

Reproduction and longevity of *Aurelia labiata* in Roscoe Bay, a small bay on the Pacific coast of Canada

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Reproduction by the moon jelly, *Aurelia labiata*, was observed in a small bay on the west coast of Canada. The bay is located in an area isolated from human contact except in the summer, is sheltered from wind and wave action by mountain ridges, and has limited tidal flushing due to a gravel bar at the entrance that dries at lower low water. Planulae appeared in brood sacs beginning in October and November. The planulae were shed by the end of March and ephyrae emerged in June. Juvenile medusae were estimated to constitute about 30–40% of medusae in the bay in each of the two years of this study. Medusae remained in the bay throughout the year. There was no major visible mortality in the adult population during the two year observation period. Medusae appear to be lost from the bay as a result of tidal flushing. It is argued that in Roscoe Bay *Aurelia labiata* medusae live for more than one year and that up to 40% of the adult medusae may be two years of age or older.

INTRODUCTION

Field studies on *Aurelia* typically report that medusae appear in the spring and disappear in the autumn (Kiel Bight [Moller, 1980; Schneider, 1989; Schneider & Behrends, 1993, 1994], Gulmar Fjord [Grondahl, 1988; Hernroth & Grondahl, 1983, 1985a,b], Kertinge Nor [Olesen et al., 1994], Southampton Water [Lucas, 1996], Tomales Bay [Hamner & Jensen, 1974] and Kagoshima Bay [Miyake, Iwao & Kakinuma, 1997]). There are a few exceptions to this pattern. *Aurelia* in Jellyfish Lake in Palau (Hamner, Gilmer, & Hamner, 1982) and in Tokyo Bay in Japan (Omori et al., 1995) survive for more than one year (however, see also Ishii et al., 1995). Nevertheless, taken together the existing evidence has led to the conclusion that *Aurelia* live for less than one year in the wild (Arai, 1997; Lucas, 2001). The species in these observations has been reported as *Aurelia aurita*. However, three morphologically distinct species of *Aurelia* are now widely recognized, *aurita*, *labiata*, and *limbata* (Wrobel & Mills, 1998) and recent DNA evidence suggests there are even more (Dawson & Jacobs, 2000; Schroth et al., 2002). The existence of numerous species of *Aurelia* raises the possibility that some of the reported differences in longevity are species differences.

The present observations were directed at describing the timing of reproductive behaviour and the longevity of a population of *Aurelia* in Roscoe Bay, British Columbia, on the west coast of Canada. Roscoe Bay provides an unusual opportunity to study *Aurelia* in a geographical region where it has not been studied previously. Located on West Redonda Island in the north-east corner of Georgia Strait, Roscoe Bay is about 1 km long, has a maximum width of about 250 m and a maximum depth of 14 m (at lower low water), although most of the bay is less than half that depth (Figure 1). Freshwater enters the bay in a small stream on the west end, and two smaller streams enter on the north side. An important feature of the bay is that tidal flushing is restricted by a gravel bar at the east end that dries at the lowest tides. From the gravel bar eastward there is a narrow channel about 500 m long connecting the bay to a large deep channel of water, Waddington Channel. A 300 m mountain ridge on the south side and higher mountains to the north produce an environment with little wind and almost no wave action. Roscoe Bay is part of a Provincial Marine Park and there is no development in the area. The bay is fairly remote and visited by recreational boaters primarily in July and August.



Figure 1. The location of Roscoe Bay (small circle to the right of center) in relation to the west coast of Canada (inset), Vancouver Island, and the islands in the north-east corner of Georgia Strait. North is at the top. The horizontal straight line is 50 degrees north latitude. The east–west distance across the detailed map is about 56 nautical miles. Depths are in fathoms; elevations are in feet.

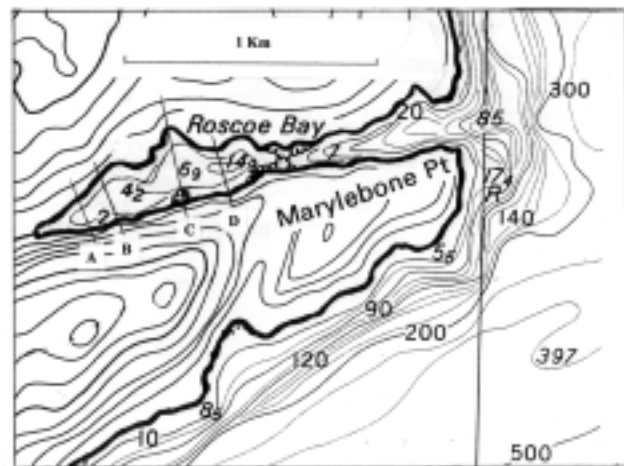


Figure 2. A diagram of Roscoe Bay showing the position of the four transects (A, B, C, and D) where medusae were counted. The A transect had five counting stops, the B transect six stops, the C transect, seven stops, and the D transect three stops. Contours in the water are depths in metres. Contours on the land are at 30-m intervals.

MATERIALS AND METHODS

Observations of medusae in Roscoe Bay were made every four to six weeks over the final year of this study and less regularly in the three previous years.

Number and distribution of medusae

Estimation of the number and distribution of medusae in the bay followed the procedure of Hamner et al. (1994) in Saanich Inlet. Four transects across the bay were established (Figure 2). Medusae were counted at five equally spaced stops along the A transect, six along the B transect, seven along the C transect and three along the D transect. Counts were made using a floating viewing box with a Plexiglas bottom (117×56×46 cm high). The box was manually pulled along the transect lines with a small rowboat (2.1 m long). Counts of medusae were made in the morning, evening, or both. An index of the total number of medusae in the bay consisted of the sum of the medusae observed at all transect stops. The number of medusae present on each day was taken as the maximum observed on a count for that day. Almost invariably medusae stayed higher in the water in the evenings and so the evening counts were usually highest.

Measurement of medusae size

In Roscoe Bay, the water is frequently still and medusae are bobbing at the surface. In locations where medusae were at the surface and densely aggregated, a clear plastic

plate with lines at 7 mm intervals was placed just above the bell. Medusa size was taken as the distance across the bell when the bell was fully extended just prior to a contraction. Measurements of medusae at any observation period were always made at two or more points in the bay.

To validate this measurement procedure, medusae were also measured by lifting them out of the water, turning them upside down, and placing them over a ruler on a glass plate. There was no substantial difference in results with the two procedures. Measuring medusae in the water using the plastic plate placed over their bell had the advantage of allowing a large number of medusae to be measured in a short period of time.

Observation of planulae in brood sacs

The number of medusae brooding planulae was evaluated when medusae were close to the surface and as they drifted by an observer in the small rowboat. The best time for this was usually early evening. The observer noted whether or not each medusa seen had planulae in the brood sacs.

Seawater temperature and salinity

Water temperature was measured midmorning using temperature probes at the end of a 15 m wire connected to a digital meter (Tempminder Digital Thermometers, Ontario, Canada). Duplicate probes were lowered on a single line and left for at least one minute at each observation depth. Measurements were taken near the west and east ends of the bay and

at a point approximately 100 m east of the gravel bar (Figure 2). Duplicate samples of seawater for salinity measurements were taken from the same points and at the same time as the temperature measurements were made. The samples were taken back to the laboratory, and read at 20°C using a refractometer (Vista, model A366ATC). Two readings were made for each salinity sample. The data reported for temperature and salinity was the average of the observations made. Temperature and salinity measurements were always made from the same positions in the bay.

RESULTS

Species identification

Medusae in Roscoe Bay have rhopalia at eight major divisions on the margin of their bell. There is secondary scalloping between the rhopalia. Fine tentacles hang from the margin of the bell. The oral arms extend to the margin of the bell. There is a frilly, conical manubrium. Females brood planulae in sacs on the manubrium. These attributes correspond to the description of *Aurelia labiata* (Wrobel & Mills, 1998; Gershwin, 2001).

Reproduction

Presence of planulae

The observations of the 2003/2004 brood year (Table 1) indicate that planulae appear in brood sacs by October and November, shedding of the planulae begins in January and is complete by the end of March (Table 1). In 2001 and 2002, first appearance of planulae in the brood sacs was also in October and November and planulae were absent from the brood sacs by the end of March. It is significant to note that virtually all females were brooding planulae in November, 2003, including those that had been juveniles during the summer. (The proportion of the total population with planulae was observed. The proportion of females brooding planulae is taken as twice the observed proportion.)

Release of ephyrae

Medusae of the autumn 2002 cohort were atypically small and remained small through the winter and into the early spring of 2003. They only grew to a small-normal adult size by the end of May, 2003 (Figure 3). In 2003, ephyrae and juvenile medusae from less than 7 mm in diameter to 45 mm in diameter were first noted on 24 June. This resulted in a medusae population with a bimodal distribution of bell diameters. A number of small medusae were still

Table 1. The percentage of females with planulae by month.

	2003					2004					
	04/09	24/09	24/10	27/11	18/01	25/02	31/03	12/05	15/06	27/07	28/08
%	-	0	6	96	72*	70	4	2	2	-	0
N	112	96	155	39	471	214	200	215			105

*, the percentage of females with planulae based on medusae in a lift net (N=39); -, an exact count was not made since the number of females with planulae was negligible.

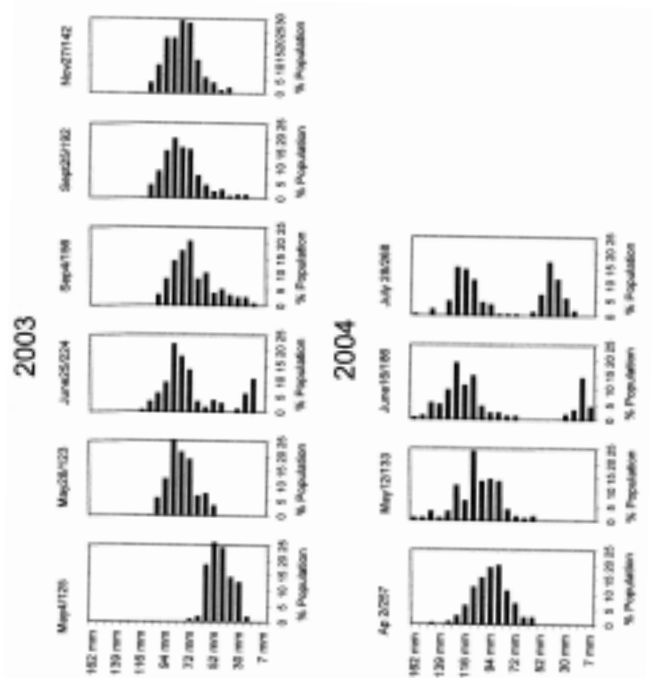


Figure 3. The distribution of bell diameters of medusae on various dates. Each bar represents the percentage of the population with bell diameters of that size. The smallest size represented is 0–7 mm; the largest 155–162 mm. The sample size (N) is shown beside the date.

present on 4 September and 25 September, 2003. By 25 November 2003, size distribution of the population had become unimodal, although there were still a number of small medusae.

In 2004, ephyrae again emerged in June, and this resulted in a bimodal distribution of bell diameters. The bimodal distribution was clearer than in 2003 because the adult population was larger. The 2004 year indicates that the release of ephyrae occurred during June but not July, since juvenile medusae, but not ephyrae, were present in July.

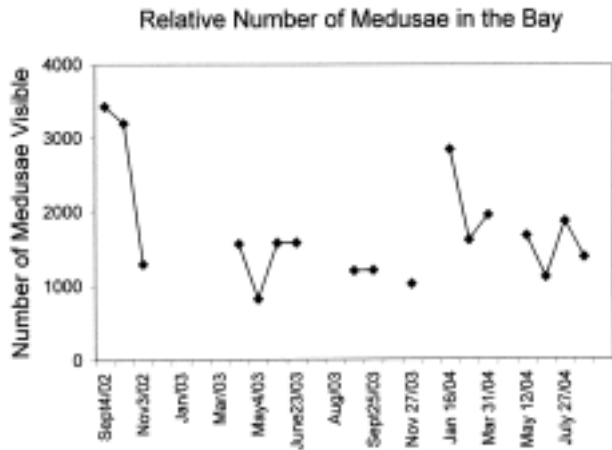


Figure 4. Relative number of medusae in the bay as represented by the sum of the number of medusae counted at each point on all of the transects. Over the two year period of this study, medusae were observed in every month except December.

Population age

The cohort of juvenile medusae present in June, 2003, constituted 29% of the medusae population. This estimate was arrived at by considering any medusae 45 mm or smaller to be a juvenile. This size was chosen because at the prior observation period (23 May, 2003), there were no medusae 45 mm or smaller. On 4 September 2003, 29% of the medusae measured were 45 mm or smaller (Figure 3). It seems reasonable to infer that the medusae in the 2003 cohort make up as much as one-third of the medusae population in the bay at the end of September, 2003. Conversely, 60 to 70% of the population in the bay would be medusae one year of age or older. The cohort emerging in June, 2004, constituted about 43%

of the medusae population (using the July census) (Figure 3). Thus, in the summer of 2004, 50 to 60% of the medusae population is one year old or older.

The inference that a substantial number of medusae in the bay are more than one year old is also supported by the observation that medusae have never been absent from the bay over the two years of this study (Figure 4). While the observations over that period have been irregular, observations have been made in the late autumn and early winter when observations from other areas would suggest that populations would fall to zero. Further, adult medusae have always been present in the early spring, when observations from other areas would also suggest that there should only be ephyrae. Over the three years of this study, December is the only month when observations have not been made. However, observations of medusae have been made at the end of November and in the middle of January.

Figure 4 can be taken as a general indication of the number of medusae in the bay but should not be considered as an accurate census. The numbers can only be approximate because the positions of the medusae swarms in the bay constantly shift while the location of the transect lines is fixed. In addition, the position of medusae in the water column is variable as is visibility in the water column. For example, in January 2004, medusae were visible from the surface to the bottom of the bay, whereas in the summer, medusae are only visible within about the top 4 m of the water column.

Water temperature and salinity

Water temperature at a depth of 2 m for the west and east sides of the bay and the channel 100 m east of the gravel bar is shown in Figure 5. In midsummer,

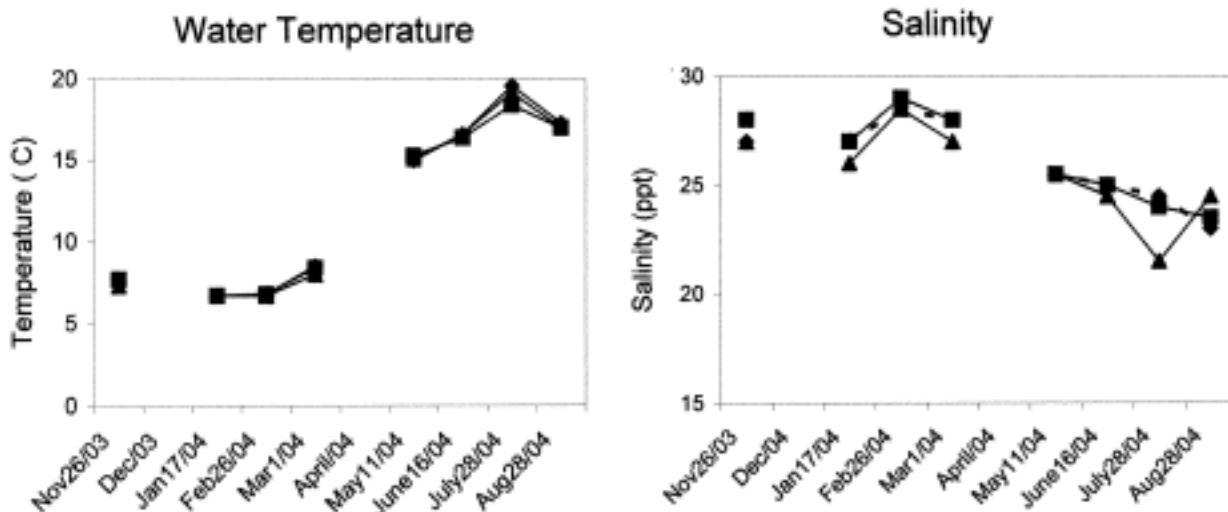


Figure 5. Water temperature and salinity at a depth of 2 m in the middle of the west side of the bay (B transect, diamonds), east side of the bay (D transect, squares), and 100 m east of the gravel bar (triangles).

there was a temperature gradient of 3°C from one metre depth to the bottom. The temperature gradient was smaller during the rest of the year and slightly reversed during the winter.

Midwinter cold water temperatures coincided with a drastic decline in material suspended in the water column and an increase in visibility. At that time, the entire bottom of the bay was visible from the surface. During the 17 January 2004 observations, the medusae were clustered at the bottom of the bay. This was verified by lift net observations. A lift net with a diameter of 0.7 m was lowered to specified depths, left for 4 min and then raised to the surface. The number of medusae in the net was noted for each of eight trials at each depth. The mean number of medusae (\pm SEM) in the net for each depth were as follows: 4 m depth: 0.0 \pm 0 medusae; 6 m depth: 1.5 \pm 0.2 medusae; 7.5 m depth (bottom): 6.5 \pm 0.3 medusae. It may be that, in the absence of other food, medusae were feeding on organic matter at the bottom of the bay (see Bamstedt et al., 2001).

Salinity varied substantially through the year (Figure 5). Drops in salinity are caused by intense rain in the fall and winter, and snow run-off in streams of adjacent fjords in the spring and summer. Since salinity tends to be lowest in summer when rainfall is lowest, freshwater run-off from mainland inlets appears to have the greatest influence on salinity in the bay. Salinity seemed to affect the distribution of medusae in the water column when it fell below 20 ppt. On 27–30 August 2004, salinity in the top 0.5 m of water fell to 18–20 ppt and medusae did not come to within \sim 0.5 m of the surface.

DISCUSSION

Medusae in Roscoe Bay have the morphological features of *Aurelia labiata*. These include the primary eight point scalloping at each of the eight rhopalia along the edge of the bell and secondary scalloping in between each rhopalia. There is a frilly manubrium and oral arms which do not drape down at the edge of the bell. Planula brood sacs are on the manubrium rather than the oral arms. Each of these features corresponds to what both Wrobel & Mills (1998) and Gershwin (2001) have identified as *A. labiata*. They contrast with more extended oral arms, eight point scalloping along the bell margin but no secondary scalloping, in *A. aurita*. Brooding of planula on the oral arms is also characteristic of *A. aurita*. Thus, the *Aurelia* in Roscoe Bay appear to be *A. labiata*, whereas *A. aurita* appears to be the species observed previously in Europe and Scandinavia (Dawson & Jacobs, 2001; Schroth et al., 2002). This conclusion is consistent with the recent

conclusions of Dawson & Jacobs (2001), Dawson (2003), and Schroth et al. (2002) using DNA findings.

Observations from 2001 through 2004 suggest that *A. labiata* medusae are year round residents in Roscoe Bay (Figure 4). The most complete records have been compiled between September 2003 and August 2004, but medusae have not been observed to be absent from the bay at any time during these three years. In contrast, in Gullmar Fjord on the west coast of Sweden (Grondahl, 1988), Kiel Bight in Germany (Moller, 1980; Schneider & Behrends, 1994), Kertinge Nor in Denmark (Olesen et al., 1994), Southampton Water in the United Kingdom (Lucas, 2001), Wadden Sea in Holland (Veer & Oorthuysen, 1985), Tokyo Bay (Ishii et al., 1995), and Elefsis Bay in Greece (Papathanassiou et al., 1987), medusae consistently appear in the spring (April–June) and disappear in the autumn (October–November). Mature medusae are present in Roscoe Bay in December, January, February and March as well, whereas in European and Scandinavian sites, adult medusae are absent at that time of year.

The temporal pattern of reproductive activity in Roscoe Bay is different from that described in other locations. In Roscoe Bay, planulae first appear in the manubrium brood sacs in October. By the end of November, virtually all females are brooding planulae. In Gulmar Fjord (Grondahl, 1988), and Southampton Water (Lucas & Williams, 1994), planulae first appear in the brood sacs in the summer. As would be expected from the appearance of planulae in the brood sacs in November, the appearance of ephyrae is also later than in European and Scandinavian locations. Roscoe Bay ephyrae appear in mid-summer (June). In Kiel Bight (Moller, 1980), Tokyo Bay (Ishii et al., 1993), Southampton Water (Lucas & Williams, 1994), Gulmar Fjord (Grondahl, 1988), Wadden Sea (Veer & Oorthuysen, 1985), Black Sea (Mutlu, 2001), Elefsis Bay (Papathanassiou et al., 1987) and Kertinge Nor (Olesen et al., 1994), they appear in winter or spring.

Ephyrae in Roscoe Bay grow and merge into a population of adult medusae, some of which were juveniles the previous year. This observation also indicates that the medusae of Roscoe Bay survive for more than one year. It is in sharp contrast to reports from Kertinge Nor (Olesen et al., 1994), the Wadden Sea (Veer & Oorthuysen, 1985), Black Sea (Mutlu, 2001), and Kiel Bight (Moller, 1980) where medusae have disappeared by the time ephyrae are released. Further, in Roscoe Bay, ephyrae released in June 2003 appear to reach sexual maturity in the autumn. By December 2003, nearly 50% of the adult population (i.e. 100% of females) are brooding planulae. This

would include medusae from the 2003 brood year that had been ephyrae a few months previously. The adult population present in June 2003 would have mated for at least the second time during the autumn of 2003.

It has been suggested that most medusae in the wild die following reproduction (Arai, 1997; Lucas, 2001). In Roscoe Bay, although a few dead medusae are observed floating on the surface or lying on exposed gravel areas at low tide in the autumn and spring, the number of dead medusae has always been a tiny fraction of one per cent of the visible population. However, medusae are swept out of the bay on ebb tides on a daily basis (D.J.A., unpublished observations). Although large numbers drift back into the bay on the following flood tide, it is reasonable to assume that not all medusae flushed out of the bay during the ebb tide make their way back in on the flood tide. Some will be swept out into the deep water channel and will not be drawn into the flood stream entering the bay.

In the two years in which ephyrae and juvenile medusae were counted in Roscoe Bay, their numbers were always less than the number of mature adults present. In June 2003, juvenile medusae constituted about 30% of the population. In July 2004, juvenile medusae constituted about 40% of the population. This replacement rate indicates that some adults in the population must be two years of age or older or the population would be declining.

Since the population of medusae in the bay has been somewhat stable over the last three years, the population of approximately 1/3 that is being produced each year is presumably replacing the approximately 1/3 that is lost through tidal flushing. Following this reasoning, at the end of two years, more than 40% of the adult medusae could be two years old or older. This would not be unreasonable since *Aurelia* in aquaria are known to live for five years (Widmer, 2004).

The present evidence that the majority of the population of *A. labiata* in Roscoe Bay survives for more than one year suggests that the results of some previous studies may have been misinterpreted. For example, observations at Tomales Bay (California) were interpreted as supporting the conclusion that *Aurelia* live for only one year. However, populations were only observed for two years, and only specimens from one season died (Hamner & Jensen, 1977). Consistent with this line of reasoning, casual observations indicate that *Aurelia* may be present throughout the year in Monterey Bay, California (C. Widmer, personal communication). Adding the present observations to these indicates that all (three) of the populations of *Aurelia* that have been observed on the west coast of North America appear to be living for more than one year.

All of these populations appear to be *A. labiata* (Wrobel & Mills, 1998; Gershwin, 2001; Dawson & Jacobs, 2001).

In most other locations where *Aurelia* have been studied they are probably not *A. labiata* and, therefore, differences in longevity may be a species difference. However, in some of these locations, deaths of medusae may be due to a parasite rather than an inherent life span limitation. Recent observations by Mutlu (2001) indicate that there is a midsummer mortality of adult *A. aurita* in the Black Sea, but the entire population is not lost. In Tokyo Bay, Ichi et al. (1995) report a substantial fall mortality of adult medusae, but once again the entire population is not lost. Moller (1980) has acknowledged that the disappearance of medusae in the Kiel Bight could be due to a parasite. Since seasonal death does not invariably occur, it is not appropriate to conclude that *Aurelia* is an annual species. The cause of these incidents of mortality merits further investigation.

In other locations, a precipitous decline in the adult population may be due to migration rather than an annual mortality. Van der Veer & Oorthuysen (1985) recognize that at least some of the medusae from the Wadden Sea population may be migrating out into the coastal North Sea rather than dying. *Aurelia* medusae in Kertinge Nor also disappear at the end of summer but these observers acknowledge that this could be due to migration out of the fjord (Olesen et al., 1994).

A substantial number of Roscoe Bay medusae are presumably lost to the bay by outward migration. There is a readily visible movement of large numbers of medusae out of the bay on the daily ebb tides (D.J.A., unpublished observations). Although large numbers return on flood tides, it is statistically unlikely that all do so. Considering that there are two ebb tides on which medusae can drift daily, the loss of a hundred at each tide can become a large number over time. In addition, had Roscoe Bay not been relatively confining, the entire population of medusae might have permanently migrated out of the bay in the winter instead of diving down to the bottom of the bay. The disappearance of medusae from the bay would then have looked like the end of a population cycle such as is seen in Kiel Bight, Kertinge Nor, and the Wadden Sea.

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