

SEASONAL OCCURRENCE OF PLANKTONIC MEDUSAE AND
CTENOPHORES IN THE SAN JUAN
ARCHIPELAGO (NE PACIFIC)

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Abstract.—Medusae and ctenophores have been recorded year-round between 1976 and 1980 in surface waters near Friday Harbor, Washington. A detailed schedule of annual occurrence has been compiled for 41 species of hydromedusae, 5 species of siphonophores, 4 species of scyphomedusae, and 11 species of ctenophores. An annotated species list provides additional information on sizes of medusae, periods of sexual maturity, special locations, and polyp stages. The Strait of Georgia-San Juan Archipelago-Puget Sound region has an unusually high diversity and abundance of medusae. Diversity reaches a maximum in late spring, thereafter a smaller number of species maintains a high biomass of medusae throughout the summer. From late autumn through early spring few medusae are present.

Introduction

Medusae and ctenophores are known to be major predators on other zooplankton. Because nutritional requirements of the various species of medusae and ctenophores are not equivalent, the effect of coelenterates as planktonic predators depends on the particular combination of species present in the plankton.

The Strait of Georgia-San Juan Archipelago-Puget Sound region (NE Pacific) is particularly rich in hydromedusae. The taxonomy of these medusae has been extensively discussed (Arai and Brinckmann-Voss, 1980; Kozloff, 1974; Mackie and Mackie, 1963; Foerster, 1923), but information on their seasonal distribution and life stages is incomplete, especially between late fall and early spring. Presented in this paper is a detailed schedule of the annual occurrence of 61 species of medusae and ctenophores. An annotated species list provides additional information. This compilation may serve as a baseline for further study of the interactions between coexisting coelenterates and other zooplankton. It also identifies when specific medusae may be collected in this locality. Several species new to the area are recorded here.

The San Juan Archipelago (Fig. 1) is composed of over one hundred islands that lie between the Strait of Juan de Fuca (south), Vancouver Island (west), the Strait of Georgia (north), and the US mainland (east). The area was heavily glaciated and islands are separated by steep-walled channels,

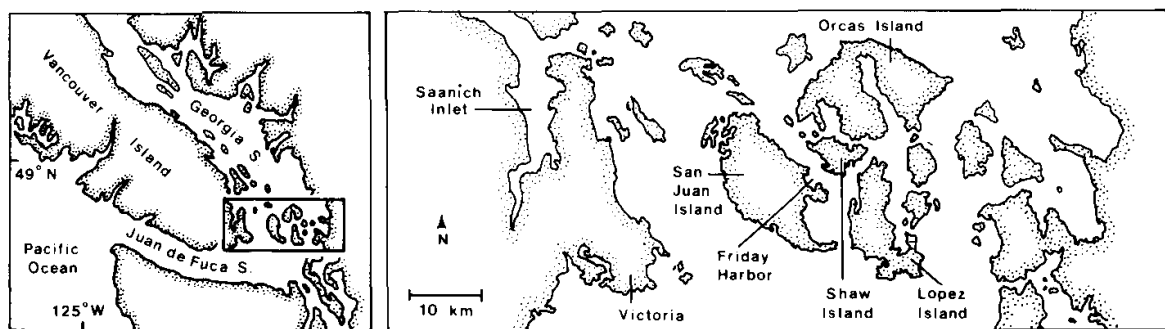


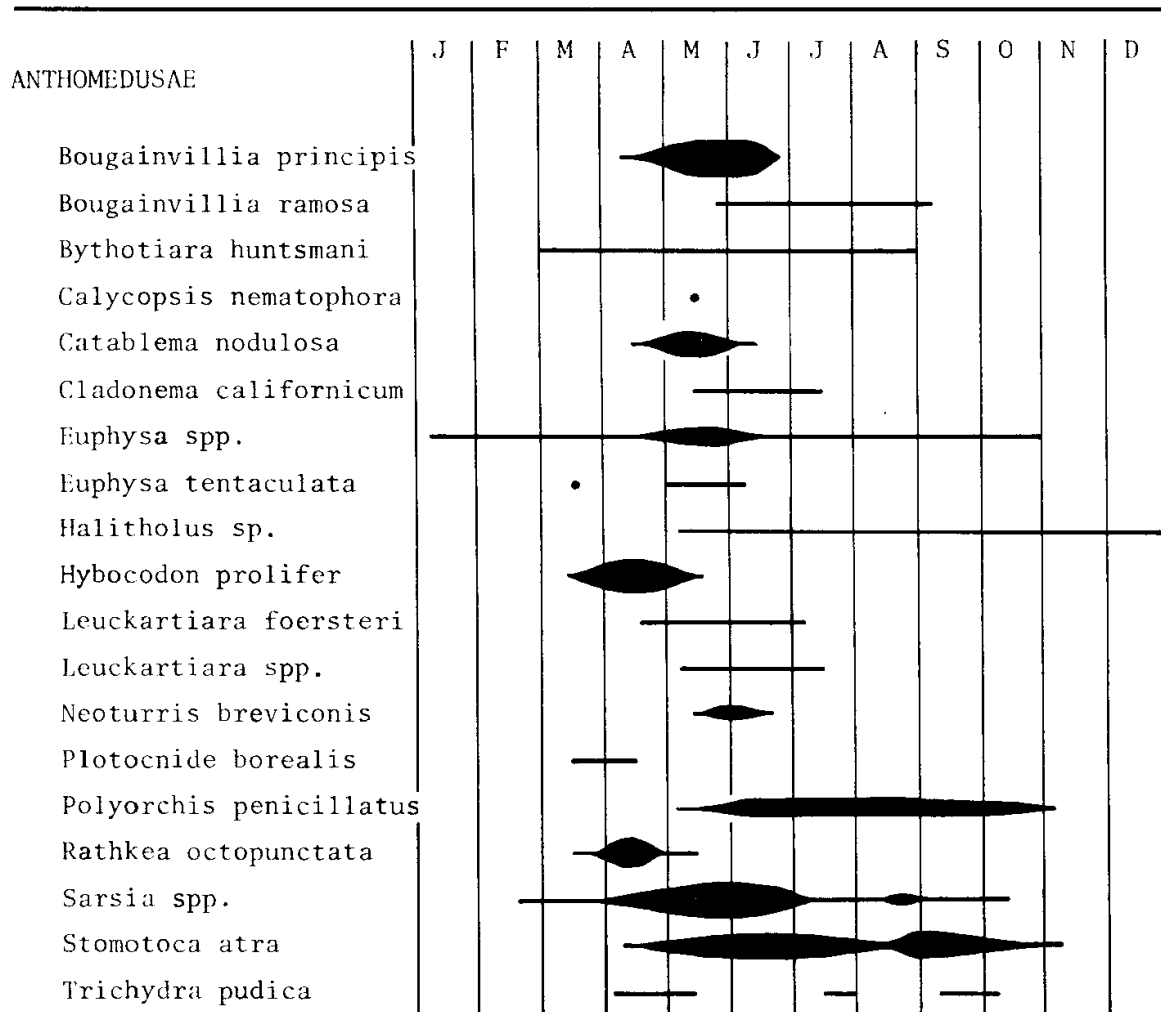
Figure 1. Map of the study area showing the southeastern portion of Vancouver Island (left), southern portion of the San Juan Archipelago (center), and west coast of the U.S. mainland (right).

some of which are greater than 200 meters deep. Some of the channels and embayments are traversed by sills. Turbulent tidal flows of 3 to 5 knots through these channels cause waters in the San Juan Archipelago to be well mixed and virtually homogeneous in vertical profile. During tidal flood, stratified water from the ocean-inlet Strait of Juan de Fuca moves into the San Juan Archipelago where shallow and deep waters mix, and is then jetted as a deep layer into the usually less saline Strait of Georgia (a body of water much influenced by seasonal freshwater discharge of the Fraser River, British Columbia). During tidal ebb, stratified waters from the Strait of Georgia are mixed thoroughly in the San Juan channels before being jetted into the Strait of Juan de Fuca (Herlinveaux and Tully, 1961). The water in Friday Harbor is continuously exchanged with adjoining channels. Continuous mixing prevents the depletion of nutrients in these waters and helps stabilize water temperature and salinity throughout the year. Surface water temperature in Friday Harbor varies between 7°C in the winter and 13°C in the summer (Pfifer and Thompson, 1937). Salinity is nearly always between 28‰ and 32‰ (Collias *et al.*, 1974), although in most years, a dilute surface layer is present for one to two weeks in late spring due to Fraser River runoff.

Methods

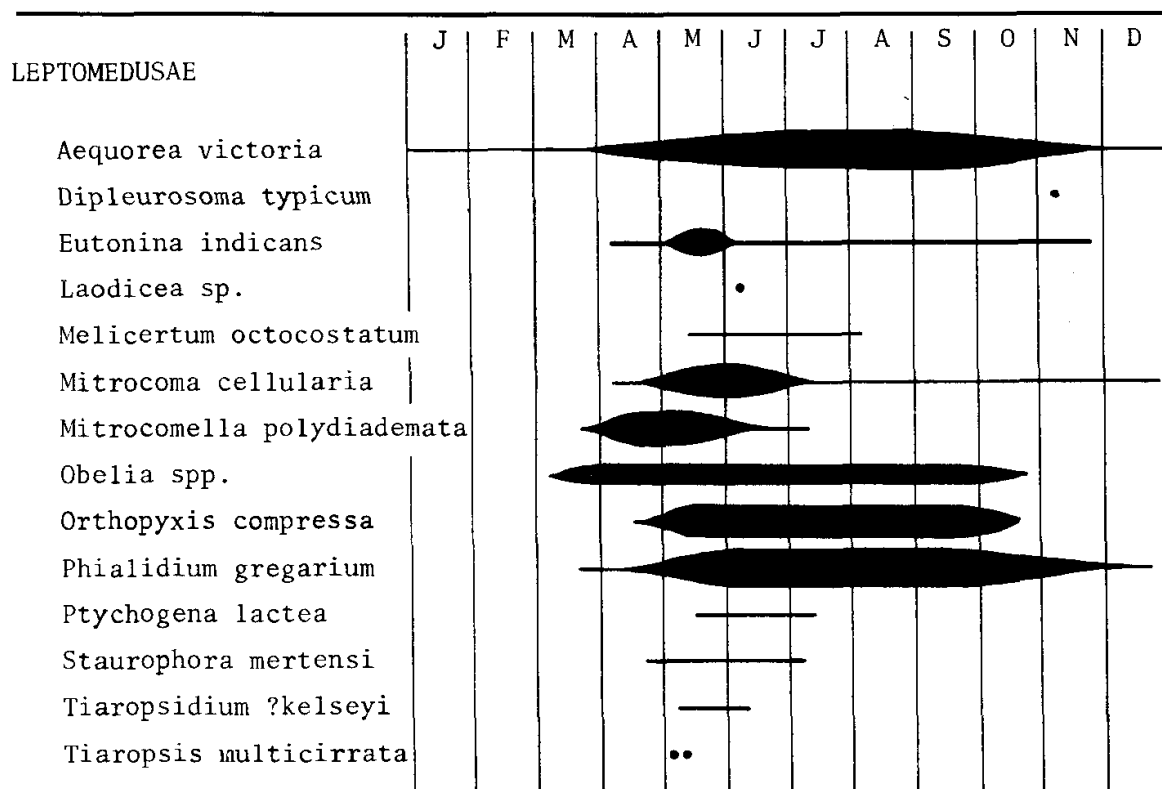
Medusae and ctenophores were recorded year-round between 1976 and 1980 in surface waters of the San Juan Archipelago near Friday Harbor, Washington (Fig. 1). Between autumn 1977 and summer 1980, observations were made approximately weekly in the winter and nearly daily in the summer. Less frequent observations were made between January 1976 and June 1977 (monthly in winter, weekly in summer). Included in my tabulations are some additional observations by Volker Schmid (personal communication) during 1975-1976, by Mackie and Mackie (1963), and some unusual specimens in the Friday Harbor Laboratories Synoptic Collection.

Table 1. Compilation of seasonal occurrence of medusae and ctenophores in the vicinity of Friday Harbor, Washington. Dots (·) indicate isolated observations of one or more individuals for one or two days. Single weight lines (—) indicate both *rare* species, for which a maximum of 1 to 2 per hour are regularly sited, although these are often not seen for many days at a time, and species in which only a *few* medusae, 3 to 6 individuals per hour, are regularly seen. Medium thickness lines (—) indicate species that are *common* for many days; usually 7 to 15 per hour can be seen. The thickest lines (■) indicate species that are *abundant* for many days; at least 15 per hour can be seen most of the time, although they may be much more numerous.



Medusae and ctenophores recorded in Table I have been observed primarily from the dock of the Friday Harbor Laboratories (FHL) on San Juan Island which extends about 75 m out into Friday Harbor. The water is 5–20 m deep under the floating parts of the dock from which observations have been made. Many observations were made at night using a suspended 100 watt lamp in a waterproof housing. Additional records of medusae came from surface plankton tows or from direct observation of surface plankton in nearby areas of the San Juan Archipelago. A few species of medusae are

Table 1. Continued.



restricted to certain bays, as indicated in the annotated species list, and are not generally found in the circulating surface waters. Seasonal distributions of *Bougainvillia ramosa*, *Bythotia huntsmani*, and *Obelia* spp. medusae were inferred from the presence in the field of polyp colonies bearing mature medusa buds.

Abundance of each species was recorded in the following categories during one-hour observation periods: *rare* (1-2 per hour), *few* (3-6 per hour), *common* (7-15 per hour), *abundant* (more than 15 per hour). In one hour, a person using a nightlight can thoroughly search approximately 50-100 m³ of surface water under most current conditions. No evidence of avoidance of the nightlight has been documented for any of these medusae or ctenophores. Even medusae measuring 1 mm in diameter can be seen by an experienced observer using a nightlight, which provides the effect of dark field illumination. Positive identification of many of the smaller medusae requires examination with a dissecting microscope.

Table 1 represents a 12-month integration of the records for all years. Seasonal distributions between years vary surprisingly little. The only noteworthy effects of compiling records from several years are that: (1) the seasonal timespan for any species may appear to be somewhat greater than should be expected for any single year because early appearances in some

Table 1. Continued.

	J	F	M	A	M	J	J	A	S	O	N	D
LIMNOMEDUSAE												
<i>Eperetmus typus</i>					•							
<i>Gonionemus vertens</i>												
<i>Proboscoidactyla flavicirrata</i>												
TRACHYMEDUSAE												
<i>Aglantha digitale</i>												
NARCOMEDUSAE												
<i>Aegina citrea</i>												
<i>Cunina</i> sp.												
<i>Solmissus marshalli</i>												
SIPHONOPHORA												
<i>Dimophyes arctica</i>					•							
<i>Lensia conoidea</i>												
<i>Muggiaea atlantica</i>												
<i>Nanomia cara</i>												
<i>Praya reticulata</i>												

years and late occurrences in other years are superimposed and (2) uncommon species are all listed although they do not occur every year.

Observations

Table 1 lists the species of medusae and ctenophores that have been observed in the vicinity of Friday Harbor, Washington, and indicates their span of occurrences (horizontal) and abundances (vertical). A discussion follows of each species with comments on sizes of medusae at various times of the year, periods of sexual maturity, identifying characteristics in the cases of uncertain species identification, special locations, and polyp stages.

Descriptions and illustrations of the species of hydromedusae mentioned in this paper can be found in the monographs by Kramp (1959, 1961, 1968) and by Arai and Brinckmann-Voss (1980). The siphonophores are described

Table 1. Continued.

	J	F	M	A	M	J	J	A	S	O	N	D
SCYPHOZOA												
Aurelia aurita				—	—	—	—	—	—	—	—	
Chrysaora fuscescens					• •	•					•	
Cyanea capillata				—	—	—	—	—	—	—	—	—
Phacellophora camtschatica				—	—	—	—	—	—	—	—	
CTENOPHORA												
Beroe abyssicola												
Beroe ?cucumis												
Beroe sp.					—							
Bolinopsis ?infundibulum	—	—	—	—	—	—	—	—	—	—	—	—
Dryodora glandiformis			—	—	—	—	—					
Haeckelia rubra					—							
Hormiphora cucumis						—	—	—	—			
Hormiphora sp.	•	•		•		•			•			
Leucothea sp.											•	
Pleurobrachia bachei	—	—	—	—	—	—	—	—	—	—	—	—
Pleurobrachia spp.			—	—	—	—	—					

and illustrated by Totton (1965). Scyphomedusae are described by Kramp (1961) and illustrated by Larson (1976) and Shih (1977).

PHYLUM CNIDARIA
CLASS HYDROZOA
Order Anthomedusae/Athecata

Bougainvillia principis (Steenstrup 1850)

This medusa may be found for about 2½ months every spring. Friday Harbor specimens correspond well to *B. principis* as described by Edwards (1966), although in Friday Harbor specimens the gonads remain interradian, not developing a secondary adradial aspect. Probably *B. principis* at Friday Harbor is the same as *B. multitentaculata* (Arai and Brinckmann-Voss, 1980; Foerster, 1923) of Vancouver Island, which is described as having 50–60 tentacles per marginal bulb. Friday Harbor specimens rarely have more than 30 tentacles per bulb (Mills, unpublished; Mackie and Mackie, 1963;

Gellerman, 1926). Small numbers of immature *B. principis* are present in the second half of April and early May. From mid-May to mid-June sexually mature *B. principis* are usually very abundant and one may see 50–100 medusae in an hour from the FHL floats. (There will also be days during this period when none or very few will be present.) *Bougainvillia principis* disappears from the plankton sometime in mid- to late June, usually rather abruptly. The medusae can survive in the laboratory in good condition for at least one month after their disappearance from the field. Since *B. principis* are often seen in *Aequorea* stomachs in June, predation by *Aequorea* may account for their disappearance. The polyp of *B. principis* (Edwards, 1966) has not been recorded from the Friday Harbor region.

Bougainvillia ramosa (van Beneden 1844)

Polyp colonies of *B. ramosa* grow luxuriantly in the summertime on the undersides and edges of the floats of the gas station dock in the town of Friday Harbor. Although the polyps are loaded with medusa buds and, in the laboratory, freely release medusae which I have raised to maturity, the medusa of *B. ramosa* has never been collected in this area. This is the first record of *B. ramosa* in the Washington-British Columbia region.

Bythotiara huntsmani (Fraser 1911) (= *Endocrypta huntsmani*)

The polyp colony of this medusa is restricted to the incurrent siphon of several species of tunicates: *Ascidia paratropa*, *A. callosa*, *Corella willmeriana*, *Halocynthia aurantium*, and *H. igaboja* (Rees, 1979b; Brinckmann-Voss, 1979). Medusa buds are seen throughout the summer in these colonies and medusae can be obtained in the laboratory. Free *B. huntsmani* medusae have never been collected in the Friday Harbor area, but I have collected two of these medusae in plankton samples in nearby Saanich Inlet, B.C. (March 1978 and December 1978). Medusa buds are known to be produced on the hydroid colonies from March through August (Brinckmann-Voss, 1979) and are probably present over an ever longer period.

Calycopsis nematophora Bigelow 1913

One mature specimen of this medusa was collected by W. Schwab from the FHL floats on 14 May 1977. This species has been collected frequently offshore in the North Pacific (Renshaw, 1965), but it is rarely seen in inland waters. Its polyp is not known.

Catablema nodulosa (Bigelow 1913)

This medusa has incorrectly been called *Leuckartiara nobilis* for many years at Friday Harbor. *Leuckartiara nobilis* apparently does not exist in

the San Juan Archipelago. *Catablema nodulosa* is a new combination (Arai and Brinckmann-Voss, 1980). Sexually mature specimens of this medusa occur between early April and early June. They may be abundant for several weeks during this period. Although specimens of all sizes may be collected in Friday Harbor, the average size of these medusae increases in the late spring. The very large and bulbous apical projection helps to distinguish this species from the several related species of *Halitholus* and *Leuckartiara* that also occur during late spring. The hydroid of *C. nodulosa* is not known.

Cladonema californicum Hyman 1947

Small numbers of nearly ripe specimens of this medusa have been collected in June 1978, June 1979, and May through July 1980. They were found in Mitchell Bay, near the north end of San Juan Island, in shallow water where *Gonionemus vertens* is abundant. *Cladonema*, like *Gonionemus*, has adhesive structures on its tentacles with which it clings to algae or other substrates, and it is primarily benthic in habitat. The *Cladonema* polyp has not been collected in the San Juan Archipelago. One *C. californicum* polyp colony has been collected on *Zostera* in Bodega Harbor, central California (Rees, 1979a).

Euphysa spp.

Sexually mature specimens of *Euphysa flammea* (Linko 1905) or *Euphysa japonica* (Maas 1909) are sometimes seen from April through October, with a peak abundance in May and early June. Very young *Euphysa* medusae have been collected in surface plankton tows as early as January. Some of these very young medusae have only one tentacle, and therefore are tentatively identified as *E. flammea*, a species released with only one tentacle, developing the remaining 3 tentacles as it grows (Kramp, 1961). Others of these very young medusae have 4 tentacles, so these are tentatively identified as *E. japonica*, a form released with 4 equal tentacles (Kramp, 1961). The adult forms of these 2 species are apparently indistinguishable. Careful life history work should be done on these *Euphysa* medusae to determine their specific identities and to determine if the differences at release are sufficient to establish them as separate species. No *Euphysa* polyps are known from the Friday Harbor area.

Euphysa tentaculata Linko 1905

This medusa is not common; mature specimens have been collected primarily during May and June. One specimen has been collected in March. Its small adult size and the fact that it looks superficially like a small *Sarsia* make *E. tentaculata* difficult to recognize in the field. It is possible that

some of the young *Euphysa* spp. medusae collected in the winter are young *E. tentaculata*, whose juvenile stages are not described. The polyp of *E. tentaculata* is not known.

Halitholus sp.

This species has incorrectly been called *Leuckartiara octona* by many workers at FHL. It is described by Arai and Brinckmann-Voss (1980) as *Halitholus* sp. I. This medusa is seen infrequently from early May through December. Although not common, it is most likely seen between May and September. One polyp colony of *Halitholus* sp. was collected near Friday Harbor in the egg mass of a *Cancer gracilis* crab in August 1979. Medusae raised to sexual maturity by the author proved to be this species. The polyp colony and newly released medusae are nearly identical to those pictured by Russell (1953) for *L. octona*.

Hybocodon prolifer L. Agassiz 1862

Hybocodon medusae are present every year from mid-March until late May. They may be quite abundant some days during this period, when as many as 50 may be collected in an hour, but their small size makes them difficult to see. The polyp (see Russell, 1953) has not been collected in the Friday Harbor area.

Leuckartiara ?foersteri Arai and Brinckmann-Voss 1980

Isolated mature specimens of a medusa tentatively identified as *L. foersteri* occur sporadically between late April and early July most years. Friday Harbor specimens are similar to those described by Arai and Brinckmann-Voss (1980) except that they have massive, much crenulated lips, and *L. foersteri* is described with slightly crenulated lips. *Leuckartiara ?foersteri* may easily be overlooked at Friday Harbor because it is superficially similar in appearance to *Catablema nodulosa*, a species more common and occurring at the same time.

Leuckartiara spp.

There are two or more additional rare species of *Leuckartiara* or *Halitholus* in the Friday Harbor region. One specimen in the FHL Synoptic Collection is probably *L. octona*. It was collected in Friday Harbor in July 1954 by H. Osborn. Another unidentified *Leuckartiara* collected by G. O. and G. V. Mackie is discussed by Arai and Brinckmann-Voss (1980).

Neoturris brevis (Murbach and Shearer 1902)

This medusa has previously been known as *Leuckartiara brevis*. Recently Arai and Brinckmann-Voss (1980) re-examined its morphology and decided that it belongs in the genus *Neoturris*. Nearly ripe and mature specimens are occasionally collected between mid-May and mid-June. The abundance is variable from year to year; one may see 10 per season or 10 per day. Its polyp is not known.

Plotocnide borealis Wagner 1885

Young specimens of this tiny medusa have been collected annually in small numbers in surface plankton tows in Parks Bay, Shaw Island. It has never been seen from the FHL floats. It is one of the first medusae to appear in the spring, being found in March and April. Because of their spherical shape and small size, young *P. borealis* medusae may be mistaken for fish eggs in plankton samples. They can be distinguished even in preserved material by the clusters of nematocysts on the bell surface, causing a vaguely spotty surface appearance. The polyp of *P. borealis* is not known.

Polyorchis penicillatus (Eschscholtz 1829)

This medusa, like *Gonionemus*, seems to be largely restricted to shallow bays and is usually associated with the seagrass *Zostera*. In most cases, *Polyorchis* and *Gonionemus* do not occur in the same bay, although Parks Bay, Shaw Island, supports small populations of each. *Polyorchis* also occurs in Mackaye Harbor and Shoal Bay, both on Lopez Island. It is infrequently collected in the surface waters of Friday Harbor. Small specimens of *Polyorchis* are found in May. Increasingly large and sexually mature specimens are found throughout the summer and into the autumn. The latest that *Polyorchis* has been seen in the San Juan Archipelago is in early November. The polyp of *Polyorchis* (Brinckmann-Voss, 1977) is not known from the Friday Harbor area.

Rathkea octopunctata (M. Sars 1835)

This medusa is seen between March and May. During this period it may be fairly abundant for one or two weeks; at other times only small numbers are found. *Rathkea* is the only species in the Friday Harbor region whose medusa asexually produces more medusa buds on its manubrium (although this is not an unusual feature of hydromedusae). The polyp of *Rathkea octopunctata* (see Russell, 1953) has not been found in the Friday Harbor area.

Sarsia spp.

Preliminary life cycle studies (Mills, unpublished) suggest that there are at least 4 species of *Sarsia* in the Friday Harbor region. Since they occur more or less simultaneously and their taxonomy has not been adequately worked out, they are considered together in this paper. Anyone working with *Sarsia* should be aware of the number of similar-looking, easily confused species. *Sarsia* medusae may be found from late February until October. In the early spring most specimens are very young. Larger, sexually mature individuals become increasingly common in April and usually remain abundant into early July. Most years there is a decline in numbers in July and August (when they may be virtually absent); sometimes another pulse of *Sarsia* medusae appears in September. Several species of *Sarsia* polyps are easily collected on floats and on intertidal and subtidal rocks, shells, and algae. Careful life history work must be completed before the identities of all species of *Sarsia* in the area are known.

Stomotoca atra A. Agassiz 1862

This species has been collected from mid-April through mid-November. Spring specimens are usually quite small, but by mid-May, adults may be abundant. Mature adults are seen in abundance throughout the summer, although there may be a period of several weeks when they are scarce. An increase in abundance of *Stomotoca* medusae in the late summer that may last well into autumn probably represents a second generation of medusae in the summer. The polyp of *Stomotoca atra* is not known.

Trichydra pudica Wright 1858 (= *Pochella polynema*)

A few immature specimens of this medusa were collected at the FHL floats in September–October 1978 and in April–May 1979. They had not been seen in previous years of this study. They were also collected in East Sound, Orcas Island (where Gellerman [1926] reported them to be numerous in late July) in April and July 1979. *Trichydra* has very fine sidebranches coming off its 4 radial canals. These may require microscopic examination to be seen. This medusa has previously been reported in the Vancouver Island area as *Pochella polynema* and as *Proboscidactyla polynema*, but has recently been shown to be the medusa of the polyp *Trichydra pudica* (Edwards, 1973a). Because the *Trichydra* name has precedence, the medusa should also take that name. The polyp has not been recorded from the Friday Harbor area.

Order Leptomedusae/Thecata

Aequorea victoria (Murbach and Shearer 1902)

This medusa, also known locally as *A. aequorea* and *A. forskalea*, has been recently re-examined by Arai and Brinckmann-Voss (1980). They have reinstated *Aequorea victoria* as the correct name. It is one of the most abundant medusae in Friday Harbor during the summertime. At times, these medusae cover acres of water, only a few cm apart. *Aequorea* has been harvested heavily in Friday Harbor; tens of thousands have been used each summer for about 15 years (R. L. Fernald, personal communication) to extract and purify the luminescent protein aequorin. Young *Aequorea* medusae are first seen in March, and by April, individuals of approximately 1 cm diameter are abundant in East Sound, Orcas Island. These medusae are probably one to two months old. Throughout the summer, *Aequorea* medusae of all sizes are seen, indicating that there is continuous release from polyps in the field over a long period. *Aequorea* medusae become quite scarce, and often are in deteriorated condition in the late fall. Isolated individuals are seen infrequently during the winter. A small *Aequorea* polyp colony producing medusae was collected in March 1979 on a *Chlamys* shell dredged in San Juan Channel.

Dipleurosoma typicum Boeck 1866

This circumpolar species has been seen only once at FHL, when many mature specimens were collected by nightlight in two evenings following a month of exceedingly windy weather (9-10 November 1977). Superficially, *D. typicum* resembles *Phialidium gregarium* which was also common in November on the nights it was collected. *Dipleurosoma* also looks somewhat like young *Aequorea* because of its numerous radial canals, but it has many more tentacles than *Aequorea* medusae of the same size. The polyp of *Dipleurosoma typicum* (Russell, 1970) has not been collected in the NE Pacific.

Eutonina indicans (Romanes 1876)

This species is most likely to be seen between April and early June, although it has been seen infrequently as late as November. Usually *Eutonina* is not very abundant around Friday Harbor, but in the spring of 1979, large numbers of sexually mature medusae (50-100 per hour) were seen. *Eutonina* is one of the most abundant spring hydromedusae elsewhere in the Vancouver Island region. The polyp is not known from Friday Harbor, but has been found on *Zostera* blades, on a crab, and on rocks in Bodega Bay, central California (Rees, 1978).

Laodicea sp.

One immature medusa identified as a *Laodicea* was collected by R. L. Miller on 7 June 1978 at the FHL nightlight. This is the only reported occurrence of *Laodicea* in the region.

Melicertum octocostatum (M. Sars 1835)

This species is seen occasionally in Friday Harbor waters. Mature medusae have been collected from May through August; usually single specimens are seen, although as many as 11 have been collected in a single evening. In some years (e.g. 1978) no *Melicertum* have been seen. The polyp of *Melicertum* (see Russell, 1953) has not been recorded from Friday Harbor.

Mitrocoma cellularia (A. Agassiz 1865) (= *Halistaura cellularia*)

Previously known as *Halistaura cellularia*, this medusa has recently been placed in the genus *Mitrocoma* by Arai and Brinckmann-Voss (1980). Most specimens reported as *M. discoidea* in the region have probably been young specimens of *M. cellularia*. *Mitrocoma cellularia* has been collected from spring through autumn, but it is most abundant during May and June. Some years it may still be found commonly in July and August (e.g. 1978), and on some days it may be as abundant as *Aequorea*. In 1979, *M. cellularia* became scarce in late June and did not reappear. There are infrequent sightings of this medusa during the autumn. R. L. Fernald (personal communication) reports that it was abundant on Christmas day 1970 in Friday Harbor. The polyp has not been collected in the Friday Harbor area.

Mitrocomella polydiademata (Romanes 1876)

This medusa is usually present from early April until early July. It is one of the most abundant medusae from mid-April until early June (along with *Bougainvillia*) and is sexually mature from mid-April until it disappears. Hundreds of these medusae may be seen from the FHL floats on days when it is particularly abundant. *Mitrocomella polydiademata* appears to be a favorite food of *Aequorea* medusae, in whose stomachs the pink color of *M. polydiademata*'s radial canals and bell margin is still evident. The polyp (Edwards, 1973b) has not been collected in the region.

Obelia spp.

Obelia is the most common hydroid that fouls floats and boat bottoms in the Friday Harbor area. Medusae are released at least between March and October. *Obelia* medusae are seen in rather small numbers in the field, but

masses can be obtained easily by collecting polyps and allowing them to release medusae in the laboratory.

Orthopyxis compressa (Clark 1876) (= *Agastra rubra*)

This medusa (*Agastra*) may be released from its hydroid (*Orthopyxis*) between late April and late October, although in some years it may have a considerably shorter season. Medusae are released in substantial numbers, but are so short-lived (persisting from several hours to probably a maximum of one day in the plankton) that they might easily go unseen. The polyp has been found growing on algae and on mussel shells under floats and in tide-pools. *Orthopyxis* hydroids (Nutting, 1915) overwinter as sparse colonies with normal hydranths, producing gonophores in the spring as they luxuriate. Medusae are liberated from gonophores in the evening shortly after dark, and spawn about 15 minutes after their release (Miller, 1978). They die within a few hours of their release.

Phialidium gregarium (A. Agassiz 1862)

Along with *Aequorea victoria*, *Phialidium gregarium* is one of the most visible and easily obtained medusae in Friday Harbor. This medusa may be found from late March until November or December. It is common from mid-April into November, although there may be a period during mid-summer when it is not very abundant. Several synchronized changes in size of *Phialidium* medusae during the summer imply that its hydroids may release medusae in pulses. The polyp of *P. gregarium* (Roosen-Runge, 1970) may be found on rocks and wood in the Friday Harbor area.

Ptychogena lactea A. Agassiz 1865

This deep-water medusa has been infrequently collected in the late spring and early summer from the FHL floats. Its occurrence is not predictable and it is not seen every year. Its hydroid (Naumov, 1960) apparently lives at depths greater than 200 m and has not been found in the Friday Harbor region.

Staurophora mertensi Brandt 1835

This species is occasionally seen in Friday Harbor. A large sexually mature specimen was collected on 9 July 1973. Immature specimens have been observed between April and July in 1978–1980. These late spring medusae do not usually have the well developed gastric diverticula on their radial canals that are very distinctive in mature specimens. They can be easily overlooked because they resemble the common *Mitrocoma cellularia*, and

therefore are perhaps not as rare as observation records indicate. The polyp (Naumov, 1960) is not known from the field in this area.

Tiaropsidium ?kelseyi Torrey 1909

A few *Tiaropsidium* specimens have been collected from the FHL floats in May and June by R. L. Miller and the author. A few similar specimens have been collected in plankton tows in Saanich Inlet in May (Mills, unpublished). Most of these specimens measured 4–6 mm in diameter, and had 4 large perradial tentacles with conical bulbs and a few rudimentary tentacles in each quadrant. One specimen was 20 mm in diameter and had 8 large tentacles. All specimens were immature with no evidence of gonads. The medusae have 8 lithocysts, each with a black ocellus. These *Tiaropsidium* medusae are most likely to be immature specimens of *T. kelseyi* which has been previously reported in the Vancouver Island area (Foerster, 1923). *Tiaropsidium kelseyi* grows to 50 mm in diameter and has 8 large tentacles as well as 40 to 64 rudimentary tentacles. Its polyp is not known.

Tiaropsis multicirrata (M. Sars 1835)

Two specimens of *Tiaropsis* were collected from the FHL floats in May 1977. They were sexually mature at about 12 mm bell diameter. The polyp (see Russell, 1953) has not been recorded in the region.

Order Limnomedusae

Eperetmus typus Bigelow 1915

Eperetmus is rarely seen in the vicinity of Friday Harbor and in many years no specimens have been observed. One specimen was collected in May (Mackie and Mackie, 1963). Other sightings have occurred between late June and November. The polyp of *Eperetmus typus* is not known (Mills *et al.*, 1976).

Gonionemus vertens A. Agassiz 1862

Gonionemus vertens lives only in certain shallow bays in association with the plants *Zostera* or *Ulva*. These bays include Mitchell Bay, False Bay, Smallpox Bay, and Griffin Bay on San Juan Island, and Parks Bay on Shaw Island. *Gonionemus* is not found in the generally circulating surface plankton of the San Juan Archipelago. Very young *G. vertens* medusae are first found in mid- to late May and continue to be released from polyps into June. The medusae grow up in these same bays for about two months; in some bays they are very abundant. The first sexually mature *G. vertens* medusae are seen in mid-June. The medusae gradually die off in August and

are generally absent by early September. The cryptic *Gonionemus* polyps (Mikulich, 1970) have been found on rocky substrates in these shallow bays.

Proboscidactyla flavicirrata Brandt 1835

This medusa may be found year-round, although it is not common during the winter. Usually *P. flavicirrata* is present in small numbers (0-3 per hour), but in May and from August through October, one may see 10-15 per hour on some days. The polyp colony of *P. flavicirrata* (see Hand, 1954) lives on the rim of the tube of the sabellid polychaete *Schizobranchia*.

Order Trachymedusae

Aglantha digitale (O. F. Müller 1776)

Aglantha is present year-round in the Friday Harbor area. Specimens occur sporadically at the surface, usually in small numbers, but from May through July they may occasionally appear in abundance at the surface. *Aglantha* is circumpolar in distribution and is associated with deep water in most localities. *Aglantha* has no polyp form.

Order Narcomedusae

Aegina citrea Eschscholtz 1829

This medusa generally lives in deep water and is not commonly seen at the surface. It has been collected throughout the year from the FHL floats, but usually only single specimens have been observed. Narcomedusae, like Trachymedusae, are holoplanktonic and have no polyp forms.

Cunina sp.

Four immature *Cunina* specimens have been collected by R. L. Miller and the author in April and May 1978 and 1980 off the FHL floats. The specimens were all about 1 cm in diameter and had 9 tentacles and 9 stomach pouches. These are the only specimens of the genus *Cunina* recorded from the area.

Solmissus marshalli Agassiz and Mayer 1902

This medusa has been observed from the FHL dock from mid-February through mid-November, but is regularly seen only from May through July. Early spring and fall observations are spotty, although individuals seen at these times appear healthy and it is presumed that a few *Solmissus* are present throughout the winter.

Order Siphonophora

Dimophyes arctica (Chun 1897)

Dimophyes is sometimes seen in the Friday Harbor surface water in the colder months. It has been taken occasionally from October through March and was seen once in May. The polygastric phase is usually seen.

Lensia conoidea (Keferstein and Ehlers 1860)

Lensia conoidea has been collected 3 times at the FHL float in late May and early June in its polygastric phase.

Muggiaea atlantica Cunningham 1892

This siphonophore has been seen off the FHL float at most times of the year, most commonly as a polygastric, but eudoxids are also seen. *Muggiaea* polygastrics are sometimes abundant during the autumn between September and November.

Nanomia cara A. Agassiz 1865

Nanomia has been seen in surface waters year-round, but is most commonly seen during the summer. One or two sightings in a few hours are about as many as can be expected.

Praya reticulata (Bigelow 1911)

One incomplete polygastric specimen of *Praya reticulata* was collected from surface waters at FHL by G. O. Mackie in June 1969.

CLASS SCYPHOZOA
Order Semaestomeae*Aurelia aurita* (Linnaeus 1758)

Although it is abundant in some areas of the Strait of Georgia-Puget Sound region, *Aurelia* is only occasionally seen in Friday Harbor. Single specimens have been observed between early April and early November. Young *Aurelia* ephyrae have been collected from the FHL floats in late October.

Chrysaora fuscescens Brandt 1835 (= *C. helvola* Brandt 1838)

This medusa is common in NE Pacific coastal areas, but is rarely seen in the inland waters. Two small *C. fuscescens* were seen near the FHL floats in May 1980. One small specimen in the FHL Synoptic Collection was collected in Friday Harbor on 24 June 1936. A few small (less than 15 cm

diameter) battered specimens were seen by SCUBA divers in early November 1979 on the west side of San Juan Island at the same time as the ctenophore *Leucothea*.

Cyanea capillata (Linnaeus 1758)

Cyanea medusae are seen in Friday Harbor between April or May, when specimens of all sizes are present, and December, when only large specimens are seen. They are not abundant; sightings of no more than 3-5 per week are usual. *Cyanea* may be reddish or yellowish and is distinguished by its short, but massive, mouth lobes and 8 crescent-shaped groups of tentacles hanging from the subumbrella near the margin.

Phacellophora camtschatica Brandt 1835

This medusa is seen between April and November, a little less frequently than *Cyanea*. *Phacellophora*, like *Cyanea*, commonly reaches 50 cm in diameter and is usually yellowish. It is distinguished from *Cyanea* by having 16 sets of marginal tentacles (although specimens with as few as 12 sets have been seen).

PHYLUM CTENOPHORA

Beroe abyssicola Mortensen 1927

This ctenophore occurs infrequently anytime during the year. Rarely is there more than a single specimen captured at one time. *Beroe abyssicola* is easily recognized by its vase-shaped stomodaeum which is lined with intense red, purple, or black pigment.

Beroe ?cucumis Fabricius 1780

Beroe ?cucumis may be found throughout the year, but it is more often seen between November and June. It is neither common nor predictable. During March 1979 there was a great intrusion of several species of ctenophores in Friday Harbor, and many *Beroe ?cucumis* could be seen at one time; this is very unusual. *Beroe ?cucumis* has arborized gastric canals, but the branches from adjacent canals are never fused. Some individuals are colorless; others have red or lilac pigment on the outer surface, or distributed throughout the mesogloea. *Beroe ?cucumis* eggs are about 1 mm in diameter.

Beroe sp.

An undescribed species of *Beroe* was fairly common off the FHL docks for about 2 weeks in early May 1980. This fairly slender, small *Beroe* is

similar to *B. gracilis* in its lack of digestive diverticula just below the body surface, but a few diverticula are present, directed inward toward the pharynx. The eggs of this species of *Beroe* are 220 μm in diameter. It is a voracious predator on *Pleurobrachia bachei*.

Bolinopsis ?infundibulum (O. F. Müller 1776)

Bolinopsis may be found throughout the year. Its occurrence is sporadic. Any month there is a possibility of finding many specimens, but *Bolinopsis* is most likely to be collected between April and November. The *Bolinopsis* specimens correspond fairly well to Agassiz' (1865) description of *B. microptera* from the nearby Rosario Strait, however a few discrepancies exist, most noteworthy of which are the prominent rows of black pigment spots which Agassiz does not mention, that are near the oral end in line with the ctene rows. *Bolinopsis microptera* is almost certainly the same as *B. infundibulum* from the Atlantic Ocean, but until living specimens of both forms can be compared, this identification cannot be verified.

Dryodora glandiformis (Mertens 1833)

Dryodora appears infrequently most years, usually in small numbers, from March into the summer (summer observations from Dunlap, 1966).

Haeckelia rubra (Köl liker 1853)

Although frequently called *Euchlora rubra*, the name *Haeckelia* predates *Euchlora* and is therefore the correct genus name for this ctenophore. *Haeckelia* is uncommon, not seen most years, and has only been collected during the month of May in the San Juan Archipelago. *Haeckelia* does not possess colloblasts on its tentacles like other ctenophores, but instead bears nematocysts extracted from narcomedusae on which it feeds (Mills, unpublished).

Hormiphora cucumis (Mertens 1833)

This ctenophore is not seen every year. Dunlap (1966) collected several specimens off San Juan Island in the summer of 1965.

Hormiphora sp.

An unidentified species of *Hormiphora* has been collected in early January 1978, late February 1979, late April and late June of 1980, and late September of 1978. This ctenophore is about the size of *Pleurobrachia bachei* and is ovoid. Its purplish tentacle sheaths are over one-half of the body length and lie against the pharynx for most of their length. The ten-

tacles, which have numerous, closely packed tentillae, are red or pinkish purple.

Leucothea sp.

Numerous specimens of *Leucothea* sp. were seen off the west side of San Juan Island in early November 1979 (C. Young and L. Cameron, personal communication). The ctenophores were present for several days. One specimen was also collected in Pedder Bay, south of Victoria, British Columbia during this period. These lobate ctenophores were large (25 cm or more in length) and had yellow-orange papillae distributed over their body surfaces. They correspond to *Leucothea pulchra*, an undescribed species, collected by L. Stanford (1931, Unpublished M.S. Thesis) off central California.

Pleurobrachia bachei A. Agassiz 1860 (= *Pleurobrachia pileus* var. *bachei*)

Pleurobrachia bachei and *P. pileus* are very similar. Bigelow (1912) chose to call *P. bachei* a variation of *P. pileus*, but I prefer to retain them as separate species. In *P. bachei*, the infundibular canal is longer than the gastric cavity; in *P. pileus* the infundibular canal is shorter than the gastric cavity. *Pleurobrachia bachei* is restricted to the West Coast of North America, whereas *P. pileus* occurs in the Atlantic and Mediterranean oceans as well as the Pacific (Bigelow, 1912).

Pleurobrachia bachei may be found throughout the year in Friday Harbor. The population increases considerably in the spring and summer during which it is usually common, but its appearance is somewhat sporadic.

Pleurobrachia spp.

Another species of *Pleurobrachia* appears infrequently between late March and July. It is distinguished by the widely-spaced tentillae on its tentacles that coil up into little pear-shaped bundles. This ctenophore appears to have been erroneously called *P. pileus* by Dunlap (1966). *Pleurobrachia pileus*, however, is very similar to *P. bachei* (see above) and does not have the peculiar coiled, sparse tentillae of the present organism.

At least two other species of *Pleurobrachia*, represented by single specimens, have been collected in Friday Harbor (Mills, unpublished; Dunlap, 1966).

Discussion

In general, medusae are unusually abundant in the Friday Harbor area. Plankton in the Strait of Georgia is extremely patchy (Parsons *et al.*, 1970) and this patchiness extends into the San Juan Archipelago so that meaning-

ful quantitative measurements of populations of medusae over time appear to be nearly impossible to obtain in most cases. Medusae may be abundant at one time, yet within an hour become rare or altogether missing; they may reappear in abundance an hour or a day later, or not at all.

In Table 1, I have indicated seasonal abundances of all species of medusae and ctenophores that have been observed over several years in the Friday Harbor area. The compiled list therefore represents all years in general and no year in particular. Specific variations from this averaged seasonal distribution are discussed in the annotated species list. Thickness of lines in Table 1 has been established by averaging semi-quantitative observations from all years. Several species whose distributions are represented by single points (e.g. *Dipleurosoma*, *Laodicea*, *Praya*) showed up on only one or two consecutive days during the entire study. These should be interpreted as rare visitors. A single weight line indicates species that are clearly present in the study area, but are still sufficiently rare that only a small number would be collected. Sightings of these organisms might be up to several weeks apart, but by superimposing all years, patterns of seasonal presence have been established. Examples of this second type are *Aegina* and *Halitholus* sp.; they are generally sighted only once or twice a month. A single weight line is also drawn for species in which a few individuals (3 to 6 per hour) can be regularly observed, although not necessarily every day (e.g. winter *Bolinopsis*). Medium thickness lines (see *Proboscoidactyla*, *Aglantha*, *Solmissus*) indicate species that are common for many days; usually 7 to 15 per hour can be seen. Thickest lines indicate that medusae are abundant (more than 15 per hour of surface observation) for many consecutive days. Extreme cases in the abundant category are represented by (1) *Aequorea* and *Phialidium* which may be present in the thousands all day long in a large spatial area, and (2) the tiny, short-lived *Orthopyxis*, whose hydroid colony lives on the FHL floats and produces 100–200 medusae daily during a one-hour period, after which the medusae will not normally be seen. The reader must refer to the individual species discussions for proper interpretations of the data in Table 1.

Special care has been devoted to making sure that the smoothing of abundance lines in Table 1 accurately reflects the average rates of increase and decrease of medusae during this study. Although a few species of medusae are released by their hydroids as early as January (*Euphysa* spp., *Proboscoidactyla*, and perhaps *Aequorea*), most juvenile medusae are not seen until March or April. The number of species occurring at one time is maximum during May and early June. Biomass of medusae increases throughout the spring. High biomass is maintained during most summers by a small number of species (although in summer 1979 very few medusae were present for nearly one month in late June and early July). In some years, an additional

pulse of medusae may appear in late summer or early autumn, but generally autumn is represented by a dwindling number of aging individuals.

Goy (1974) found that near Villefranche-sur-Mer in the Mediterranean Sea, coelenterate plankton in the spring was dominated by Anthomedusae and in the autumn by Leptomedusae. This dichotomy does not strictly hold true for the NE Pacific as represented by the planktonic coelenterates of the San Juan Archipelago. Individuals of many species of hydromedusae here live for several months, probably because of the cold sea water temperature. Many species of both Anthomedusae and Leptomedusae first appear in the spring and persist into late summer, although in the spring there are a few short-lived species of Anthomedusae, and in the autumn one sees mostly aging summer Leptomedusae.

Studies of surface plankton in most global localities would provide an incomplete picture of all species present in the water column. Due to the peculiar geography of the San Juan Archipelago, tidal turbulence causes homogeneity of shallow and deep waters and allows surface observers access to all species present in the area. As a disadvantage, turbulence renders this area useless for field studies of vertical stratification and vertical migration.

Acknowledgments

I am grateful for the assistance of the staff and colleagues at the Friday Harbor Laboratories during this study. I would like to thank the various colleagues, especially Richard Miller, who drew my attention to interesting specimens. This work was partially supported by Canadian NSERC Grant #GO226 to G. O. Mackie and by a University of Victoria Graduate Fellowship.

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