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Abundance and Vertical Distribution of Siphonophores (Cnidaria) from the Central Strait of Georgia, British Columbia, During Spring and Summer

Gillian M. Mapstone and Mary Needler Arai
Department of Biological Sciences, The University of Calgary,
2500 University Drive N.W., Calgary, Alberta T2N 1N4

Abstract: *Dimophyes arctica* (Chun, 1897) was the dominant siphonophore in the central Strait of Georgia, British Columbia, in samples taken between March and May 1979 at various depths down to 345 m. Anterior nectophores were most abundant between 50 and 100 m and increased tenfold from March to May to a maximum of 4810 individuals per 1000 m^3. Eudoxids peaked earlier in smaller numbers in deeper water. *Nanomia bijuga* (Chiaje, 1841) was the second most abundant siphonophore, reaching a maximum density of 841 nectophores per 1000 m^3 at 200 m in May. In addition *Lensia baryi* Totton, 1965 was present in all series and *Lensia conoidea* (Keferstein and Ehlers, 1860) in April and May.

Key Words: *Dimophyes arctica*, *Nanomia bijuga*, siphonophores, population, Strait of Georgia, depth.

Introduction

The central Strait of Georgia is one of the most extensively investigated marine locations for productivity studies. Harrison et al. (1983), reviewing the biological oceanography of the area, stated that "standing stock associations of the dominant species in the food web of the Strait are reasonably well known." Nevertheless, populations of siphonophores have not been previously examined. They are shown in the present study to be major invertebrate predators in the spring nektonic community of the Strait.

Siphonophores have been studied in the various inlets around the Strait of Georgia and Vancouver Island from the submersible *Pisces IV* by Mackie and Mills (1983) and Mackie (1985). Although most of their work was done in inlets, Mackie (1985) established that the midwater species of the central Strait are *Dimophyes arctica* (Chun, 1897), *Nanomia cara* (A. Agassiz, 1865), *Lensia baryi* Totton, 1965 and *Cordagalma cordiformis* Totton, 1932. Gardner (1977) also stated that the siphonophores *Nanomia bijuga* (Delle Chiaje, 1841) and *Muggiaea atlantica* Cunningham, 1892 were present in zooplankton samples from the central Strait. Since Mackie and Gardner only briefly examined the central Strait in the autumn, nothing is known of the abundance and vertical distribution of species in this area during the spring plankton bloom. A comprehensive survey of hydromedusae from the central Strait of Georgia was carried out by Arai and Mason (1982). Siphonophores collected at the same time as these hydromedusae were used for the present study. New information is provided on population abundance and vertical distribution for four siphonophore species.

Materials and Methods

Horizontal tows were made during daylight hours using non-closing 350 µm bongo samplers. Data from the tows were corrected, for mean depth using the angle of the wire, and to a standard volume of 1000 m^3 using flow meters. Specimens were fixed in 5% formalin buffered in sodium borate. Five series of almost horizontal tows, (oblique over 50 m intervals), were made at 49°16'N, 123°40'W (Arai and Mason 1982, Fig. 1A). Four of these series were carried out from March to May 1979 and the fifth was taken in July 1980. In addition, isolated horizontal series were obtained in April 1979 at 49°16'N, 123°49'W, and in July 1980 at 49°14'N, 123°41'W.

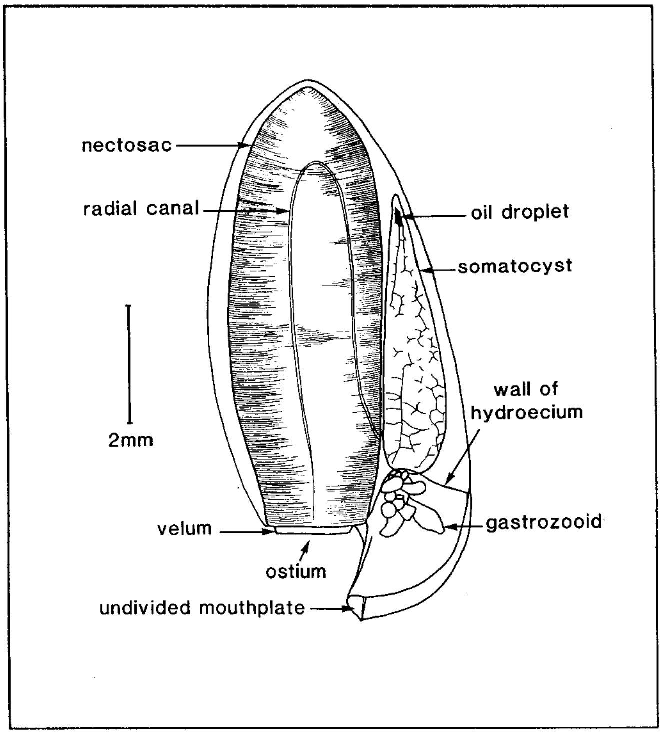

Fig. 1 ***Dimophyes arctica*** **anterior nectophore**

Siphonophores consist of one or more nectophores or swimming bells, which usually become separated during collection. Calycophoran species typically include an anterior and a posterior nectophore. The structure of an anterior nectophore of *Dimophyes arctica* is shown in Fig. 1. A stem from the anterior nectophore (contracted in the preserved specimen in Fig. 1) bears feeding gastrozooids. In the mature animal it also develops the sexual or eudoxid stage. Eudoxids, which in *D. arctica* consist of a bract and a gonophore (Fig. 2), detach and become free-living. Anterior nectophores and eudoxids were sorted and recorded for each of the calycophoran species found. Physonect siphonophores, when alive, consist of a number of nectophores attached to a stem, the apex of which is expanded to form a gas-filled float called the pneumatophore. Because these animals break up into

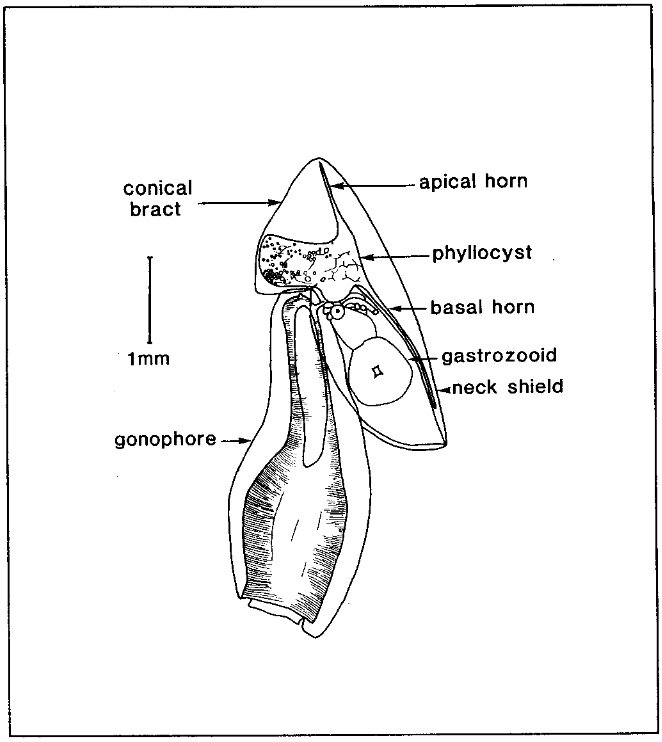

Fig. 2 ***Dimophyes arctica*** **eudoxid**

pieces when caught in tow nets, counts of the numbers of individuals is difficult. Both nectophores (Fig. 3) and pneumatophores (Fig. 4) of *Nanomia bijuga* were sorted and recorded in the present samples. An adult *N. bijuga* individual will have one pneumatophore and usually 8-25 nectophores (Totton 1965a, Daniel 1985). Pneumatophores give the most accurate estimate of population density, but because they are small they are sometimes missed in net samples. Although the number of nectophores per individual varies with age, nectophores have been used for population abundance estimates by other workers (Lakkis 1971, Gili et al. 1988) and are included here for comparative purposes.

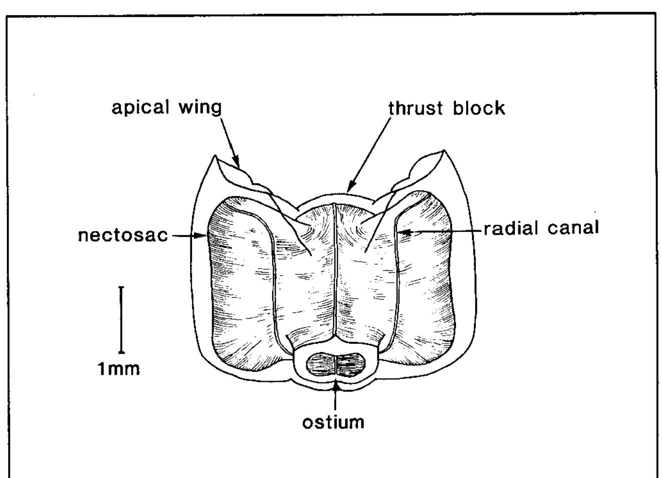

Fig. 3 ***Nanomia bijuga*** **nectophore**

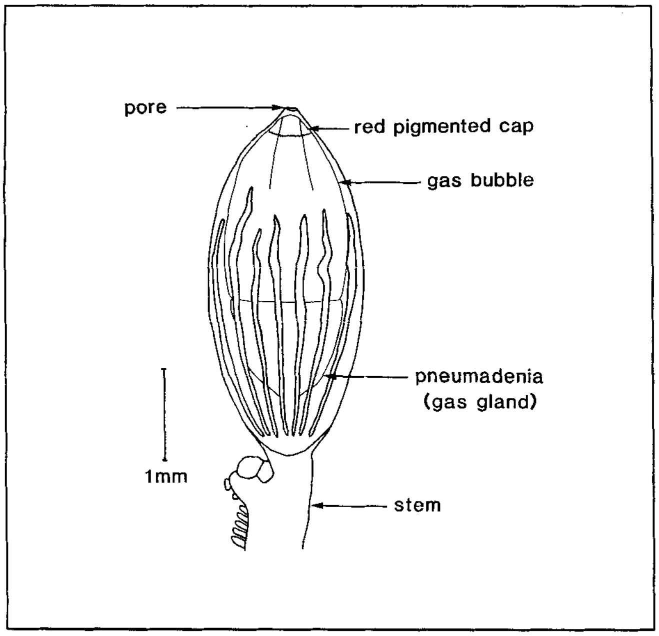

Fig. 4 *Nanomia bijuga* **pneumatophore**

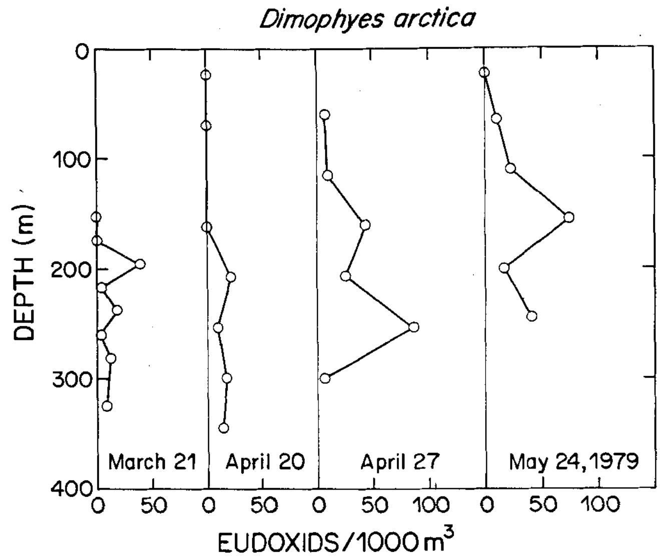

Fig. 5b Depth profile of *Dimophyes arctica* **eudoxids**

Results

Dimophyes arctica

Vertical distribution:

Dimophyes arctica was the most abundant siphonophore species to be found in the central Strait of Georgia during the spring and summer of 1979 and 1980. Anterior nectophores of *D. arctica* (Fig. 1) were found in every sample taken at 49°16'N, 123°40'W, from 23 to 345 m, with population maxima occurring between 50 and 100 m from April to July (Fig. 5a). (March samples were from 150 m downwards.) Mackie (1985) found anterior nectophores in a similar zone (30 to 160 m) in November 1982. Eudoxids (Fig. 2) were present from March to May 1979, but in much smaller numbers and only from 66 m downwards. Eudoxid population maxima were deeper, between 155 and 253 m (Fig. 5b).

Seasonal distribution:

A spring bloom of anterior nectophores is clear from Fig. 5a. Maximum numbers in 1979 increased tenfold

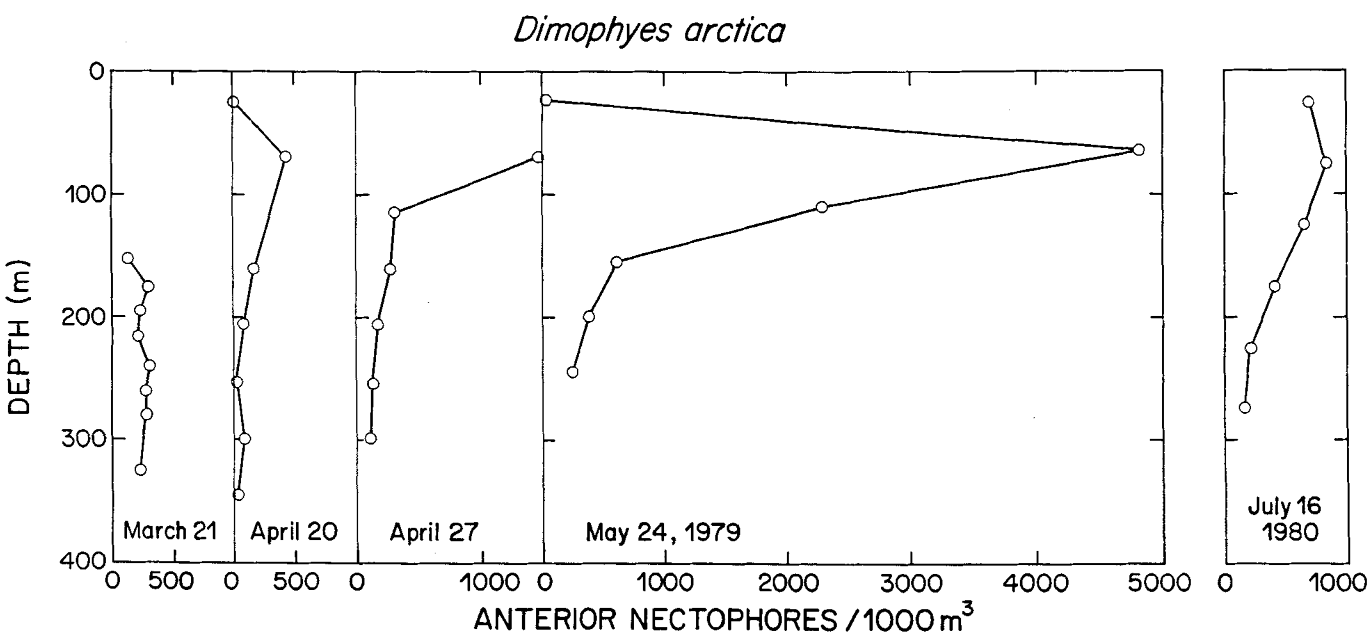

Fig. 5a Depth profile of *Dimophyes arctica* **anterior nectophores**

from 439 per 1000 m³ in April to 4810 per 1000 m³ in May. In 1980 the summer level was much lower: 840 per 1000 m³ in July. Eudoxid numbers also increased in 1979, from 40 per 1000 m³ in March to a peak of 87 per 1000 m³ in April (Fig. 5b). By May eudoxids had dropped to 75/1000 m³. None were found in the 1980 July sample. Mills also found the seasonal maximum of eudoxids to precede that of anterior nectophores in Saanich Inlet (Mackie et al. 1987).

A number of large, detached gonophores (16-39 per 1000 m³) were found in the March sample, from 195 to 345 m (the deepest sample depth). Calycophoran eudoxids can release their gonophores once they become mature (Totton 1965a), although this has not yet been reported for *Dimophyes arctica*. Perhaps these gonophores were detached from large overwintering eudoxids in February. However, for *D. arctica* in the Strait of Georgia, the eudoxids released in April must be the main progenitors of the new generation of anterior nectophores which form the enormous bloom in May.

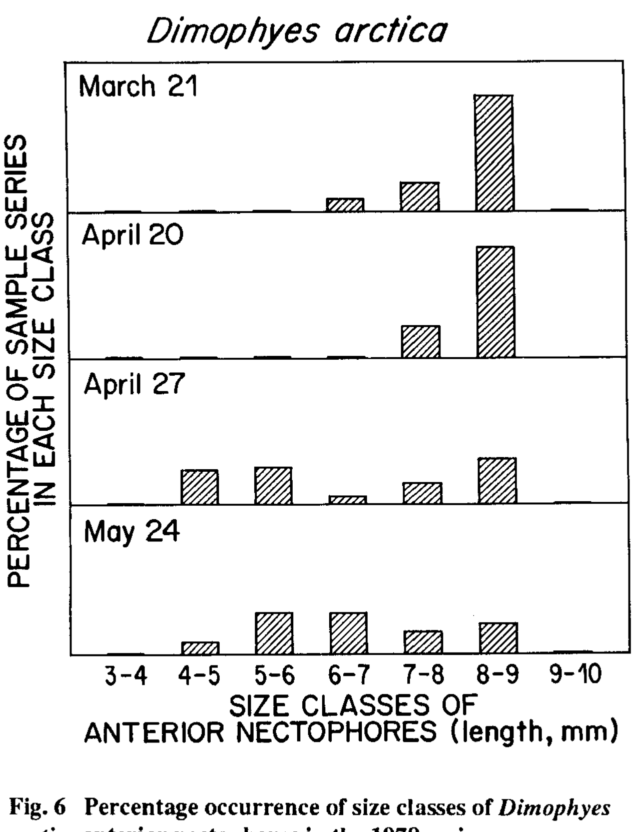

Fig. 6 Percentage occurrence of size classes of *Dimophyes arctica* anterior nectophores in the 1979 series

Size classes:

Lengths of anterior nectophores were measured for all specimens from the four 1979 series tows. Lengths ranged from 3 to 10 mm and were allocated to 1 mm size classes. The number of individuals in each size class was expressed as a percentage of the total number present in each series as shown in Fig. 6. In early spring (March 21 and April 20 series) 75-77% of individuals were of large size (8-9 mm). By April 27, the 8-9 mm class contained only 30% of individuals, with the smaller 4-5 mm and 5-6 mm groups forming 22% and 26% of the total respectively. By May, the 8-9 mm class was even smaller (20%) and maximum numbers occurred in the 5-6 mm and 6-7 mm classes (27% in each). These small individuals presumably grow steadily until they reach adult size (8-9 mm for most individuals). The appearance of the smaller size class in late April probably represents the new generation of anterior nectophores which have developed from the March and early April eudoxids. By May, these are in a larger size class, and the 5-6 mm class contains anterior nectophores which have developed from the late April eudoxids.

Individuals of *Dimophyes arctica* varied in several features, the most notable being nectosac musculature. Some individuals had distinct opaque muscles, while others had very few or no visible nectosac muscles. There were also differences in the shape of the hydroecium (details given in Pugh 1974). However, none of these features could be related to the size of the individual in the present specimens and could not therefore be used to distinguish different growth stages as implied by Pugh (1974). Stepanyants and Lobanov (1989) also question this concept.

Nanomia bijuga

Some confusion exists between *Nanomia bijuga*, which is common in the Pacific (see Alvarino (1971) as *Stephanomia bijuga*), and the closely related *N. cara*, but the two species can be distinguished by nectophore shape (Totton 1954, Stepanyants 1967, Daniel 1985). *N. bijuga* has been recorded around Vancouver Island (Berkeley & Berkeley 1960) and in the Strait of Georgia (Gardner 1977), although Mackie, who has worked extensively on *Nanomia*, has only found *N. cara* in this area (Mackie 1964, 1985; Mackie & Mills 1983). The nectophores found in the present study (Fig. 3) fit the description of those for *N. bijuga* given by Totton (1954) and Daniel (1985). *N. bijuga* is a cosmopolitan warmer water species (Stepanyants 1967) and in the eastern Pacific is a typical species off the United States and Baja California (Alvarino 1971), while *N. cara* is a northern boreal species (Mackie 1964; Margulis 1972, 1976). However, both species coexist in cooler north Atlantic waters southeast of Greenland (Margulis 1978) as well as in the waters around Vancouver Island.

Numbers of nectophores and pneumatophores indicate that *Nanomia bijuga* was the second most abundant siphonophore species in the central Strait of Georgia in 1979 and 1980 (Fig. 7), occurring throughout the depth range of samples from 23 m to 345 m. Nectophores were

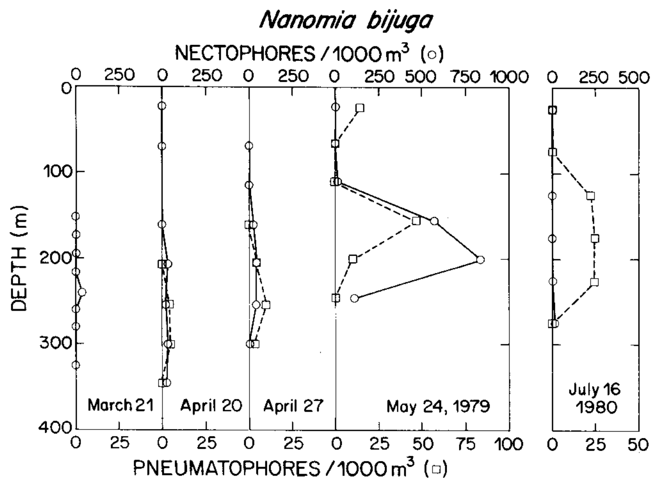

Fig. 7 Depth profiles of *Nanomia bijuga* pneumatophores and nectophores

present in all seven series from the Strait of Georgia, and pneumatophores in all except the March series. Maximum abundance in daylight samples in May was 841 nectophores per 1000 m^3 and 47 pneumatophores per 1000 m^3 at 200 and 155 m respectively, deeper than that of *Dimophyes arctica.* However, depths at which population maxima occur may be variable for *N. bijuga* since this species may exhibit a diel migration (Alvarino 1967, Pickwell et al. 1970).

Other species:

Anterior nectophores of *Lensia baryi* Totton, 1965 were also present in every series at 49°16'N, 123°40'W, at depths ranging from 207 to 345 m, but in much smaller numbers than *Dimophyes arctica* or *Nanomia bijuga.* Several posterior nectophores were also found. Abundance varied from 3 individuals per 1000 m^3 in March 1979 to a maximum of 14 per 1000 m^3 in May. *L. baryi* was first described by Totton (1965b) from Burke Inlet and has since been recorded at a number of other sites in the Strait of Georgia region by Mackie (1985).

Three anterior nectophores of *Lensia conoidea* (Keferstein and Ehlers, 1860) were also found in the central Strait of Georgia, between 155 and 253 m, during April and May 1979. The only other record of this species in the area is from the surface at Friday Harbour (Mills 1981). It seems probable that *L. conoidea* is replaced in the Strait of Georgia at most locations by the more successful species *L. baryi.*

Cordagalma cordiformis, which was recorded in the central Strait by Mackie (1985), was not found. It is a delicate species (Mackie 1985) and may have been damaged beyond recognition during collection. *Muggiaea atlantica*, also recorded in the Central Strait (Gardner 1977), at Friday Harbour (Mills 1981) and in Saanich Inlet (Larson 1986), would not have been taken in the present samples since it is an epipelagic species which only occurs above 50 m (Mackie 1985).

Discussion

Dimophyes arctica dominated the siphonophore fauna in the spring of 1979 in the central Strait of Georgia. It is known to be a eurybiotic species living in all biogeographical areas (Margulis 1976). In the N.E. Pacific, most records are from the subarctic region in the upper 200 m of water (Berkeley and Berkeley 1960; Bigelow 1913; Alvarino 1967, 1971; Mackie and Mills 1983; Mackie 1985). Records are sparser in the tropico-equatorial Pacific because at lower latitudes this species inhabits much deeper water where fewer hauls have been taken. The deepest Pacific record was taken from 3040 m off San Diego, California (Alvarino 1967).

As stated above, the vertical distribution of *Dimophyes arctica* in the Strait of Georgia in the spring of 1979 was similar to that found by Mackie (1985) in November. In more oceanic water in the western Pacific, Stepanyants (1970) also found maximum numbers of anterior nectophores between 100 and 200 m, and maximum numbers of eudoxids in deeper water, from 300 to 500 m. Population abundance of anterior nectophores was also similar, but she found a higher density of eudoxids. In the temperate North Atlantic, the vertical distribution of this species is even more similar to the present findings in the Strait of Georgia, with anterior nectophores being most abundant higher in the water column, and eudoxids being deeper and much less abundant (Pugh 1974, 1977). *D. arctica* is known to inhabit waters with a temperature range of -1°C to +22°C (Totton 1954, Stepanyants 1967, Casanova 1980), although it can only reproduce between 1.5°C and 10°C (Stepanyants 1967). The water below 50 m in the Strait of Georgia falls within both these ranges, being virtually isothermal at 8-8.5°C (Thomson 1981), and provides ideal conditions for a large bloom of *D. arctica.*

The spring bloom of *Dimophyes arctica* in the Strait of Georgia was similar to that observed in the northeast Atlantic by Williams & Conway (1981). They took seasonal samples over a twelve year period and analyzed them for *D. arctica*, April to October 1973. They found that numbers of *D. arctica* started to increase in early April, peaked in June, and then dropped fairly sharply to a low level at which they remained until the following spring. It also resembles a bloom of *D. arctica* in an open-ended fiord in Sweden from February to April 1978 (Bamstedt 1985). There *D. arctica* was a dominant species below 30 m in these months, reaching similar maximum numbers to those found in the Strait of Georgia. Zelickman (1972), studying *D. arctica* in the southern Barents Sea over an eight year period, found it to be common below 100 m in winter and spring, although there it was more abundant at a lower temperature (1-2°C) than in the Strait of Georgia.

A plentiful supply of food must be available in the central strait water to facilitate such an enormous increase in numbers of *Dimophyes arctica* during spring and early summer. The diet has not yet been studied, but *D. arctica* almost certainly feeds on copepods, since these make up the main prey of all the calycophoran siphonophores so far investigated (Purcell 1981). Diphyids have fairly small gastrozooids (Purcell 1981) so *D. arctica* is probably only capable of ingesting prey in the 0.1 to 1.0 mm range. In the central Strait, nauplii and early copepodite stages of *Neocalanus plumchrus* dominate the zooplankton in the top 100 m during mid-April and May (LeBrasseur et al. 1969, Fulton 1973), and almost certainly form the main food source of *D. arctica*. *N. plumchrus* migrates up from deeper water before the start of the spring bloom (Fulton 1973), as do *Calanus marshallae*, *C. pacificus* and *Metridia pacifica* (LeBrasseur et al. 1969). *Pseudocalanus minutus* and other very small copepods are also present (LeBrasseur et al. 1969), and most stages of these together with nauplii and early copepodites of *C. marshallae*, *C. pacificus* and *M. pacifica* could all contribute to the diet of *D. arctica*.

Dimophyes arctica reached much higher numbers in May 1979 than the hydromedusae *Aglantha digitale* and *Aegina citrea* taken from the same daylight samples, and its population maximum was at 66 m, while those of *Aglantha* and *Aegina* were deeper at 150 m (Arai and Mason 1982). *Aglantha* is also a copepod feeder (Lebour 1922; Smedstad 1972), but competition for food may be eliminated by the differential depth distributions of these coelenterates. At night, however, the situation may change, because *Aglantha* moves into the upper layers (Arai and Fulton 1973), whereas *Dimophyes* makes no such diel migration (Pugh 1984, Stepanyants and Lobanov 1989).

Nanomia bijuga was the only other siphonophore species common in the central Strait of Georgia during the spring plankton bloom of 1979 and its population density was much lower than that of *Dimophyes artica*. *N. bijuga* has been cultured on arthropod food in the laboratory (Carré 1969, Biggs 1977). Prey actually captured and ingested by this species includes copepods, decapod larvae, shrimps and chaetognaths (Purcell 1981) and mysids (Biggs 1977). *N. bijuga* has larger gastrozooids and therefore feeds mostly on larger prey than *Dimophyes arctica*. In spring in the Strait of Georgia, while *D. arctica* is feeding on the smaller forms of *Neocalanus plumchrus* and other copepods, *N. bijuga* is probably consuming the larger copepodite stages, thus avoiding competition for food. It may also feed on chaetognaths, euphausids and other larger plankton species occurring in the central Strait of Georgia (Légaré 1957).

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