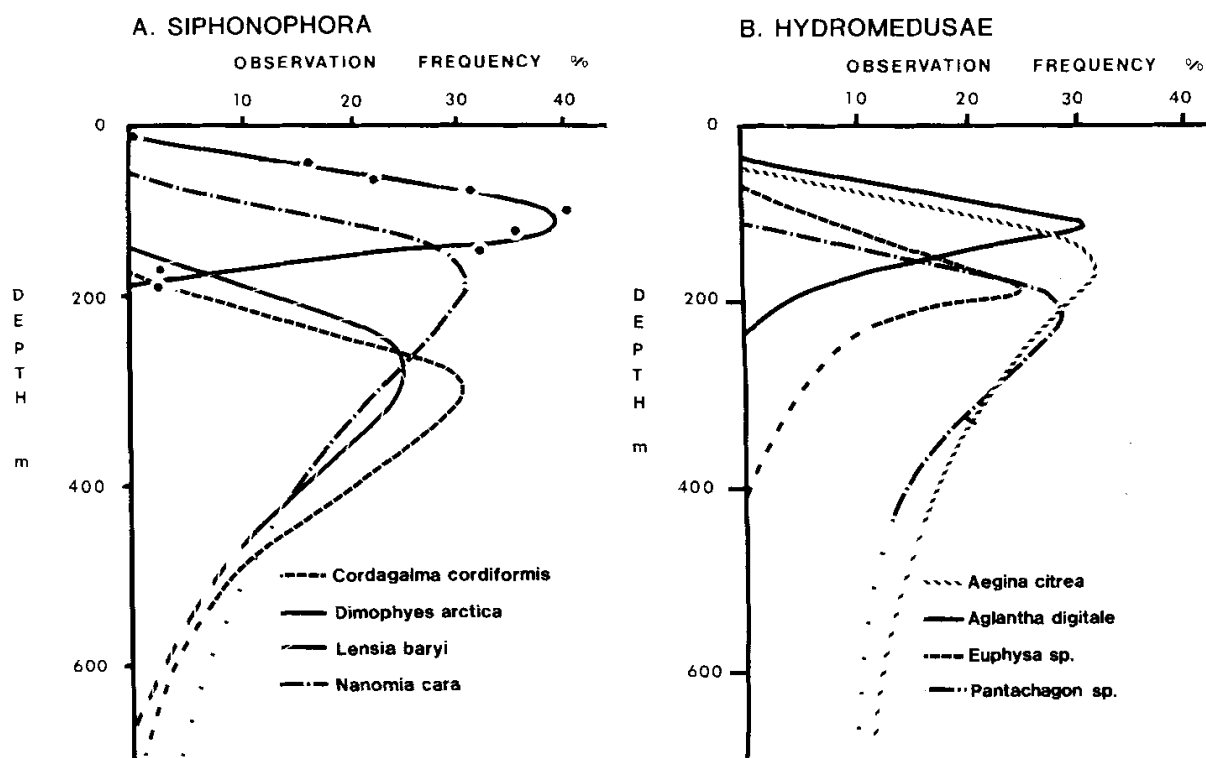


Fig. 11. Summary distribution curves for (A) Siphonophora and (B) Hydromedusae.

Fulton (1973) describes the life cycle of this species for the Strait of Georgia. The adults overwinter in deep water, producing eggs in February – April. The nauplii rise to the surface where early copepodite stages are found in March and April. The stage V copepodites then start to descend to deeper water and from October on the bulk of the population lies below 200 m. Adults are present again from January to mid April below 350 m.

Our *PISCES* observations from Jarvis Inlet, Howe and Desolation Sounds and from an open strait near Texada Island are fully consistent with this picture except that adult females with ripe eggs were observed (J.D.Fulton, personal communication) below 500 m in Jarvis Inlet in late May 1983, which suggests that the species has a longer breeding span here than in the open strait.

The data summarized in Figure 10 were compiled from five dives in November and December in Jarvis Inlet. A special effort was made to enumerate *N. plumchrus* at all depths in these dives, and densities were estimated using a formula based on estimated mean nearest-neighbour distances (Mackie and Mills, 1983). *N. plumchrus* was found between 80 m and 520 m, with a peak concentration of $11\,280\text{ m}^{-3}$ at 260–280 m depth.

N. plumchrus greatly outnumbers all other crustacean plankton in the midwater zone and is probably the chief food of many of the gelatinous predators living in the same water mass.

Other crustaceans. The conspicuous red conchostracan *Conchoecia elegans* was seen frequently, though never in great numbers, between 60 and 580 m. Sergestid shrimps (*Pasiphaea pacifica*) were seen from 140–680 m, usually singly, but tending to aggregate near the bottom. Galatheid crab juveniles (*Munida quadrispina*) lie in a narrow belt close to 100 m as noted previously (Mackie and Mills, 1983). Amphipods

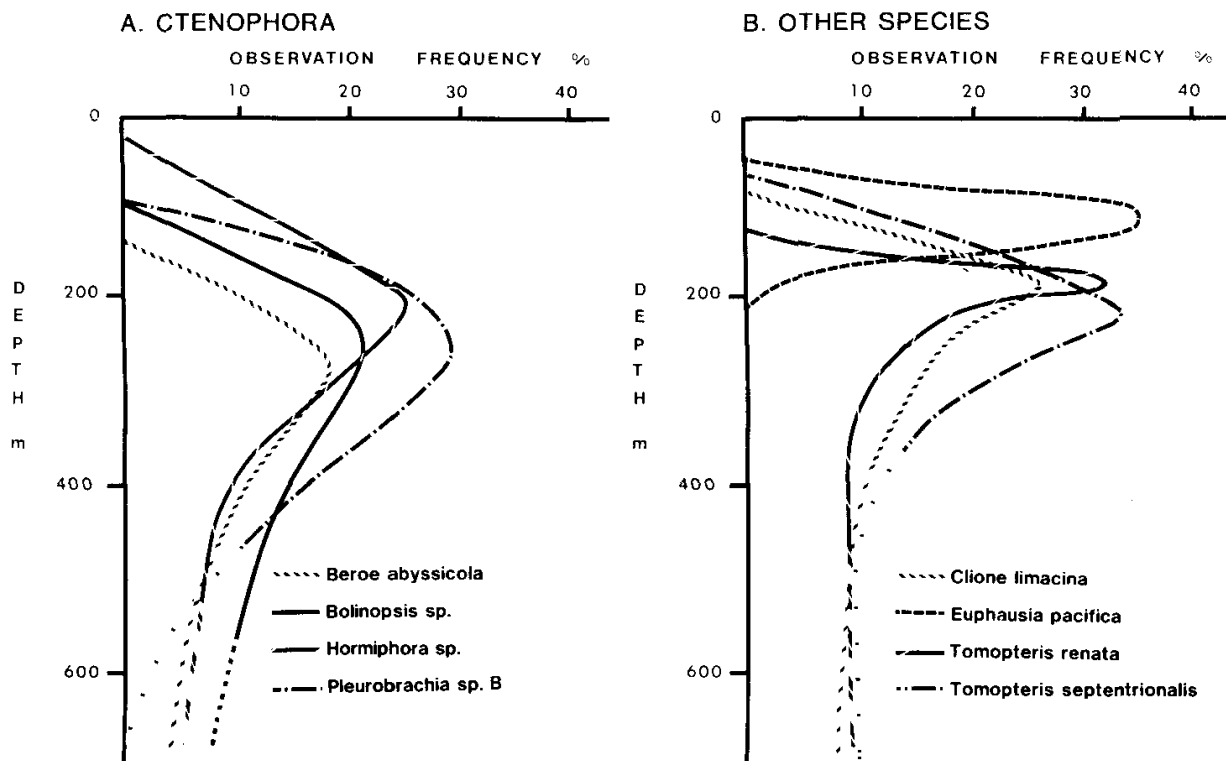


Fig. 12. Summary distribution curves for (A) Ctenophora and (B) other species.

(*Cyphocaris challengerii*, *Parathemisto pacifica*, *Orchomene obtusa*) were often observed, sometimes in considerable numbers, but attraction to the submersible's lights is a complicating factor, and amphipod data are not reported here in detail.

Summary distribution curves

These curves (Figures 11 and 12) were made as described in Methods and summarize the distributions of twelve major species from sightings made throughout the study and in all months when dives were made. Less commonly seen species are omitted.

The siphonophores (Figure 11A) are represented by one upper, narrow band form *D. arctica*, peaking at 100 m, two deep forms, *C. cordiformis* (290 m) and *L. baryi* (280 m) and one intermediate form, *N. cara* (170 m). *S. gracilis* (90 m) appears to have a distribution similar to *D. arctica*, but is omitted because of inadequate data. The *D. arctica* curve is a tall, symmetrical bell curve. The others are wider, and skewed toward the surface.

A similar picture is seen with the hydromedusae (Figure 11B), where there is an upper, narrow band form *A. digitale* (110 m), a deep species *Pantachogon* sp. (200 m) and two intermediate forms: *Aegina citrea* (160 m) and *Euphysa* sp. (180 m).

The ctenophores (Figure 12A) have no 'upper', narrow band representative. Three species can be considered as deep. *Bolinopsis* sp. (250 m), *Pleurobrachia* sp. B (250 m) and *B. abyssicola* (310 m). *Hormiphora* sp. (200 m) is in the intermediate category, extending well into the upper zone. *Beroe* sp. B (150 m) may also be in this category.

The species shown in Figure 12B include an upper, narrow band form *E. pacifica* (110 m) and three intermediate forms *C. limacina* (180 m), *T. renata* (180 m) and *T. septentrionalis* (210 m). *L. helicina* (not shown) peaks near *Clione* at ~190 m.

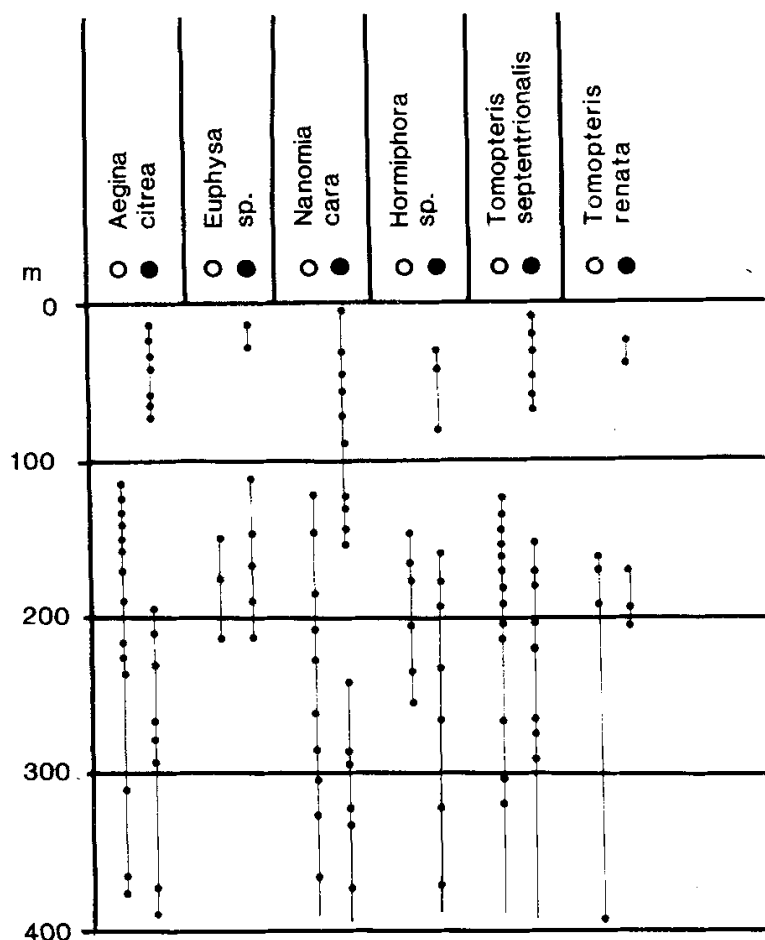


Fig. 13. Examples of species showing markedly differing (○) daytime and (●) night-time distributions, Jervis Inlet, Foley Head, November 8, 1330 h, November 9, 1930 h, 1982. Lines drawn through the points emphasize apparent depopulation of an upper midwater zone due to surfaceward migration of part of the population at night.

Nocturnal redistribution

Evidence of nocturnal migration to the surface is shown for six species in Figure 13. It will be noted that these are all species characterized in the preceding section as 'intermediate' (i.e., having daytime distributions in both 'upper' and 'deep' midwater zones). A noteworthy feature is that in all cases the population appears to split into two groups at night, an upper migratory component which moves to the surface and a lower component which remains deep. The top of the deep component lies at a mean depth of ~175 m for these six species, which is some 40 m deeper than the mean upper daytime limit of 135 m for the same species. The possible significance of these two depth lines in terms of light penetration and the effects of light on the biology of the organisms concerned is discussed below. Data for *C. limacina* and *L. helicina* are too scanty to warrant their inclusion in Figure 13 but both species were found to migrate to the surface at night, *Clione* from a daytime range of 120–175 m, *Limacina* from 155–180 m. No specimens were seen at night in these depths, which may mean that the whole population migrated. For the upper, 'narrow band' species *A. digitale*, *E. pacifica* and *Munida quadrispina* there is insufficient new data to report, but all three were previously observed to migrate (Mackie and Mills, 1983). It is noteworthy

that not all species in this category migrate. For instance *D. arctica* is not a migrator, as elsewhere noted by Pugh (1977).

Discussion

Uniformity of midwater environment

Despite the fact that observations were made at different seasons in many different regions over several years, sightings of the common gelatinous plankton species proved to be fairly consistent as to depth range, and the same species were found repeatedly in widely separated areas. This leads to the conclusion that the midwater environment in this area of deep, narrow straits and fjords, is quite stable, and is populated on a year round basis by more or less permanent animal communities.

The stability of the midwater ecosystem of the Strait of Georgia and the deep inlets running off it suggest that the region should be thought of more as an 'inner sea' than as a mere stretch of coastal water disorganized by mixing and run off.

Divisions of the pelagosphere

Although the terms epi-, meso- and bathypelagic are not usually applied to the pelagic realm in coastal areas, there seems no reason why these terms should not be used in the present case, given the stability of the environment and the predictability of the species encountered.

Epipelagic zone. This will here be considered to include the top 50 m, the so-called 'mixed' layer in which temperatures and salinities are quite variable owing to seasonal factors, tides, wind effects and river run off (Thomson, 1981).

Mesopelagic zone. Conventionally, this term is defined in terms of light penetration as the 'twilight' zone of the sea where there is not enough light for photosynthesis but enough to affect animal behaviour. If, as generally assumed (Raymont, 1983), animal migration to the surface at night is triggered by a change (decrease) in light intensity it can be inferred from the data given in Figure 13 that the point where the daytime range of a species splits at night into two components (an upper migrating one and a lower, non-migrating one) is determined by the photosensitivity of the species and by the amount of light which penetrates to that point. Taking a number of species into account, such data can be used to define the boundary line between the mesopelagic zone and the bathypelagic zone. As noted above, the animals here are 'telling' us that the boundary line lies at ~175 m.

Bathypelagic zone. It follows from the above that the bathypelagic, or aphotic, zone lies below 175 m.

Planktonic occupants of the three zones

The animals whose distributions are reported here do not fall tidily into three groups corresponding to the three pelagic zones recognized. A substantial number occupy both meso- and the bathypelagic zones. Thus we have to consider not three, but four categories of plankton (Figure 14). This classification is the logical development of the breakdown

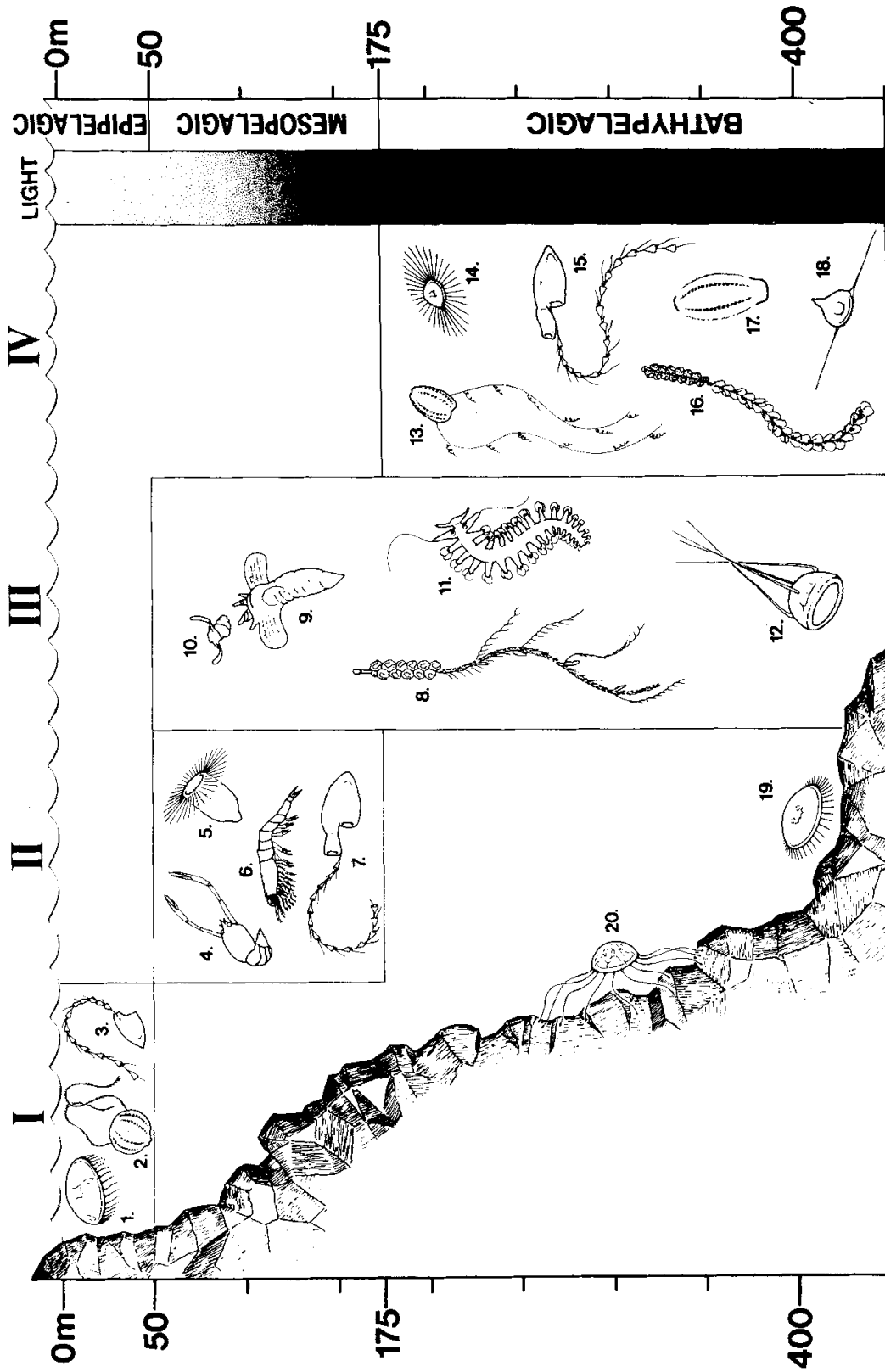


Fig. 14. The major macroplankton species shown grouped into four categories: I epipelagic, II mesopelagic, III meso-bathypelagic, IV bathypelagic. Key to species: 1 *Phialidium gregarium*, 2 *Pleurobrachia bachei*, 3 *Muggiaea atlantica*, 4 *Munida quadrispina*, 5 *Aglantha digitale*, 6 *Euphausia pacifica*, 7 *Dimophyes arctica*, 8 *Nanomia cara*, 9 *Clione limacina*, in pursuit of 10 *Limacina helicina*, 11 *Tomopteris septentrionalis*, 12 *Aegina citrea*, 13 *Pleurobrachia* sp. B, 14 *Pantachogon* sp., 15 *Lensia baryi*, 16 *Cordagalma cordiformis*, 17 *Beroe abyssicola*, 18 *Amphinema plathyedus*. Also shown are a suprabenthic species (19 *Foersteria purpurea*) and an epilithic species (20 *Ptychogasteria polaris*). This drawing was inspired by Figure 12 in Marshall (1979).

given in Mackie and Mills (1983) taking much new data into account, and it supercedes the latter.

Epipelagic forms. These are forms which live permanently in surface waters down to ~50 m, but which are typically concentrated above 25 m. Among the commoner epipelagic species are medusae of the genera *Aequorea*, *Proboscoidactyla*, *Sarsia*, *Eutonina*, *Mitrocoma*, *Mitrocomella*, *Phialidium*, *Stomotoca* and *Bougainvillea*, the ctenophore *Pleurobrachia bachei* and the siphonophore *Muggiaea atlantica* (Mills, 1981). The listings compiled by Mills testify to the extraordinary richness of the jellyfish fauna in the surface waters around the San Juan Islands. These waters are, however, subject to much turbulent mixing due to tides and currents entering through the Strait of Juan de Fuca (Thomson, 1981). Several of the species listed by Mills, including *Ptychogena lactea*, *Aglantha digitale*, *Aegina citrea*, *Lensia conoidea* (= ?*L. baryi*), *Dimophyes arctica*, *Nanomia cara*, *Beroe abyssicola* and several other ctenophores are meso- or bathypelagic species which are presumably brought to the surface by mixing, or migrate to the surface at night and become trapped in shallow bays. Likewise, *Clione*, *Tomopteris* and *Euphausia* are also found at the surface in some areas during daylight hours. The much studied surface macroplankton at Friday Harbor, San Juan Islands, is therefore by no means purely representative of the epipelagic community of the southern Strait of Georgia, but is a mixture of bathy-, meso- and epipelagic species found in the Strait, with some additions from the ocean.

Mesopelagic forms. These forms are distributed in 'narrow bands' (Mackie and Mills, 1983) of ~100 m. Their numbers fall off rapidly and symmetrically on either side of the peak depth. They are *S. gracilis* (peaking at 90 m), *A. digitale*, *D. arctica* and *E. pacifica* (100 m). *E. pacifica* is a herbivore which presumably obtains much of its food during nocturnal migrations to the surface. The other three species are predators, too small to capture euphausiids, and probably feeding on coepods such as *Metridia pacifica*, which are concentrated in the 75–200 m zone (Gardner, 1977). Juveniles of the galatheid crab *M. quadrispina* also fall within the mesopelagic category (Mackie and Mills, 1983).

Meso-bathypelagic forms. These forms live in both meso- and bathypelagic zones. Individuals located high enough in the water column respond to changes in ambient light intensity and perform nocturnal migrations. Those that lie too low behave like bathypelagic species, hence the splitting of the population at nightfall. Species in this category are *A. citrea* (160 m), *Nanomia cara* (170 m), *Euphysa* sp. (180 m), *T. renata* (180 m), *L. helicina* (190 m), *C. limacina* (180 m), *Hormiphora* sp. (200 m) and *T. septentrionalis* (210 m). Individuals of these species migrate if high enough in the water column. *Pantachogon* sp. (200 m) peaks in the same area, but is not a migrator, has few individuals as high as 175 m, and is best considered in the bathypelagic category.

Bathypelagic forms. These forms are concentrated well below 175 m, and if some individuals occur above this point, they do not migrate. *Pantachogon* sp. (200 m), *Pleurobrachia* sp. B (250 m) and *Bolinopsis* sp. (250 m) are concentrated near the top of the aphotic zone. *L. baryi* (280 m), *C. cordiformis* (290 m) and *B. abyssicola* (310 m)

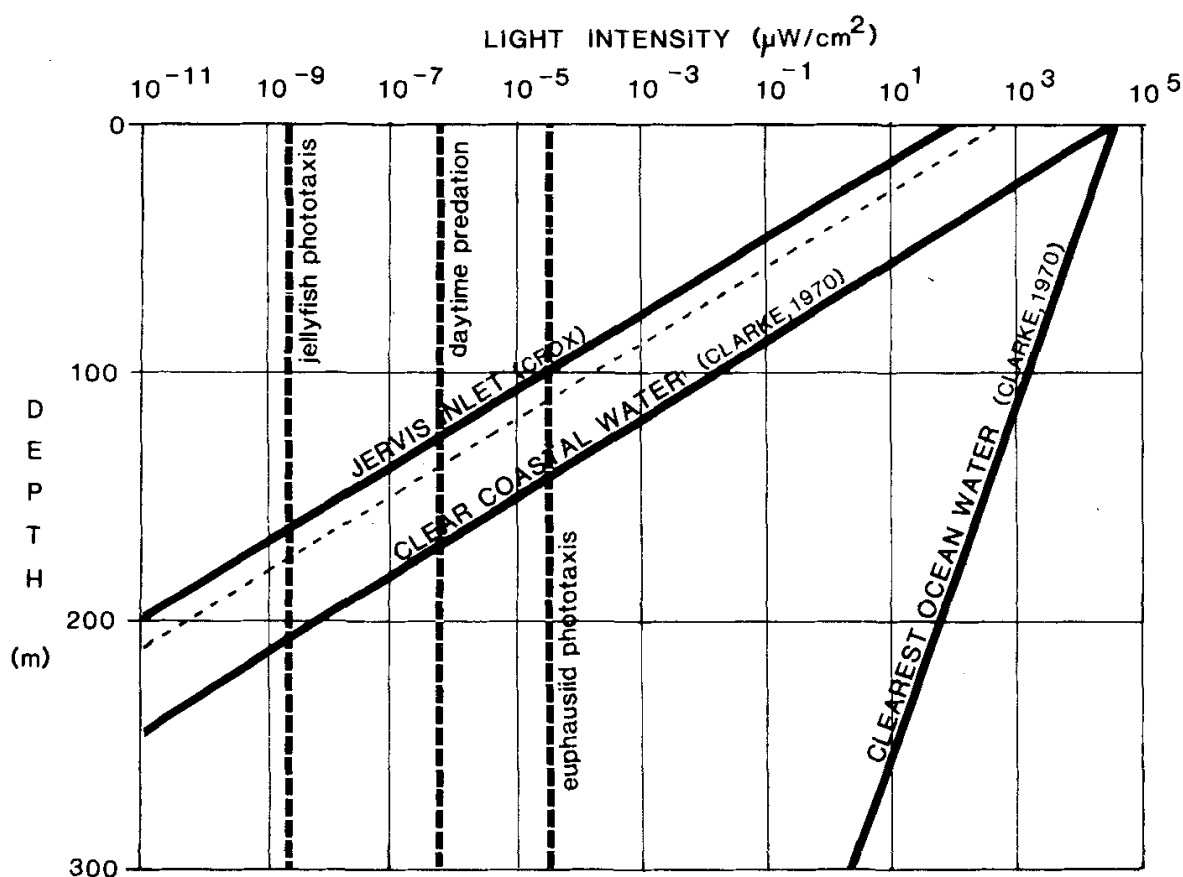


Fig. 15. Light penetration (480 nm), Jervis Inlet, from Campagne CFOX (1979) data, with curves from Clarke (1970) for comparison as explained in the text. Phototaxis and predation limits shown are approximations for the whole study area over the whole study period.

lie deeper. *Amphinema platyhedos*, for which data are scant, peaks even deeper than *B. abyssicola*, at 450–500 m. It is a true pelagic species, unlike *Foersteria purpurea* and *Ptychogastria polaris*, which are supra- or epibenthic medusae.

Gardner (1977) used various analytical techniques on zooplankton collected by vertical and horizontal net hauls in the Strait of Georgia. Groups of species with common distribution patterns were apparent, but they were not sufficiently well defined to suggest the presence of separate communities. Study of Gardner's data shows several points where the distributions of his species differed markedly from those determined in the present study. For example, *Aegina* is shown with 57% of its members near the surface and none below 200 m, directly contrary to what our data would predict. No *Aequorea* were found above 75 m, while 70% of them were below 200 m, which again runs directly counter to the present findings and to those of other workers. Gardner's 'Medusa sp. A' is without any obvious counterpart in our sightings and his '*Muggia atlantica*' shows a distribution which could be reconciled with the present observations only on the assumption that his '*Muggia*' is an amalgum of all three of our diphyid calycophorans. Gardner's *E. pacifica* is shown with a bimodal distribution, and only 2% of its numbers in the 75–200 m zone where 98% of our sightings located it. In view of these astonishing discrepancies, is difficult to avoid the conclusion that the material in Gardner's net samples was too poorly preserved to allow reliable identification of the gelatinous species.

We know very little about trophic relationships in the midwater zone, but most of the macroplankton species studied in this investigation are known to be predators, relying chiefly on crustacean microplankton as a food source. It is therefore significant that the copepod, *Neocalanus plumchrus* is abundant throughout the greater part of the year in the meso- and bathypelagic zones. When overwintering in Jervis Inlet this species occurred in great numbers from 80 m down to 520 m, peaking at 260–280 m with densities $> 10\,000\text{ m}^{-3}$. Except for two or three months of the year, *N. plumchrus* is probably always abundant, and may be the principal food item for many of the mid-water forms reviewed in this account.

Light penetration and vertical zonation

We have proposed above that the boundary between the meso- and bathypelagic realms corresponds to the mean depth at which meso-bathypelagic populations split at nightfall into migrating and non-migrating components, on the assumption that those which do not migrate lie below 175 m, just too deep for the light change to trigger phototaxis. Without bathyphotometric measurements it would be impossible to establish accurate values in absolute terms for light penetrating to this depth. However, consideration of existing data suggests a value in the range $10^{-8} - 10^{-9}\text{ }\mu\text{W cm}^{-2}$. This was calculated using: (i) data from irradiance measurements in Jervis Inlet (Campagne CFOX, 1979); (ii) a mean value of 100 m for euphausiid daytime depth as established in the present study; and (iii) the assumed preference of euphausiids for the $10^{-4} - 10^{-5}\text{ }\mu\text{W cm}^{-2}$ isolume (Boden and Kampa, 1974). Irradiance data for 480 nm were plotted as an attenuation curve from the surface to 50 m, extrapolated down to 200 m, giving the upper line in Figure 15. This line was found to run parallel to Clarke's (1970) curve for clear coastal water. It intersects the euphausiid depth of 100 m at $\sim 10^{-5}\text{ }\mu\text{W cm}^{-2}$, according to expectations. The dotted line below it intersects the euphausiid line at $10^{-4}\text{ }\mu\text{W cm}^{-2}$. A first approximation to a 'mean' light penetration curve for the study area would therefore be delimited by the two upper lines in Figure 15, from which we get the value of $10^{-8} - 10^{-9}\text{ }\mu\text{W cm}^{-2}$ at 175 m, proposed above as the limit of phototaxis for *Aegina*, *Tomopteris* spp., *Nanomia* and *Hormiphora*. This represents a level of photosensitivity slightly superior to that of human broad field vision, but inferior to that of deep-sea fishes (Clarke, 1970). Such acute photosensitivity is remarkable, especially as some of the species in question lack ocelli. However, it is known that the neurones controlling locomotion in jellyfish may themselves be photoreceptors (Anderson and Mackie, 1977).

It was noted earlier that the ranges of the five species used for calculation of the 175 m datum line extends some 40 m higher during the day, to 135 m. This would correspond to an irradiance level of $\sim 10^{-6}\text{ }\mu\text{W cm}^{-2}$. Tentatively, we may regard this as a relatively 'safe' amount of light in terms of susceptibility to fish predators. There is a group of mesopelagic forms higher up in the 'danger' zone but some of these (e.g., *Aglantha*, *Euphausia*), are agile, transparent, powerful swimmers, with well-developed escape responses.

It will be appreciated that the values given here are intended to serve only as a rough estimate of the amounts of light affecting animal behaviour in the study region. The isolumes will of course move up and down over a wide range depending on location, season, weather conditions, etc.

Shapes of distribution curves

The distribution curves for the group of true mesopelagic species are narrow, symmetrical bell curves. This implies that the upper and lower sides of the distribution are both 'controlled', presumably by light, as in the case of euphausiids, or because of trophic or other biological interaction with species whose distribution is so determined. These species probably lie within the effective foraging range of visual predators.

The distribution curves of meso-bathy and bathypelagic species are broad bell curves skewed toward the surface (flattened on top). The reasons for this asymmetry are not clear. If the animals are photosensitive, they might show negative phototaxis or photokinesis near the top of their distribution range, which would have the effect of compressing the upper part of the curve. Alternatively, where the upper part of the curve lies within the zone where visual predators can operate effectively, the flattening effect could represent loss of individuals due to predation. A third possibility is that the distribution is related to the abundance of prey organisms.

Some midwater species, such as *Pleurobrachia* sp. B, have a reasonably clear lower limit to their range while others (e.g., *Bolinopsis* sp.) continue right to the bottom in the deepest places giving the impression that their distribution is limited not by any inherent features of the pelagic environment, but by the bottom itself. Regardless of these differences, a steady diminution in numbers with increasing depth is apparent in all cases. This presumably reflects the gradual using up of food energy as it passes through successive cycles at ever-increasing depths.

Conclusions

The apparently 'structureless' character of the sea itself has led some (e.g., Elton, 1966) to suggest that marine animal communities are equally unstructured. Study of open water habitats has shown that this is far from being the case (e.g., Ebeling *et al.*, 1970). Likewise the distribution of gelatinous midwater predators in the Strait of Georgia and its inlets is certainly not indicative of structurelessness. Here, as elsewhere, the basic structure can best be understood in terms of light effects. The picture is complicated by the existence of a large group of animals living simultaneously in the aphotic and disphotic zones, with nocturnal excursions to the surface, which tends to blur the epi-, meso-bathypelagic divisions. The narrowness of the epi- and meso-pelagic zones, which is due to poor light penetration, results in some bathypelagic species lying, in part, near enough to the surface to behave as mesopelagic forms.

Madin and Harbison (1978) went down in *ALVIN* in the Atlantic Ocean and were 'immediately impressed by the abundance and diversity of many forms of gelatinous zooplankton at great depths'. Many species seen were probably new to science. The French pioneers of submersible research in the 1950s [F. Bernard, J.M. Pérès, J. Picard and G. Trégouboff (see Fage, 1958)] recorded similar impressions. Plankton net hauls completely fail to do justice to these fragile species. The realization that there are so many gelatinous predators in the midwater zone should lead to an intensification of efforts to study their feeding biology and nutritional physiology along the lines of Purcell and Kremer (1983). Many food chains probably end, not in squids and fishes, but in jellyfish and ctenophores.

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