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**BIOLOGICAL CYCLE
OF *BOTRYLLOIDES LEACHI* (SAVIGNY)
(ASCIDIACEA) IN THE VENETIAN LAGOON (*)**

by Riccardo BRUNETTI

Istituto di Biologia Animale, Università di Padova, Italy

ABSTRACT

The work presented here is part of a program designed to study the distribution and ecology of ascidians in the Venetian Lagoon (northeast coast of Italy). The area studied, including its principal hydrographic parameters, has been described in a prior publication devoted to *Botryllus schlosseri* (BRUNETTI, 1974).

MATERIALS AND METHODS

Botrylloides leachi is an hermaphroditic, viviparous, colonial ascidian. The colony originates from a "tadpole" larva which, following attachment, undergoes a process of budding referred to as blastogenesis. The development of the buds is similar to that described for the closely related genus *Botryllus* (BERRILL, 1941, 1947; SABBADIN, 1955). The development of the buds is synchronous throughout the colony. The buds, in turn, produce secondary buds even before the former have developed to the stage of being capable of filtering water. Normally, three successive blastogenetic generations coexist in any particular colony. It is, hence, possible to apply to *Botrylloides* the sequence of developmental stages developed by BERRILL (1941) and SABBADIN (1955) for *Botryllus schlosseri*.

The seasonal variations of the populations of the Lagoon were followed by monthly observations of colonies forming part of the biocoenoses on 20 × 30 cm asbestos-cement (Eternit) panels main-

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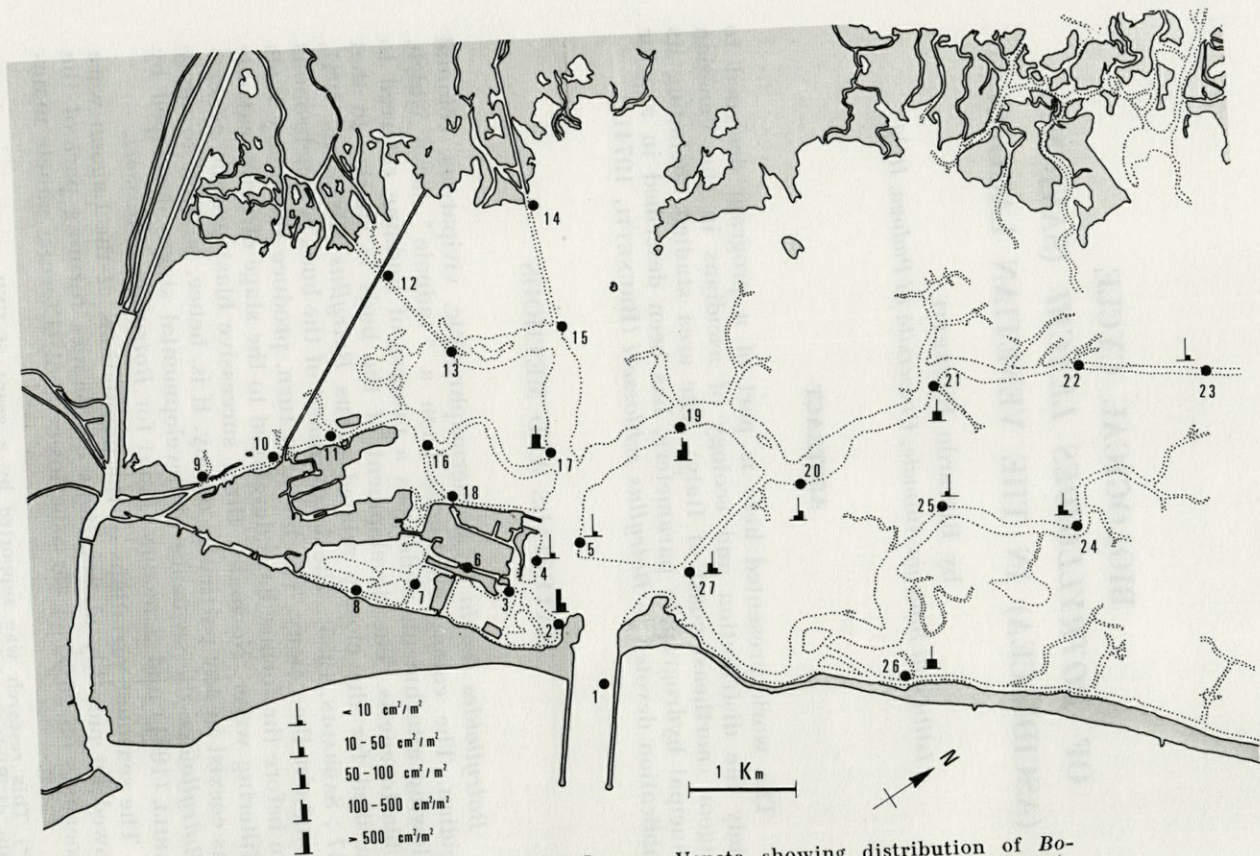


FIG. 1. — Lower basin of the Laguna Veneta showing distribution of *Botrylloides leachi* for end of March (left column) and end of July (right column).

tained at about 1 m below low water at stations 1, 2, 3, 5, and 19 shown in Fig. 1.

The duration of the period of sexual reproduction at these same 5 stations was studied by examination of colonies removed from pilings as well by observations on a second set of panels changed at monthly intervals.

The pattern and intensity of settling was established by counts of new colonies on the lower surface of glass plates (12×12 cm). These were held in a horizontal position in a plastic frame and changed at intervals of about 10 days.

RESULTS

DISTRIBUTION AND TEMPORAL VARIATION.

Initial observations on the distribution of *Botrylloides leachi* were performed in 1971-1972. During 1973 a quantitative and more systematic survey of the entire southern basin of the Lagoon was carried out. In that period 27 stations were sampled, from each of which we removed the fouling organisms from about 1 m² of surface. The results are displayed in Table I, expressed as the surface, in cm², occupied by colonies. As can be seen in Fig. 1, *B. leachi* is most abundant along the larger canals of the northern portion of the basin. Such areas are subject to the highest current velocities, have the least domestic pollution input and have the greatest stability in terms of salinity and temperature. In the port entrance channel direct diver observations during May and June revealed an abundance of vigorous colonies from a depth of 50 cm below low water to the bottom (~ 10 m) for the entire length out to its sea end.

The colonies, always in an incrusting form, are to be found on a variety of available surfaces. Well developed colonies often have the surface thrown up in folds so as to resemble the convoluted surface of a brain (Fig. 2). On the muddy partially consolidated bottoms in, and adjacent to, the port entrance channel *B. leachi* settles on any available solid material that is somewhat raised above the surface, often the shells of bivalves. The colonies cover these isolated substrates completely, assuming a spherical aspect. In no case have we observed colonies of the pendant type that is so commonly encountered in the case of *Botryllus schlosseri* (BRUNETTI, 1974).

During the coldest part of the winter the colonies do not possess zooids capable of filtering, but are composed entirely of

TABLEAU I

Surface, in cm^2/m^2 , occupied by colonies of *Botrylloides leachi* at the various stations in the Laguna Veneta (see Fig. 1) for two periods of the year.

Stations	End of March	End of July
1	none collected	
2	>1000	14
3	0	0
4	0	10
5	0	9
from 6 to 16	0	0
17	52	76
18	0	0
19	18	190
20	3	30
21	45	42
22	0	0
23	0	2
24	18	4
25	6	0
26	15	48
27	23	2

ampullae and assume the homogeneous aspect of a carpet (Fig. 3-4). These hibernating colonies are often covered with a film of colonial diatoms and other benthonic organisms (Fig. 5).

Examination on 3 July 1972 of the panels set out at station 3 on 7 May 1971 revealed a few (< 10) small colonies of *B. leachi*; these, however, were no longer present on the subsequent examination of 7 September. All other collections of material indicated that stable populations of this ascidian were absent at this station.

At stations 1, 2, 5, and 19 collections of material from surfaces indicated the presence of *B. leachi*.

At station 2, on a panel set out on 31 July 1971, we noted development of newly settled colonies only in the month of May of 1972. At stations 1, 5, 19 a development of young colonies was noted within the first month on panels set out on 1 June 1971. For brevity, we will describe only the observations on the panels of station 2 since the progression of events was similar, though the populations less dense, at the other two stations.

At the end of June 1971, after about a month of exposure, there were numerous small colonies none of which exceeded 1 cm^2 in area. Taken as a whole these colonies occupied slightly less than half of the available surface. At the end of August the population appeared somewhat reduced in overall area. The young colonies

had grown very little, being on average only 1-2 cm² in area and were less in number. There appeared to be considerable spatial competition by other foulers, especially tube-forming amphipods.

At the end of September there were only about 40 colonies remaining per panel. Growth had been quite modest, only about 12 % of the colonies had reached a size of 5 cm², the rest being between 1 to 3 cm²; *B. leachi* occupied less than 1/3 of the overall available surface of the panels. At the end of October examination revealed that the colonies had achieved a notable increment of growth; some had reached a size of 30 cm². On 10 December there was little evidence of further change in area and some colonies (18 % of 55 examined) no longer possessed filtering zooids, i.e. were in the hibernation phase.

On 8 March, an examination of the panels indicated that only about 1/4 of the colonies had survived the winter, and, of these, 1/3 were still in the hibernation phase. Successive observation of 10 April, and in particular those of 2 May, indicated that the colonies had entered a phase of very active growth. By 11 June *B. leachi* was obviously the dominant species on the panels and by 3 July the colonies occupied 70 % of the available surface. It was necessary to interrupt observations of the panels in July. However, collection of material from nearby surfaces has indicated that from the second half of July into August there was an extensive mortality of the large colonies and by the end of August the populations of *B. leachi* were composed almost exclusively of small (newly settled) colonies of the new generation.

SEXUAL REPRODUCTION.

An analysis of the condition of the gonads in the colonies collected at station 2 (Fig. 6), as well as the data relating to the settling and development of new colonies (Table II and III) indicate a period of sexual reproduction of about 2 months, from the second half of May to the first half of July. The initiation and termination of the periods of sexual reproduction of *B. leachi* as determined by our observations in the lower Laguna Veneta for 1971-1974 are as follows :

	Initiation	Termination
1971	—	10 July
1972	10 - 20 May	20 - 30 July
1973	24 May - 5 June	10 - 15 July
1974	16 - 20 May	10 - 16 July

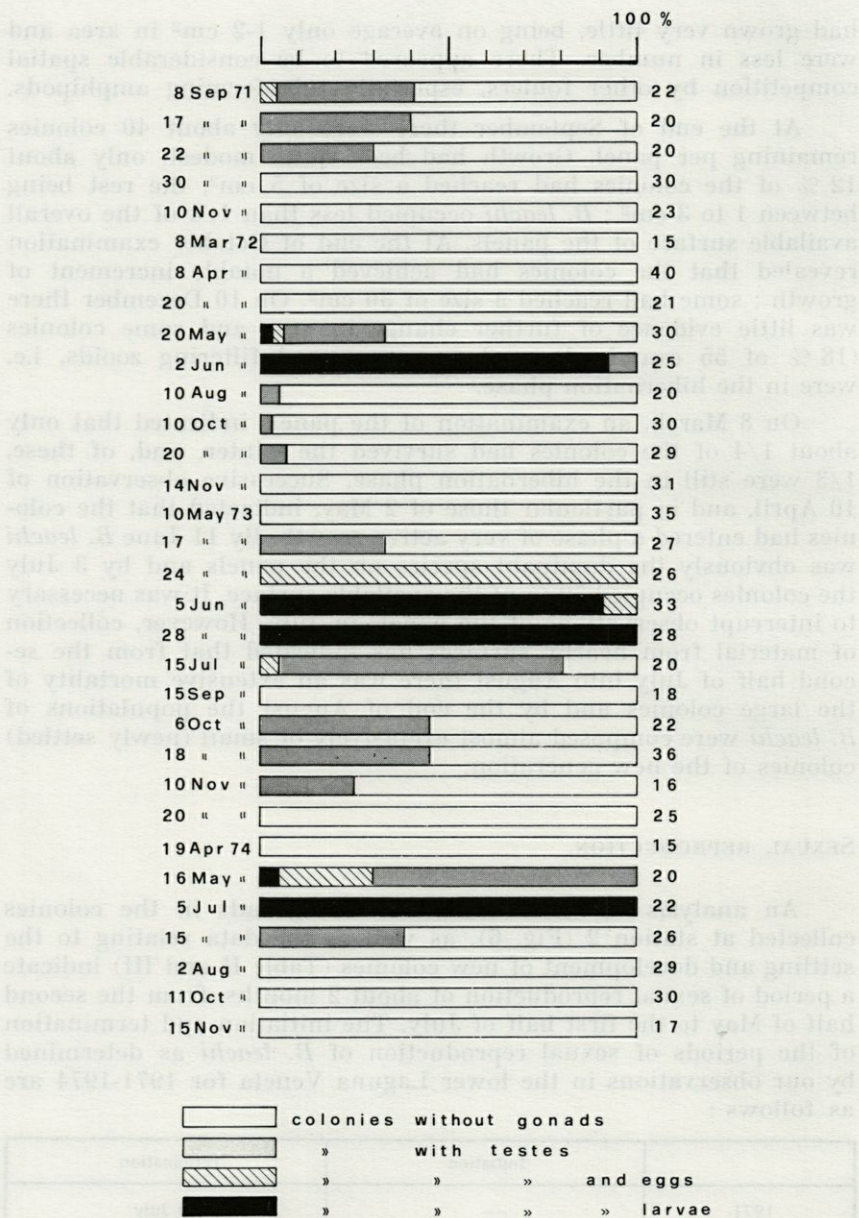


FIG. 6. — Analysis of gonad condition in colonies collected at Station 2 (expressed in percent). The number on the right represents the total number examined.

Considering the water temperatures recorded for the months of May, June and July (Fig. 7), it appears that the period of sexual reproduction for *B. leachi* is initiated when the temperature reaches 17-18 °C and is terminated when the temperature reaches 24-25 °C.

It should be pointed out that in this context sexual reproduction refers to sequential events of gonad maturation, larval development

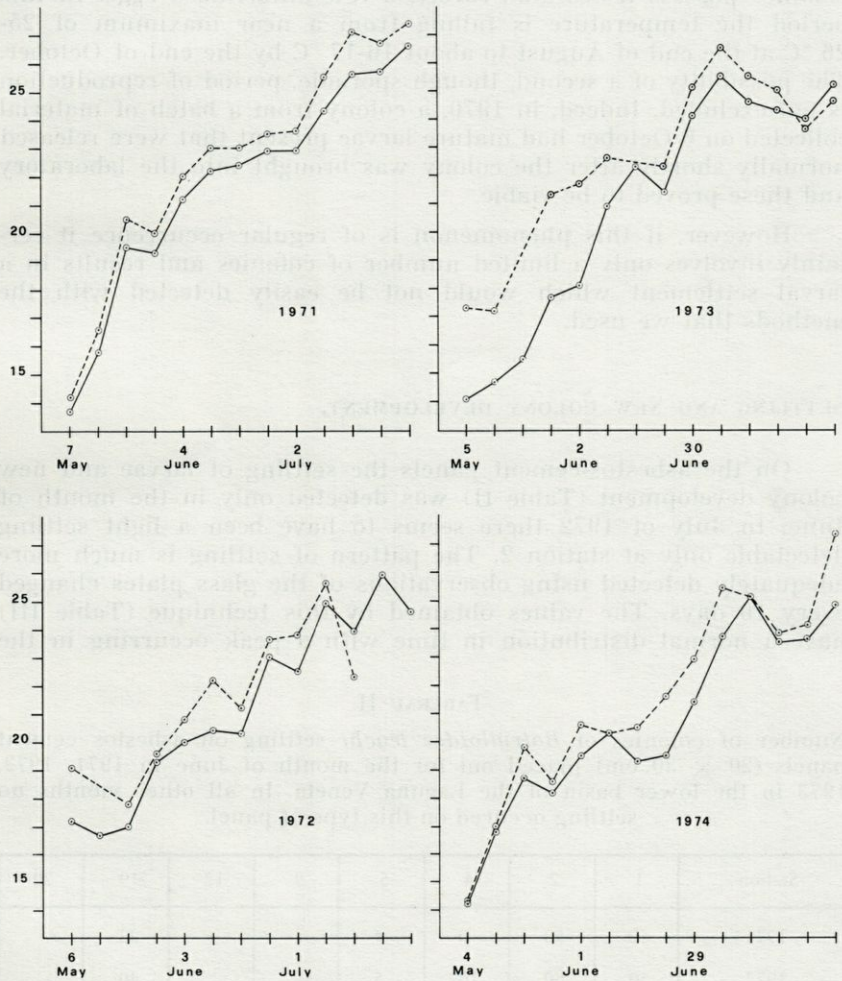


FIG. 7. — Mean weekly temperatures for months of May, June and July 1971-74 for the lower basin of the Laguna Veneta. Solid line : Flood; Dashed line : Ebb.

and release, and subsequent settling. These events all occur within a period of only a few days.

In the colonies examined we have never observed eggs in the absence of mature testes, though the reverse situation is a fairly common occurrence. This indicates that the male elements probably mature considerably in advance of the female gonadal tissues. Occasionally, during the months of September and October some colonies possess testes and, rarely, a few unfertilized eggs. In this period the temperature is falling from a near maximum of 25-26 °C at the end of August to about 16-17 °C by the end of October. The possibility of a second, though sporadic, period of reproduction is not excluded. Indeed, in 1970, a colony from a batch of material collected on 6 October had mature larvae present that were released normally shortly after the colony was brought into the laboratory and these proved to be viable.

However, if this phenomenon is of regular occurrence it certainly involves only a limited number of colonies and results in a larval settlement which would not be easily detected with the methods that we used.

SETTLING AND NEW COLONY DEVELOPMENT.

On the asbestos-cement panels the settling of larvae and new colony development (Table II) was detected only in the month of June. In July of 1972 there seems to have been a light settling detectable only at station 2. The pattern of settling is much more adequately detected using observations of the glass plates changed every 10 days. The values obtained by this technique (Table III) have a normal distribution in time with a peak occurring in the

TABLEAU II

Number of colonies of *Botrylloides leachi* settling on asbestos cement panels (20 × 30 cm) placed out for the month of June in 1971, 1972, 1973 in the lower basin of the Laguna Veneta. In all other months no settling occurred on this type of panel.

Station	1	2	4	5	9	12	19	20
1971	40	50	0	4	—	—	22	—
1972	50	60	10	5	—	—	40	—
1973	44	46	0	—	0	0	—	0

TABLEAU III

Accumulated settlement of *Botrylloides leachi* on glass plates (144 cm²) for approximate 10 days periods. The divisions of the successive periods of the months (first column) are indicated by I, II and III.

1972	Station 19			Station 2		
	Mean	Stand. dev.	N. plates	Mean	Stand. dev.	N. plates
May I	0.00		6	0.00		6
May II	0.16	0.408	6	0.50	0.836	6
May III	0.80	0.447	5	0.66	0.516	6
June I	1.17	1.690	6	15.66	3.444	6
June II	3.00	1.897	6	176.66	69.436	6
June III	13.00	10.984	4	580.00	70.649	4
July I	0.00		6	101.66	20.373	6
July II	0.50	0.547	6	6.50	4.722	6
July III	0.00		6	0.66	0.816	6
August I	0.00		6	0.00		6
August II	0.00		6	0.00		6

last 10 days of June (Fig. 8). These observations, covering with regularity the period from July 1971 throughout all of 1972, have not indicated other periods of settling.

HIBERNATION PHASE.

During the coldest portion of the winter, the colonies of *B. leachi* are lacking completely functional filtering zooids. They resemble a carpet composed of small rounded ampullae completely filled with highly pigmented cells (Figs. 3 and 4). As water temperature drops the colonies undergo a succession of changes culminating in a condition of winter quiescence. Initially there is a notable reduction in general activity: the filtering zooids are less sensitive to mechanical stimuli and the rate of blastogenic development decreases. Under such conditions change in generation is slower, often requiring many days.

In this phase not all the buds reach the stage of filtering zooid, many in fact degenerate together with the parent zooids resulting in an overall reduction in the number of components in the colony. After a series of changes of generations, the number of which depends on environmental factors (temperature and food), none of the buds are capable of functionally replacing the parent zooids and the vascular ampullae, full of pigmented hemocytes, occupy the entire surface of the colony.

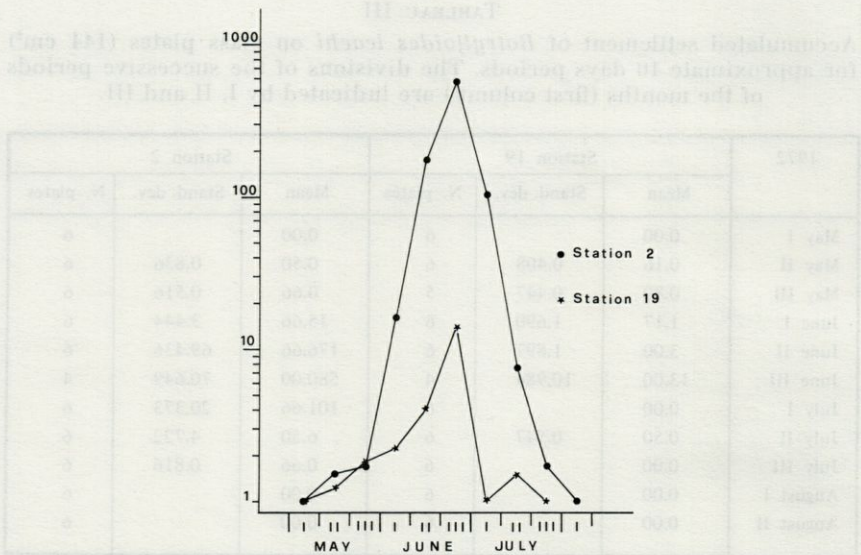


FIG. 8. — Accumulated settlement of *B. leachi* on glass plates (144 cm²) for approximate 10 days periods. The divisions of the successive periods of the months are indicated by I, II and III. The values on the log axis are mean numbers of individuals/plate + 1; i.e. : 0 = 1.

In the spring a few zooids make their appearance at isolated positions on the surface of the colony and from these are reformed small new systems that have no obvious interconnections with each other (Fig. 5). With renewed blastogenic activity there are several changes of generation which lead to a rapid repopulation of the colony surface. At the same time the marginal ampullae assume the elongated appearance typical of a colony in the phase of expansion. By observations of colonies on Eternit panels and of a large volume of material collected periodically from pilings at the different stations (Fig. 9) it was possible to determine the time of initiation and termination of hibernation from 1971-1974.

In 1971 the first signs of reduced activity were noted in November. By the beginning of December about half the colonies examined were already in hibernation or an advanced phase of the precursor stages. By January no active colonies were encountered.

Reactivation began at the beginning of March in 1972. In that year the colonies began to enter into hibernation during December. Reactivation was initiated between 23 March and 5 April of 1973. As in previous years hibernation was first noted somewhat earlier, 15 February, in 1974.

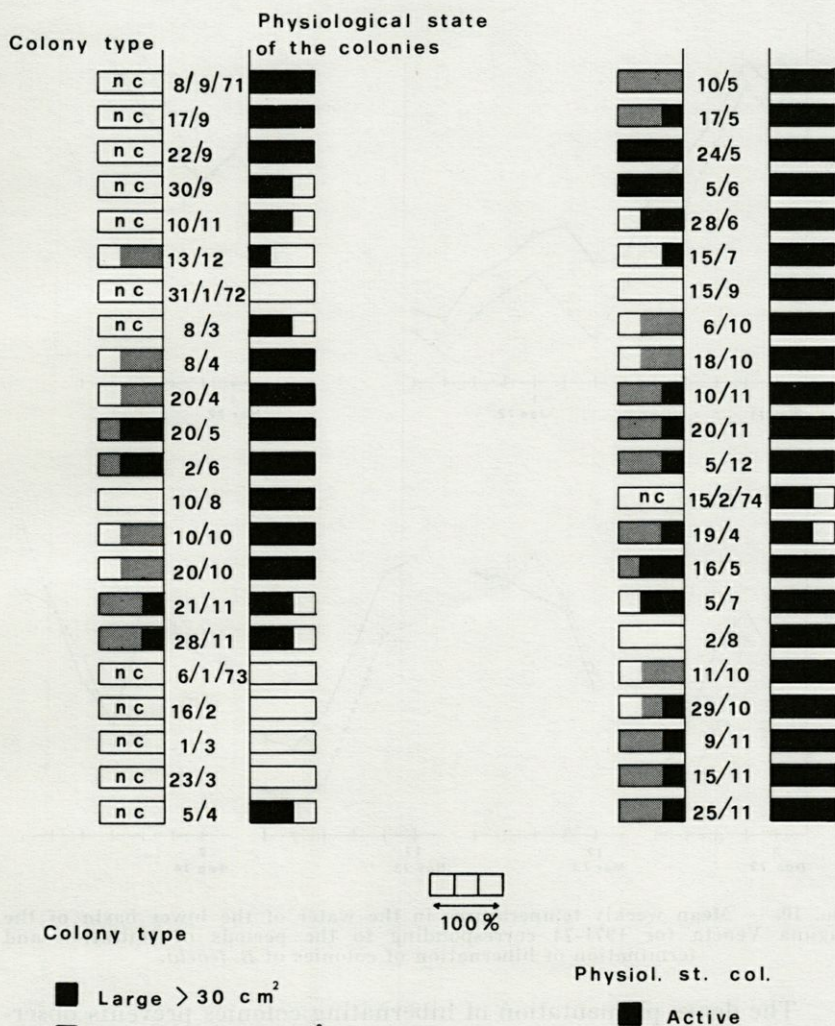


FIG. 9. — Pattern of change in the composition of population with time.

The water temperatures for these periods of observation are illustrated in Fig. 10. It can be seen that the initiation of hibernation was noted as the temperature approached 10 °C and was complete by the time the temperature had dropped consistently below this level.

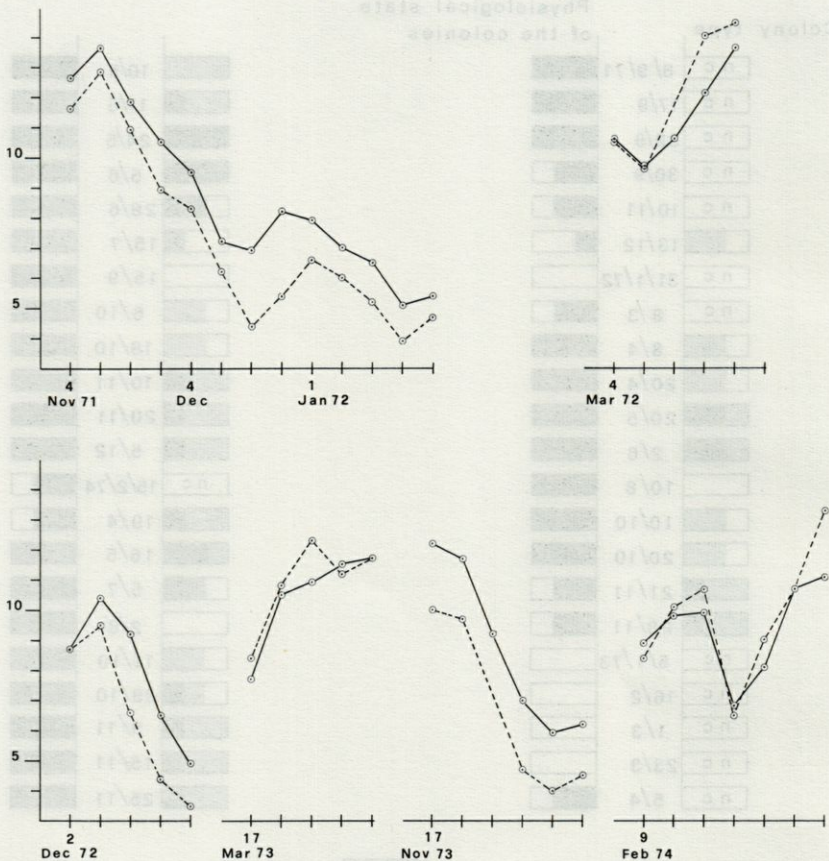


FIG. 10. — Mean weekly temperatures in the water of the lower basin of the Laguna Veneta for 1971-74 corresponding to the periods of initiation and termination of hibernation of colonies of *B. leachi*.

The dense pigmentation of hibernating colonies prevents observation *in vivo* of internal organization. A series of observations on sectioned material was therefore initiated, the detailed results of which are reported elsewhere (BURIGHEL *et al.*, 1976).

Based on these observations it was determined that this phenomenon consists in a general regression of the colonies during which the organs of the zooids and buds break down and are resorbed by the numerous phagocytes present in the hemolymph. In spring the reactivation of the colonies is initiated by the reconstruction of zooids that arise from newly-formed buds that appear along the walls of vessels of the tunic vascular network.

DISCUSSION

Botrylloides leachi undergoes a period of sexual reproduction in the Laguna Veneta that begins in about the second half of May and lasts through the first half of July. This corresponds to the interval in the thermal regime between 17° and 25 °C.

During its life span of about 12 months the colony exhibits several distinct phases of physiological activity. The young colony, established in late spring, undergoes a brief period of blastogenic development that corresponds approximately with the month of June. Growth is rather slow from July through September. In this period of maximum water temperature the colonies often exhibit signs of stress. This period is followed by a period of recovery in autumn that persists until blastogenic development is slowed when the temperature drops below 15°C. After the temperature drops below 10°C the zooids undergo a general regression and the colony, no longer containing filtering zooids, enters into a state of hibernation. In this condition the colonies pass the winter with no indication of overt activity; the tunic surface often becoming covered with detritus and other organisms. During this phase there is a considerable mortality. In spring, with the temperature consistently above 10°C, the colonies enter into a phase of reactivation. This is first signalled by the appearance in the old colonial matrix of small isolated groups of zooids that probably arise from small buds of the vascular type that had formed during the period of hibernation. This reactivation occurs in the Laguna Veneta sometime during March. This reactivation is followed by a period of rapid new blastogenic growth that increases with the rise in water temperature. By the end of May the colonies, already sexually mature, have reached maximum dimensions. After a brief period of sexual reproduction, towards the end of July, the colonies of the preceding year are subject to a new period of high mortality. Thus, during mid-summer, large colonies are encountered only rarely, whereas the small newly-formed colonies are quite abundant.

The possibility of a second period of sexual reproduction in autumn, though not noted by us for the years 1971-1974, cannot be entirely discounted. There were indications of potential larval production, the magnitude of which probably depends on the rate at which water temperature declines and the availability of adequate food in this period.

The phenomenon we have referred to as *hibernation* has been noted by BANCROFT (1903) in one colony he transferred to laboratory aquaria. It is somewhat strange that, after his mention of

this manifestation of response to stress, it has not since been reported by others working with *Botrylloides*. BANCROFT hypothesized that the phenomenon, labelled by him "aestivation", was caused by a rise in temperature though he had no adequate controls on his observations. In fact, under conditions of laboratory rearing, this phenomenon of "aestivation" or "hibernation" can be provoked quite readily by a variety of environmental factors : e.g. a scarcity of food ; presence of toxic materials ; low levels of dissolved oxygen. It therefore appears to be a non-specific response to unfavourable environmental conditions.

BANCROFT attributed considerable significance to his observation of the development of a small "lobe" within the degenerating colony. This "lobe", he hypothesized, was the only portion of the colony that would survive and later serve as the starting point for the reconstruction of the colony. We have never noted such "lobe" formation in the overwintering colonies under natural conditions. It should be pointed out, however, that such "lobe" formation is commonly observed in colonies maintained in aquaria. This is easily explained by the fact that in such closed systems the regression of the colonies usually does not proceed uniformly or with continuity due to variations in the stressing factors. Hence the stressed colonies are capable of occasional spurts of growth in the marginal areas whereas degeneration is more or less irreversible in the more internal areas.

BANCROFT also noted that the pigmentation of the colony resulting from such involution resembled that of *Botrylloides luteum* Von Drasche, whereas the original pigmentation was typical of *Botrylloides gascoi* Della Vale (at present both these species are recognized as synonyms of *B. leachi*). This rather interesting observation might be an indication of some variation in the metabolism of the colony under the conditions leading to "aestivation". We have never noted such variation in pigmentation in the colonies collected from the Laguna, which, regardless of phase, are consistently of a red-orange colour.

Our observations on the distribution of this species in the Laguna Veneta indicate that it is consistently absent in the lower portions of the Southern basin, where the water is quite shallow (0.5-2.0 m) and subject to considerable extremes of both temperature and salinity. The most profuse distribution is in correspondence with the larger and deeper canals in the upper portion of the area studied. Such a distribution, in addition to the restricted seasonal activity of the species, indicates a rather limited thermal range for normal function as well as a rather restricted tolerance to low salinities. This conclusion is somewhat contrary to the observations of DYBERN (1969) who found *B. leachi* to be most

abundant in the innermost reaches and at shallow depths in some Norwegian fjords. It is quite probable that the two populations (Norway and Laguna) represent two distinct geographical races, each of which reflects in its physiological profile considerable selection for tolerance to general hydrographic conditions prevailing in their respective habitats. In fact, DYBERN (1967) has demonstrated just such a pattern of physiological selection in several distinct populations of *Ciona intestinalis*.

In all probability salinity and temperature are not the only factors that influence the distribution of *B. leachi*. We suspect, as suggested by our observations, that dissolved oxygen and the abundance of the proper planctonic material are also significant factors. However, it would be hazardous to draw any definitive conclusion concerning this based only on field observations made in the not easily characterized environment of the Laguna Veneta.

SUMMARY

The biological cycle of *Botrylloides leachi* was studied in the Laguna Veneta by observations on populations attached to both artificial surfaces (fouling plates) and to natural substrates. The duration of the colonial life span, the period of sexual reproduction and the settling rates were determined over a period of more than 3 years.

During its life span of about one year a colony of *B. leachi* passes through several distinct physiological stages. The colonies newly settled in spring and early summer grow quite slowly during the months of Aug.-Sept. In the autumn blastogenic growth is quite rapid until it ceases rapidly with a drop of temperature below 15°C.

At temperatures below 10°C the colonies are in a stage of hibernation during which filtering zooids are absent. In March the colonial matrix is repopulated with zooids derived from small buds of the vascular type that had developed during the phase of hibernation. This blastogenic development occurs quite rapidly and by May the colonies are at a maximum size.

Sexual reproduction takes place from May to July, corresponding to the thermal interval between 17 and 25°C. This is followed by a period of high mortality for the colonies of the previous year class. The distribution of the species in the Laguna indicates that optimal conditions are provided by an environment free of both high and low extremes of temperature and with a relatively high salinity.

RÉSUMÉ

Le cycle biologique de *Botrylloides leachi* dans la Lagune de Venise a été étudié à l'aide d'observations périodiques des populations vivant sur des plaques immergées ou dans le milieu naturel.

On a déterminé pendant trois ans la durée du cycle vital, la période et la durée de la reproduction sexuée, les valeurs d'établissement des nouvelles colonies.

En général le cycle biologique des colonies de *Botrylloides leachi* dure un an et présente différents stades physiologiques. Les colonies nées au printemps se développent très lentement pendant les mois chauds d'août jusqu'à septembre. En automne l'accroissement blastogénétique devient plus marqué mais il ralentit brusquement lorsque la température baisse fin automne. Pendant l'hiver, avec des températures inférieures à dix degrés centigrades, les colonies se trouvent en phase d'hibernation, c'est-à-dire qu'elles sont dépourvues de zooïdes filtrants. Au mois de mars suivant, la matrice de la colonie se peuple de nouveaux zooïdes provenant du développement de petits bourgeons de type vasculaire formés pendant la phase d'hibernation. Ensuite le développement blastogénétique se produit très rapidement et, au mois de mai, les colonies atteignent leurs dimensions maximales. De mai jusqu'à juillet, dans un intervalle entre 17° et 25°C a lieu la reproduction sexuée qui est suivie par une période de haute mortalité.

La distribution de *Botrylloides leachi* dans la Lagune de Venise suggère l'hypothèse que cette espèce s'adapte mal aux basses salinités et aux températures extrêmes (hautes ou basses).

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FIG. 2. — Colony of *B. leachi* during period of rapid growth on abestos-cement panel at station 2.

FIG. 3. — Colony of *B. leachi* in hibernation. Some filtering zooids are still visible.

FIG. 4. — Colony of *B. leachi* in hibernation.

FIG. 5. — Colony of *B. leachi* at time of reactivation. Small groups of zooids are seen emerging through a layer of sediment that had accumulated on the colony surface during the winter.

