The Egg Masses and Veligers of Thirty Northeast Pacific Opisthobranchs

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(Plates 26 to 38; 31 Text figures)

INTRODUCTION

Since the veligers of opisthobranchs are released in huge numbers from rather conspicuous egg masses, it is somewhat surprising that little has been systematically recorded concerning these or other young stages. Identification is thus a formidable task. While an exhaustive survey is required to cover the problem, the present work provides new information in a format suitable for organized use of further comparative data. Amongst previous authors O'Donoghue & O'Donoghue (1922) working on Northeast Pacific forms, Thorson (1946), Thompson (1961) and Hadfield (1963) have summarized much of the information available.

The animals included here were collected off the San Juan Islands, Washington, in the vicinity of the Friday Harbor Laboratories. Adults, egg masses and veligers were kept in running or frequently renewed sea water. Most species are common in the area but a few have not been recorded there previously: these are marked with an asterisk in the following list.

Acanthodoris brunnea MacFarland, 1905
Acanthodoris hudsoni MacFarland, 1905
Acanthodoris nanaimoensis O'Donoghue, 1921
Acolidia papillosa (Linnaeus, 1761)
Aglaja diomedea (Bergh, 1893)
Archidoris montereyensis (Cooper, 1862)
Armina californica (Cooper, 1862)
* *Austrodoris odhneri* MacFarland, 1966
* *Catriona aurantia* (Alder & Hancock, 1842)
* *Chelidonura phocae* Marcus, 1961
Coryphella fusca O'Donoghue, 1921
? *Coryphella rufibranchialis* (Johnston, 1832)
* *Cratena albocrusta* MacFarland, 1966
* *Cumanotus beaumonti* (Eliot, 1908)
Dendronotus frondosus (Ascanius, 1774)
Dendronotus iris Cooper, 1863
Diaulula sandiegensis (Cooper, 1862)
Dirona albolineata Cockerell & Eliot, 1905
Dirona aurantia Hurst, 1966
Eubranchus olivaceus (O'Donoghue, 1922)
Gastropteron pacificum Bergh, 1894
Haminoea virescens (Sowerby, 1833)
Hermissenda crassicornis (Eschscholtz, 1831)
Melibe leonina (Gould, 1853)
Olea hansineensis Agersborg, 1923
Onchidoris bilamellata (Linnaeus, 1767)
* *Onchidoris muricata* (Müller, 1776)
Rostanga pulchra MacFarland, 1905
Triopha carpenteri (Stearns, 1873)
Tritonia exsulans Bergh, 1894

EGG MASSES

The eggs of opisthobranchs are enclosed in capsules which in turn are deposited within a jelly-like material which swells to a variable extent in contact with sea water, as described by Pruvot-Fol (1954). A definite egg string containing the capsules is often visible within the jelly as described by O'Donoghue & O'Donoghue (1922) but it is not always readily apparent. The egg mass may take one of several forms, depending on the manner of laying and the anatomy of the reproductive tract. The most usual forms are as follows:

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Type A: The egg mass is in the form of a ribbon attached along the length of one edge, capsules occurring throughout most of it. This is common amongst dorids, which whilst laying may grip the mass between foot and mantle edge (Text figure 4b) tending to flatten it, as mentioned by FRETTER & GRAHAM (1964). This is probably not the sole cause of the flattened shape.

Type B: The egg mass is in the form of a cylindrical capsule-filled cord usually attached along one side by a thin jelly sheet (free of capsules) which may be wide or narrow. This is the usual form produced by aeolids and sacoglossans, the egg masses of the latter being particularly closely attached to the substratum (i. e. the jelly-free sheet is very narrow).

Types A and B are usually coiled since the parent crawls in a spiral whilst laying its eggs, as described by ALDER & HANCOCK (1845 - 1855). As these authors noted, however, the coiling may be more or less completely disguised when the mass is laid on other than a flat substratum.

Type C: The egg mass is in the form of an ovoid or globular jelly bag attached by a jelly string. This is common amongst cephalaspideans.

Type D: The egg mass is a small structure, often sac-like, and attached at one side. It may be similar to Type A or B but if coiled turns less than one complete circuit. It is typical of very small aeolids.

The egg masses of the species listed in the introduction will be considered in these four groups. The possession of a particular complex of characteristics distinguishes the egg mass of any species: the most useful diagnostic features of opisthobranch egg masses are tabulated for each type (Tables 1 - 8) and additional comparative notes and illustrations given below. The months in which egg masses were found (Tables 1, 3, 5, 7) represent, to some extent, times of observation and may not reflect seasonal laying except where stated. Seasonal laying in this area may be different from that of other regions with different seasonal or ecological conditions. The variety of months in which opisthobranchs lay their eggs is much wider than supposed by O'DONOGHUE & O'DONOGHUE (1922).

The number of egg masses examined for each species varied from 1 to 14 and averaged 6. Where great intraspecific variation occurred it has been noted. In cases where several egg masses were laid by the same animal wide variation occurred at times between the first and last egg mass observed – the last often contained many fewer eggs, but the dimensions of both eggs and capsules (Tables 2, 4, 6, 8) remained constant. The terminal part of the last egg mass very frequently had less eggs per capsule and sometimes empty capsules, presumably because no more eggs were available. The size of the mass laid (Tables 1, 3, 5, 7) also varied to some extent with the size of the parent, as noted by O'DONOGHUE & O'DONOGHUE (1922). Thus the maximum, minimum and average measurements given do not represent absolutes, but do provide a reliable guide to sizes involved. The number of eggs per egg mass has not been included since it has not proved particularly constant or diagnostic.

The colour of the egg masses (Tables 1, 3, 5, 7) sometimes varies with age but not to any great extent in the species included here. Water temperature has not fluctuated widely (8° to 11° C) but hatching time (Tables 2, 3, 6, 8) has sometimes been variable. However, time taken to hatch has been similar to comparable times found by previous workers which have been summarized by HADFIELD (1963). Hatching time is influenced by other factors besides temperature: egg masses hatch earlier if placed in a strong water current and may be caused to hatch by addition of fresh sea water. This may be due to the effect of a good oxygen supply, change in osmotic conditions. or to a mechanical cause. Egg masses are less infested by such animals as copepods and protozoans when placed in a good water circulation and the contents of many become unhealthy where this is not available. The veliger type (using the terminology of THOMPSON, 1961) has been included in the egg mass tables (Tables 2, 3, 6, 8) and is further discussed below.

Egg Masses of Type A

In this type the appearance of the ribbon depends greatly on the relative lengths of the free and attached edges. Thus in the egg mass of *Acanthodoris hudsoni* (Text figure 2) the longer free edge is fluted resembling a rosette, whilst that of *Diaulula sandiegensis* (Text figure 4a) is only slightly wavy at intervals since there is little difference in length between the free and attached edges. Where the free edge is shorter than the attached one the ribbon slopes inwards to the centre of the coil as in *Onchidoris muricata* (Text figure 8). The degree of stiffness of the ribbon (largely depending on its thickness) also affects the general appearance of the egg mass – whether it flops in folds as in that of *Austrodoris odhneri* (Text figure 5) and *Melibe leonina* (Text figure 7a), or stands erect as does that of *Haminoea virescens* (Text figures 6a, b). The closeness and regularity of coiling is variable although some species habitually lay very neat coils e. g. *Acanthodoris hudsoni* (Text figure 2), *A. nanaimoensis* (Text figure 3), *Onchidoris muricata* (Text figure 8); others rarely lay in a spiral e. g. *Onchidoris bilamellata*; others as commonly lay in a random direction as in a regular coil e. g. *Haminoea virescens* (Text figure 6a), *Melibe leonina* (Text figure 7a). In some egg masses the egg string is so easily detected in the field that the ribbon appears to be striated as in those of *Triopha*

carpenteri and *Haminoea virescens* (Text figures 6a, b). In several cases the situation of the egg mass is helpful. Such gross observations are summarized in Table 1 and Text figures 1 - 9, whilst those based on more detailed study are included in Table 2 and Plates 26 - 28.

Acanthodoris brunnea, Text figure 1; Plate 26, Figure 1

The egg masses are found on intertidal rocks in great abundance in early summer. The ribbon is laid in an

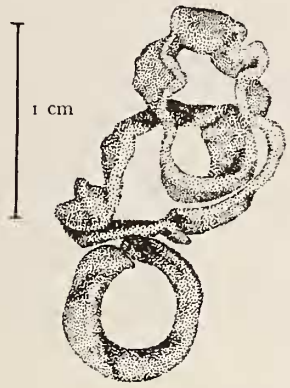

Figure 1

Egg Mass of *Acanthodoris brunnea*

untidy criss-crossing coil and is often almost as thick as it is wide. There is a narrow, clear area of jelly along both its edges. The capsules are well-spaced, frequently by almost their own width and their walls are thick and smooth.

Acanthodoris hudsoni, Text figure 2; Plate 26, Figure 2

The white ribbon forms a neat, closely coiled egg mass, usually with 1½ to 2 whorls. Its free edge is considerably longer than the attached one and since the ribbon is fairly

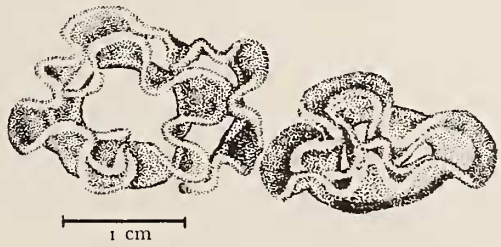

Figure 2

Two Egg Masses of *Acanthodoris hudsoni*

thick and stiff, the whole mass forms a fluted rosette. The capsules are spaced as in *Acanthodoris brunnea,* tending to be relatively thicker-walled and, in some specimens, more oval. The eggs are yellowish.

Acanthodoris nanaimoensis, Text figure 3; Plate 26, Fig. 3

Egg masses were laid on rocks and empty shells in the laboratory. The ribbon is very closely coiled, fairly thick and upright, taking a rounded course of 2 to 3 whorls, depending on the size of the parent. O'Donoghue & O'Donoghue (1922) reported the ribbon as yellow, with a wide, transparent margin, but in the present study all egg masses

Figure 3

Egg Mass of *Acanthodoris nanaimoensis*

were creamy-white with a narrow transparent margin at the free edge. Whereas the O'Donoghues' ribbons were 0.89 cm in width, the present ones were 0.45 to 0.50 cm. A ribbon of 9.20 cm length formed a spiral of about 1.50 cm diameter. The capsules are spaced out as in other acanthodorids.They are widely oval, with smooth, thick walls, and some are pointed at one end. Capsule dimensions (Table 2) were a little larger than those measured by O'Donoghue & O'Donoghue (the 1922 measurements were: 80 to 90μ by 90 to 100μ).

Archidoris montereyensis, Text figs. 4 a, b; Plate 27, Fig. 5

The egg mass of this species may be found at any time of year, usually on rocks where there is a strong current flow. Varying from bright yellow to very pale cream, the mass is laid in a fairly close coil occasionally trailing off to a straight terminal part. The ribbon is relatively thicker than that of *Austrodoris* and hence more erect (masses often consist of several more whorls than that in Text figure 4a). The free edge is a little longer than the attached one and splays out but is not usually fluted. It is also often the thicker edge and has a narrow, transparent margin. The usual ribbon width is 1.50 to 2.50 cm. As O'Donoghue & O'Donoghue (1922) mentioned, an egg string is present within the ribbon, but usually it is not at all obvious in the field. Each rounded capsule has a very thick, sculptured wall and contains 1 to 2 eggs, though in some masses capsules may contain 3 eggs. O'Donoghue

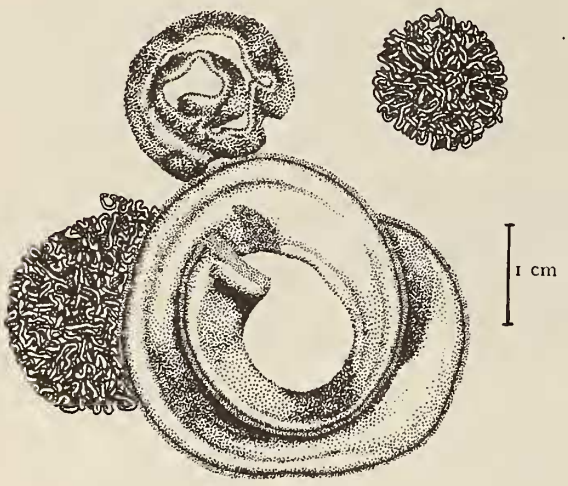

Figure 4 a

Egg Masses of *Archidoris montereyensis* (lower right), *Diaulula sandiegensis* (upper left), *Hermissenda crassicornis* (upper right and lower left)

& O'Donoghue found only 1 egg per capsule and the capsule size (120 to 160μ by 140 to 210μ) is at variance with present measurements (Table 2).

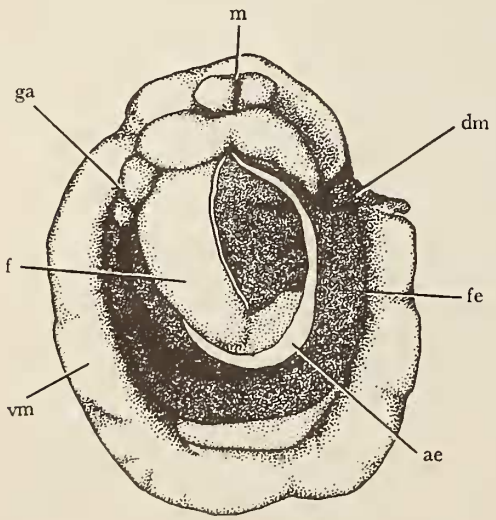

Figure 4 b

Ventral View of *Archidoris montereyensis* laying an Egg Mass
ae – attached edge of egg mass fe – free edge of egg mass
dm – dorsal side of mantle ga – genital aperture
f – foot m – mouth
vm – ventral side of mantle

Austrodoris odhneri, Text figure 5; Plate 26, Figure 4

In the aquarium, the egg masses were always deposited where there was a rather strong current flow. This is advantageous in keeping the ribbon clean of infesting animals, particularly useful in this case since the ribbon is relatively thin as well as wide and flops in folds which otherwise cling together closely, forming a sheltered hab-

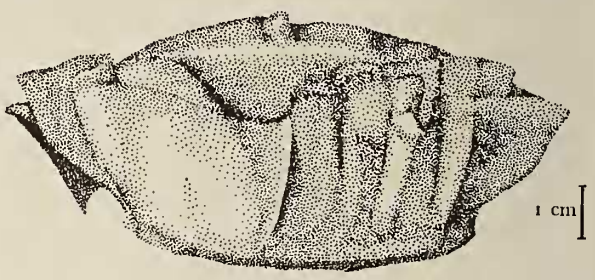

Figure 5

Egg Mass of *Austrodoris odhneri*

itat for protozoans and copepods. The very wide ribbon (3.30 to 4.70 cm) is laid in an oval spiral, and its free edge is longer than the attached one. The capsules are closely packed, sometimes touching. They are rather rounded with smooth, thick walls and usually contain 8 to 12 eggs, but sometimes there are fewer, particularly at the outermost, ultimate part of the ribbon.

Diaulula sandiegensis, Text figure 4 a; Plate 27, Figure 6

The egg masses were found attached below overhanging edges of intertidal rocks. The white (much less commonly cream) ribbon is relatively narrow, (about 0.40 cm) and has 3 to 8 whorls, according to the size of the adult. (The egg mass in Text figure 4 a was the third laid by one animal and is thus unusually short.) A coil with diameters 2.0 and 3.50 cm took three hours to lay and was laid in a typically oval spiral. The turns of the coil are rather close and sometimes appear crowded due to waviness of the upper edge, which is not, however, much longer than the attached edge. The egg string is usually fairly obvious and may sometimes be detected in the field. The slightly oval capsules are arranged closely, overlapping but not joining. There are 1 to 2 eggs per capsule. Capsule dimensions overlapped with those measured by O'Donoghue & O'Donoghue (1922) whose capsules were a little smaller.

Haminoea virescens, Text figures 6 a, b, c

The untidy yellow egg masses were found on *Ulva, Vaucheria* and *Zostera* in sheltered bays and lagoons with

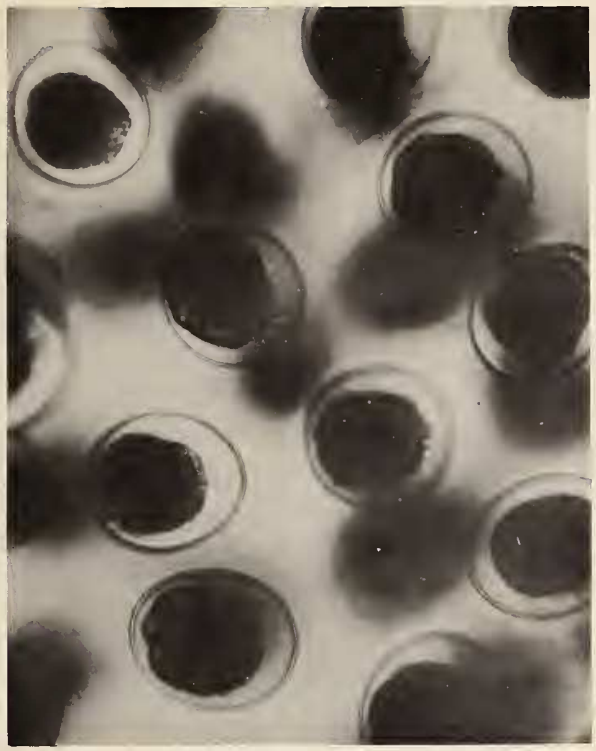

Figure 1: Egg Mass of *Acanthodoris brunnea*

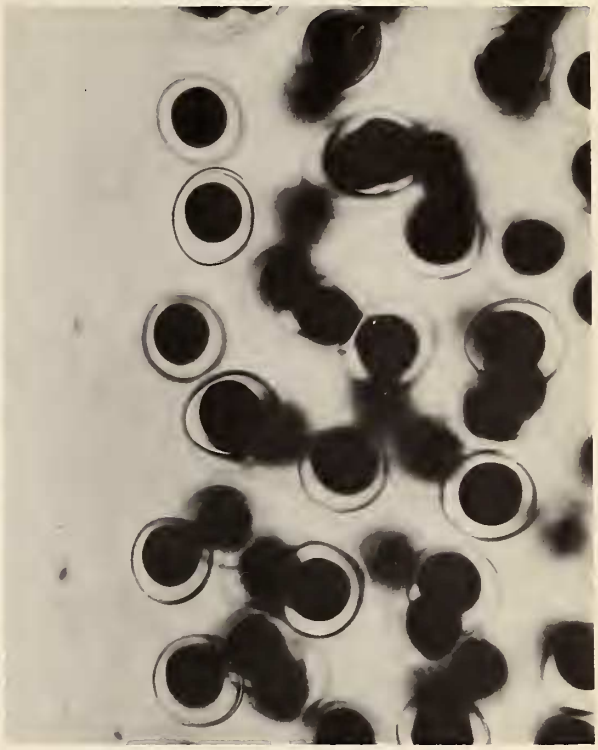

Figure 2: Egg Mass of *Acanthodoris hudsoni*

Figure 3: Egg Mass of *Acanthodoris nanaimoensis*

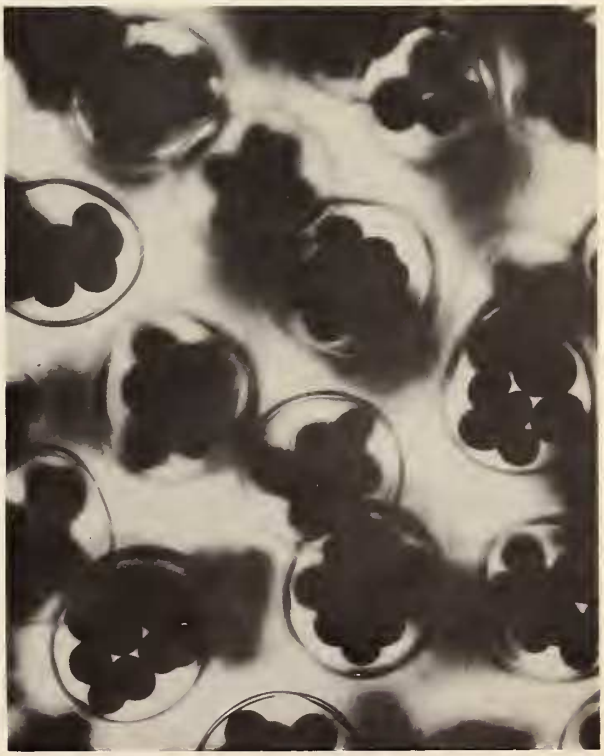

Figure 4: Egg Mass of *Austrodoris odhneri*

Figure 5: Egg Mass of *Archidoris montereyensis*

Figure 6: Egg Mass of *Diaulula sandiegensis*

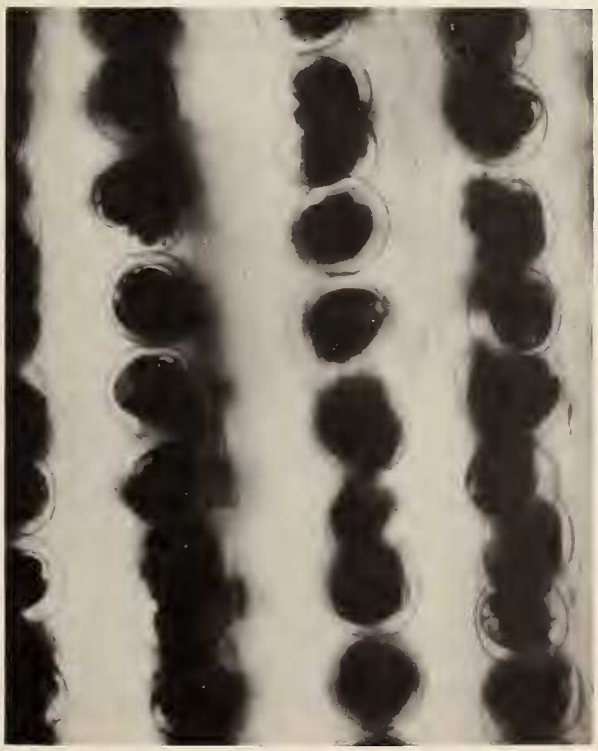

Figure 7: Egg Mass of *Haminoea virescens*

Figure 8: Egg Mass of *Melibe leonina*

Figure 9: Egg Mass of *Onchidoris bilamellata*

Figure 10: Egg Mass of *Onchidoris muricata*

Figure 11: Egg Mass of *Rostanga pulchra*

Figure 12: Egg Mass of *Triopha carpenteri*

a fine gravel or sandy substratum. They were attached in an unevenly coiled or meandering line and were striated in appearance due to the very obvious egg string. The free edge has a clear margin and is equal in length to the

Figure 6a

Two Egg Masses of *Haminoea virescens*

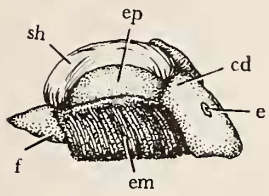

Figure 6b

Right Lateral View of *Haminoea virescens* laying an Egg Mass

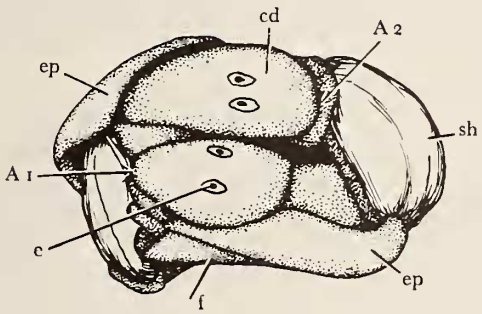

Figure 6c

Dorsal View of Two *Haminoea virescens in coitus*

A 1 – anterior end of first animal em – egg mass
A 2 – anterior end of second animal ep – epipodium
cd – cephalic disc f – foot
e – eye sh – shell

attached edge. The ribbon stands erect, being about 0.2 cm thick and 0.8 to 1.10 cm wide. The average length of an egg mass is 5 to 6 cm. The capsules touch each other along the egg string but not between adjacent coils of this. Individual capsules may be attached to their neighbour by a fine connection as is frequent in cephalaspidean egg masses, and also in *Elysia* (Reid, 1964). The capsule walls are smooth and either rounded or oval in outline. In most egg masses there was 1 egg per capsule but a few contained many capsules with 2 eggs. The characteristic yellow colour is due to the contents of the developing eggs and later to those of the the veliger digestive glands.

Melibe leonina, Text figures 7a, b; Plate 27, Figure 8

The egg masses are attached to kelp, or, more commonly, to *Zostera* well below the tidal region. They are very distinctive although width varies (less than 1.0 to 3.50 to 4.50 cm) and so does length (2.50 to 12.50 cm). The larger dimensions are more common and colour is

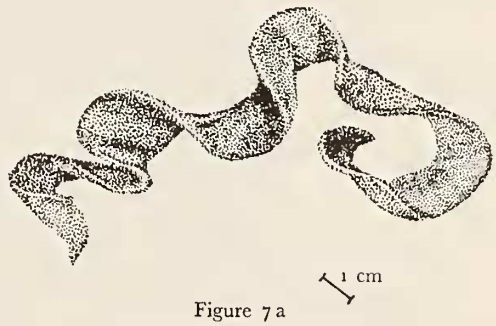

Figure 7a

Egg Mass of *Melibe leonina*

usually cream. The free edge of the egg mass is longer than the attached one, as Agersborg (1921) and O'Donoghue & O'Donoghue (1922) have reported. This often results in a funnel-shaped appearance (as in Agersborg's photograph), but the mass is not necessarily laid in a tight coil and may hang in wavy folds as in Text figure 7a and in the O'Donoghues' photograph. A wide basal area of the ribbon may be free of capsules, as may be its terminal end. The capsules may be close-packed or narrowly separated. They are large and oval, but frequently have flattened sides if much crowded. Most contain 15 to 25 eggs and only sometimes appear arranged in fairly regular lines as Agersborg described. Smaller egg masses may have fewer eggs per capsule, especially if the mass is the last laid over a short period of several layings by one adult. As few as 5 eggs per capsule may occur and frequently only 8 occur – less than has previously been described. However the general size range of egg masses, capsule size and number of eggs per capsule agree with earlier observations.

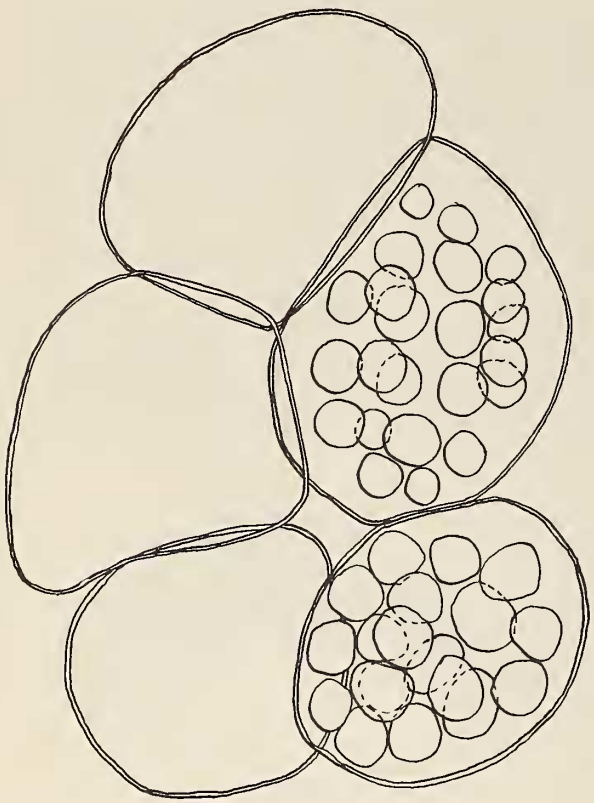

Figure 7 b

Five Capsules from the Egg Mass of *Melibe leonina*

Onchidoris bilamellata, Plate 28, Figure 9

The adults appear gregarious, laying preferentially where other *Onchidoris bilamellata* are already present – in the field the site is usually a barnacle-covered rock where adults are common. There was no apparent difference between egg masses laid by the usual dark-coloured adult and the occasional albino or light-coloured one. The egg masses were extremely common in winter only. They are usually laid in an irregular curve and the ribbon flares out at the longer free edge (as photographed by O'Donoghue & O'Donoghue, 1922). The ribbon is about 0.20 cm thick and eggs occupy the central 0.15 cm. Its length is commonly around 3 cm and width is 0.70 to 1.0 cm. It is sometimes possible to detect the egg string in the field, but due to the extreme crowding of capsules this is not easy. Some larger capsules contained two eggs, but these were not as large as O'Donoghue & O'Donoghue measured (140 to 180μ by 230 to 260μ). The size of capsules with only 1 egg agreed with the O'Donoghues' measurements, but most of the egg masses used by these authors were larger than those of the present study. In the majority of masses, capsules with 1 to 2 eggs prevailed, but in some, all capsules had only 1 egg; in a very few a high proportion of capsules had 3 eggs.

Onchidoris muricata, Text figure 8; Plate 28, Figure 10

The small egg masses of this species were laid in the aquarium. The ribbon was relatively thick (0.1 cm) and stood erect although it sloped inwards due to the shortness of the free edge relative to the attached one. The coil was quite wide, varying from 1.25 to 2.50 whorls, the largest mass being 0.5 cm in basal diameter. The free edge of the ribbon is transparent and the capsules are irregularly spaced, being 2 deep across the thickness of the ribbon.

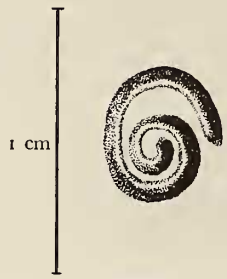

Figure 8

Egg Mass of *Onchidoris muricata*

Rostanga pulchra, Text figure 9; Plate 28, Figure 11

The vermilion or orange coils of this species' egg masses are found on or near the red food sponge, *Ophlitaspongia,* of the adults. They were found mainly during the summer months, none earlier than March, which is at variance with the year round occurrence mentioned by Ricketts

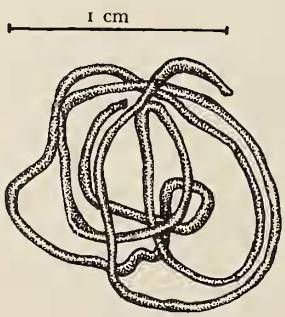

Figure 9

Egg Mass of *Rostanga pulchra*

& CALVIN (1962) in the region between San Diego and Monterey Bay. This difference is probably due to a minimum temperature requirement only attained at Friday Harbor in the summertime. The ribbon is so thick and narrow that it appears almost cylindrical and the many-whorled form of the mass (usually much neater than the one figured) is similar to that described for *Rostanga arbutus* in the Iranian Gulf (THORSON, 1940). As in this species, the egg mass grows paler with age as the red colour fades within the digestive glands of the veligers. On hatching these retain a pink colouration. The total diameter of an average coil – almost circular in disposition – is 1.25 by 1.25 cm, while ribbon width is 0.08 to 0.09 cm. The capsules are not in contact with each other, are rounded and extremely thick-walled. Most contain a single egg.

Triopha carpenteri, Plate 28, Figure 12

Egg masses were laid in the laboratory only between April and June although specimens had been kept at all other times of year. The white or cream ribbon is laid in a loose coil and its wavy free edge is considerably longer than the attached one. The egg string is very obvious causing a striated appearance as in *Haminoea.* The ribbon is about 1.4 cm wide. Capsules are smooth-walled and may contain 1 or 2 eggs, those with 2 being larger and more oval, some being pointed at one end. Capsules with only 1 egg are more numerous, but in a few egg masses capsules with from 5 to 7 eggs were frequent.

Egg Masses of Type B

Type B egg masses consist of three main parts, firstly a capsule-free jelly sheet (Text figures 10b, 11c, 15, 17a, 18b: js) which is usually attached to the substratum and along its free edge bears a cylindrical cord-like area (cf) containing the egg string (Text figure 11c: es). The egg string may double to and fro (denoted here as secondary twisting) and is always crowded with capsules in contact with each other and often joining along at least part of their walls. Type B egg masses are less homogeneous than those of Type A since the relative lengths and widths of the three component parts vary widely between species and affect the general appearance considerably. The simplest form of Type B egg mass is that of *Coryphella ?rufibranchialis* (Text fig. 13b) and *Olea hansineensis* in which the jelly-free sheet is very narrow, attached to the substratum (if flat) in a close coil and the eggstring lies untwisted in the cylindrical free edge of the mass. A more complex form is represented by *Coryphella fusca* (Text figure 12a), *Hermissenda crassicornis* (Text figure 4a) and *Dirona aurantia* – the egg masses of these are similar except that the egg string is secondarily twisted. Greater degrees of complication in appearance are also common. Where the capsule-filled area of the free edge is much longer than the capsule-free attaching sheet, the latter is usually relatively wider, allowing the free edge to double to and fro upon itself. This makes the egg mass appear much wider and more complex, also the eggs are raised further above the substratum, probably allowing a better water circulation. The egg masses of *Aeolidia papillosa* (Text figure 10a, b), *Dendronotus frondosus* (Text figure 15) and *Tritonia exsulans* (Text figures 18a, b) represent a series within which these characteristics are progressively more marked. In the most extreme cases of disparity in length between the shorter capsule-free edge of the mass and the other, opposite, capsule-filled edge, the egg mass may of necessity become tangled into a ball as in *Dendronotus iris* and *Armina californica* (Text figure 11a). It is then attached to the substratum by one or more mucous strings, resembling the method of attachment of egg masses of Type C. Another example of a free coil attached by mucous strings, is the egg mass of *Cumanotus beaumonti* (Text figure 14). Here the egg string is not secondarily twisted and there is no attaching jelly-sheet, so that the appearance is very simple.

Aeolidia papillosa, Text figs. 10a, b, c, d; Plate 29, Fig. 13

This species lays a large untidy pink or white coil, frequently attached to *Zostera* and about 6.0 by 3.50 cm in diameter. The capsules are extremely crowded and

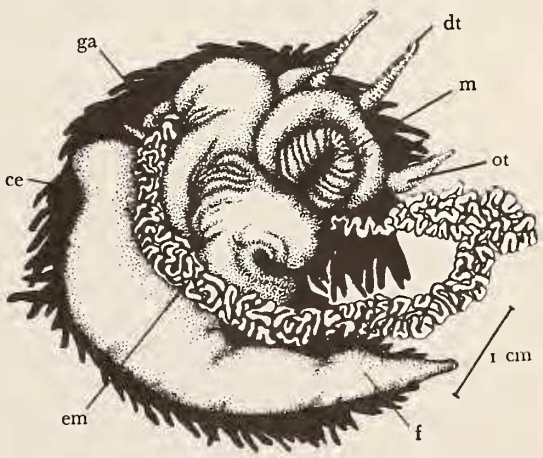

Figure 10a

Ventral View of *Aeolidia papillosa* laying an Egg Mass

ce – cerata
dt – dorsal tentacle
em – egg mass
f – foot
ga – genital aperture
m – mouth
ot – oral tentacle

thin-walled, thus are often crumpled and always pushed out of shape. The capsule walls often appear pinched together at one end (Text figure 10d). The number of

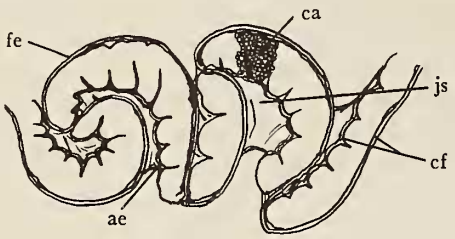

Figure 10b

Small Portion of the Egg Mass of *Aeolidia papillosa*
ae – attached edge of egg mass cf – capsule-filled area
ca – capsules fe – free edge of egg mass
js – capsule-free jelly sheet

Figure 10c

One Capsule containing Six Developing Eggs of *Aeolidia papillosa*

Figure 10d

Small Area of a Capsule Wall of *Aeolidia papillosa*

eggs per capsule is rather variable, but usually fairly consistent within one egg mass. Thus in one egg mass, 6 is a common number of eggs per capsule (less may occur in a few capsules) but another mass may have 10 to 15 eggs per capsule throughout and no capsules with as few as 6. O'Donoghue & O'Donoghue (1922) described *Aeolidia* egg masses with smaller capsules containing 1 to 3 eggs. As the egg develops into a morula, the cells protrude so that it is not smoothly spherical (Text figure 10c).

Armina californica, Text figs. 11a, b, c; Plate 29, Fig. 14

The dingy cream egg mass is laid in an untidy bundle of about 3.0 to 5.0 cm diameter. It is attached only by one

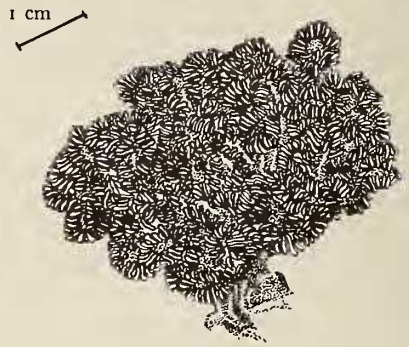

Figure 11a

Egg Mass of *Armina californica*

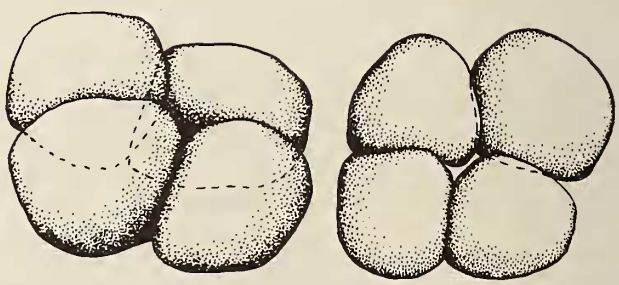

Figure 11b

Developing Eggs of *Armina californica* – at 4-cell stage

or more mucous strings from the ends of the ribbon. These may be secured by burrowing into the substratum as is the case with Type C egg masses. The capsule-free part of the egg mass is much wider and shorter than the outermost, capsule-filled part, which gives the mass its colour and lies in folds, obscuring the capsule-free jelly sheet. The egg string is secondarily twisted, looping to and fro and occasionally spiralling within the outer part

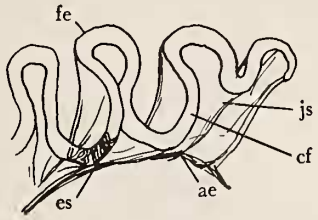

Figure 11 c

Small Portion of the Egg Mass of *Armina californica*
ae – attached edge of egg mass es – egg string
cf – capsule-filled area fe – free edge of egg mass
js – capsule-free jelly sheet

of the ribbon. In the earliest part of the egg mass, capsules are sometimes scattered down to the base of the jelly sheet (normally capsule-free), but in later areas the capsules are confined to the outer edge of the mass as in other Type B masses. At the terminal end of the mass there is sometimes a short portion without capsules, presumably because no more were available. The capsules are large, rounded and thin-walled, usually containing 12 to 15 yellowish eggs.

Coryphella fusca, Text figures 12 a, b; Plate 29, Figure 15

This species lays a pale pink, evenly coiled egg mass, in which the capsule-filled area is closely attached to the substratum by a narrow capsule-free sheet. The egg string

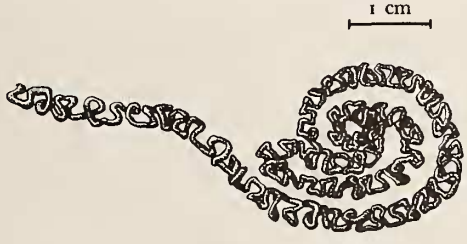

Figure 12 a

Egg Mass of *Coryphella fusca*
(drawn from the attached edge – the transparent jelly enclosing and attaching the egg string has not been shown)

is very evenly folded within the free edge of the mass and its diameter is rather constant throughout, constrictions or empty areas being rare, unlike some other species' egg masses e. g. *Hermissenda crassicornis.* The mass presents a very neat appearance. The capsule walls are quite stout and adjacent ones sometimes join (Text figure 12 b). Each oval capsule contains 1 to 2 brownish-yellow eggs.

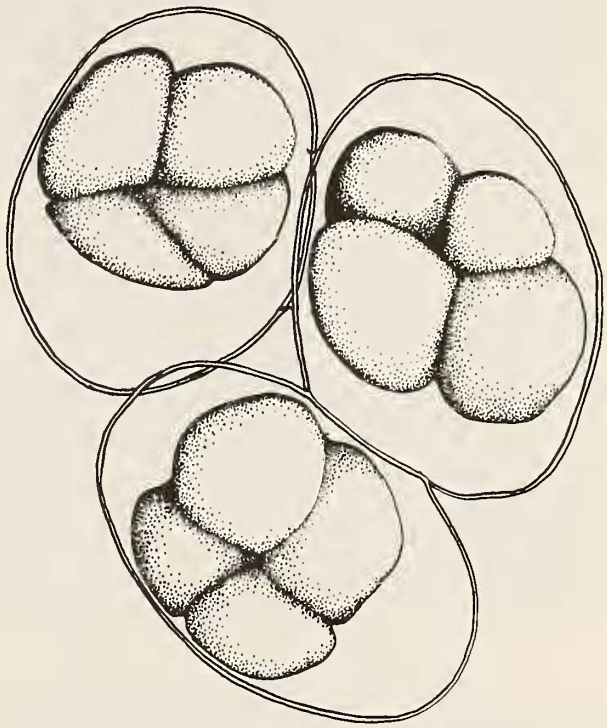

Figure 12 b

Three Capsules of *Coryphella fusca* with Eggs at 4-Cell Stage

Coryphella ?rufibranchialis, Text figures 13 a, b; Plate 29, Figure 16

(The identification of this species has caused some confusion as it also has characteristics in common with *Coryphella trilineata* and *C. lineata.* The name suggested is following the conclusions of E. and E. Marcus on their examination of the animal.) The egg masses are found intertidally at low water, frequently in groups on rocks or weed, and they also occur on floats. In aquaria adults frequently laid eggs on the surface film, in undisturbed conditions. The white egg mass is laid in an extremely neat coil, looking like a watch-spring just over 1 cm in diameter. The capsule-free attaching sheet is narrower than the capsule-filled area. The egg string is not secondarily twisted and contains somewhat rounded capsules, 4 or 5 deep. Each has a thick, smooth wall and contains one almost spherical egg.

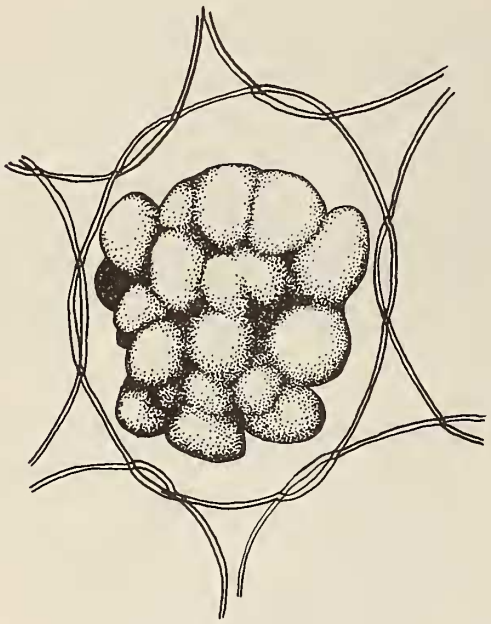

Figure 13 a

One Capsule, and Parts of Surrounding Capsules of *Coryphella ?rufibranchialis*

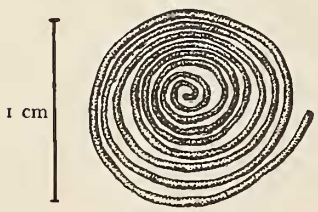

Figure 13 b

Egg Mass of *Coryphella ?rufibranchialis*

Cumanotus beaumonti, Text figure 14; Plate 30, Figure 17

This species has not been recorded previously from the North-East Pacific region and both it and its egg mass are quite distinctive. The egg mass is pale pink when first laid and becomes paler with age. It consists of a cylindrical cord containing an untwisted egg string, and there is no capsule-free sheet to attach it. Instead the mass is attached by a mucous string. The coiled mass comprises a series of parallel loops of similar diameter, so that it looks like a spring. The large oval capsules are spaced out and are thin-walled, usually becoming pushed out of shape when they do touch. They contain a variable number of eggs (4 to 14). As each egg develops to a morula the cells can

Figure 14

Egg Mass of *Cumanotus beaumonti*

be clearly distinguished and stick out slightly, but not so markedly as those of *Aeolidia* (Text figure 10 c).

Dendronotus frondosus, Text figure 15; Plate 30, Figure 18

This species lays an untidy coil varying from pale to dark pink. Generally the mass is quite small in diameter, although that shown in Text figure 15 consists of a shorter ribbon than is customary. The capsule-free attaching sheet is often folded at the base and thus appears shorter than it is. The capsules are in contact and sometimes joined. They are rather rounded with thin walls which are usually creased. Each capsule contains one egg.

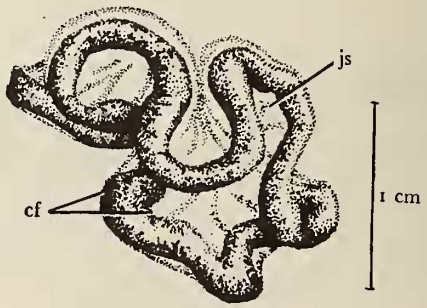

Figure 15

Egg Mass of *Dendronotus frondosus*
cf – capsule-filled area js – capsule-free jelly sheet

Dendronotus iris, Plate 30, Figure 19

Only one specimen has been observed laying eggs and it laid a large rounded bundle of about 5 to 6 cm diameter. This was pure white and attached to the aquarium wall by mucous strings. The width of the capsule-free sheet relative to the outer, capsule-filled part of the mass was great and it was also much shorter than the capsule-filled region.

Figure 13: Egg Mass of *Aeolidia papillosa*

Figure 14: Egg Mass of *Armina californica*

Figure 15: Egg Mass of *Coryphella fusca*

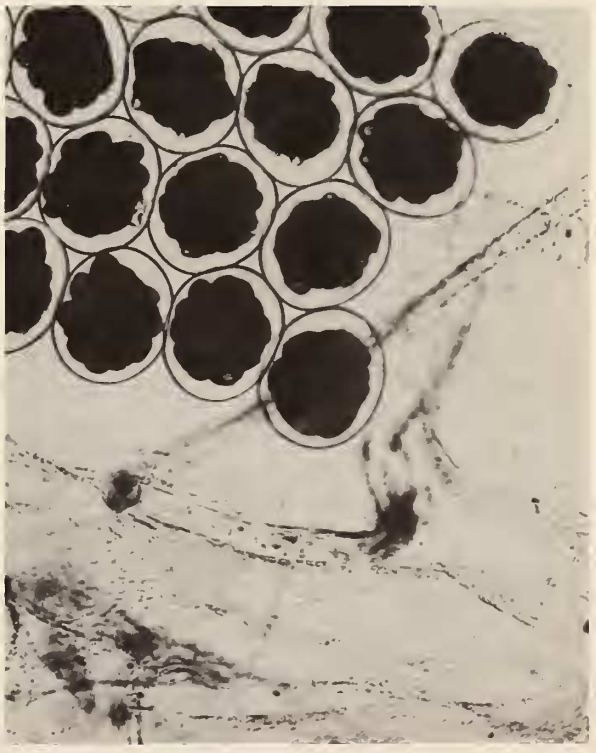

Figure 16: Egg Mass of *Coryphella ?rufibranchialis*

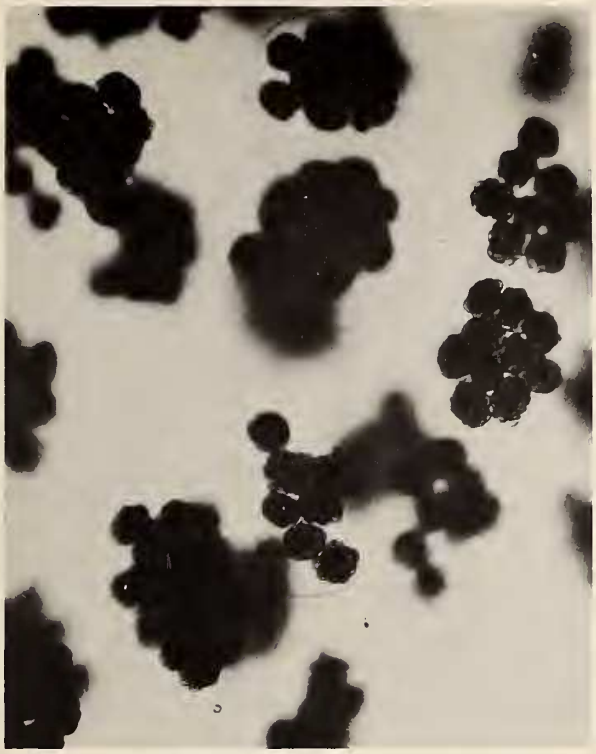

Figure 17: Egg Mass of *Cumanotus beaumonti*

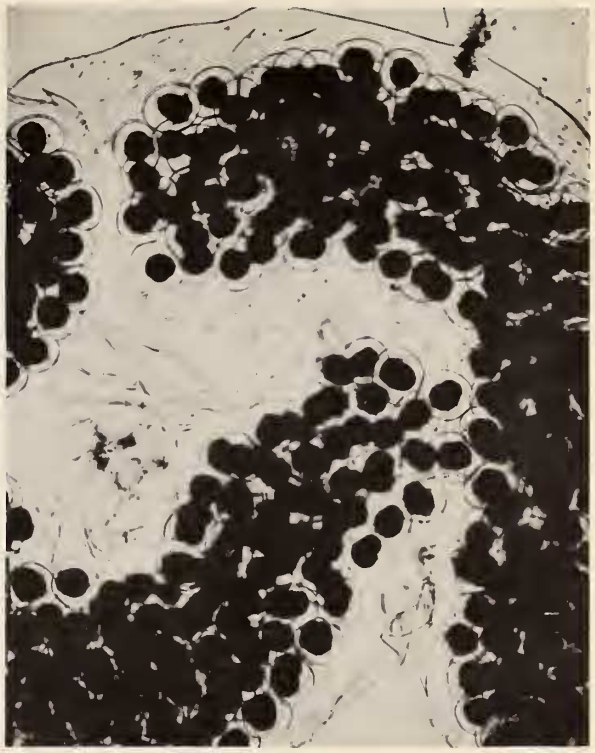

Figure 18: Egg Mass of *Dendronotus frondosus*

Figure 19: Egg Mass of *Dendronotus iris*

Figure 20: Egg Mass of *Dirona albolineata*

Figure 21: Egg Mass of *Dirona aurantia*

Figure 22: Egg Mass of *Hermissenda crassicornis*

Figure 23: Egg Mass of *Olea hansineensis*

Figure 24: Egg Mass of *Tritonia exsulans*

Thus the mass automatically formed a bundle as in *Armina*. The large round capsules were arranged neatly, from 3 to 5 overlapping capsules, crossing the capsule-filled area in rather regular rows. Large numbers of eggs – more than have been observed in other species of the genus – clump together within each capsule, rarely touching its walls. The capsule walls are a little stouter than those of other dendronotid species and although adjacent walls may be slightly flattened against one another, they are rarely creased. In other dendronotids creasing is very frequent or universal amongst the thin-walled capsules.

Dirona albolineata, Text figure 16; Plate 30, Figure 20

The egg mass of this species is untidy in appearance and superficially similar to that of *Aeolidia*. The secondarily twisted egg string is enclosed in striated jelly in which the apparent striations are caused by greenish bodies on its surface (Text figure 16, insert). The mass has been well described by O'Donoghue & O'Donoghue (1922) in whose specimens capsules were larger (390μ by 260μ to 520μ by 350μ) and number of eggs per capsule (17 to 27) higher. In the present masses the capsules were in contact and were smooth-walled, each being oval and containing only 8 to 12 eggs per capsule.

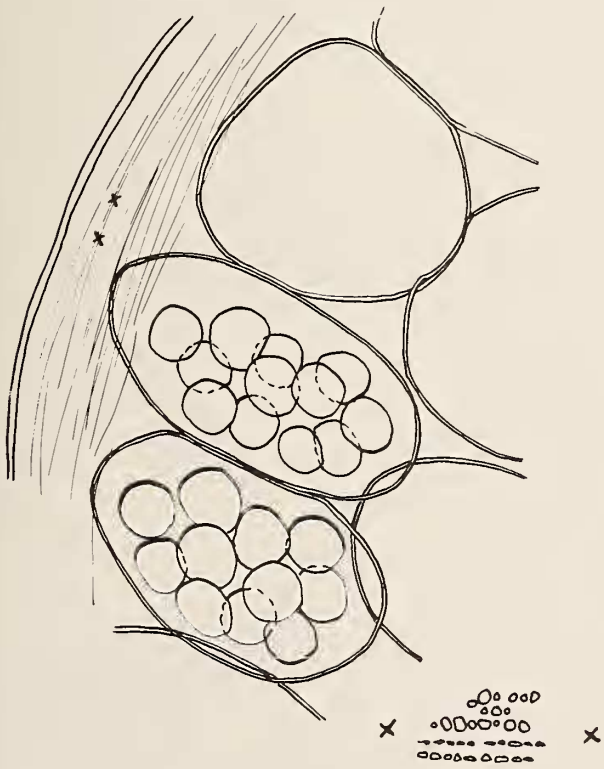

Figure 16

Several Capsules and Surrounding Jelly from the Egg Mass of *Dirona albolineata* with Detail (x-x insert) of Markings on the Jelly

Dirona aurantia, Text figures 17a, b; Plate 31, Figure 21

The salmon-pink egg mass of this species is laid in a loose coil (Hurst, 1966), characterized by its small size relative to that of the parent. Its general appearance recalls that of *Coryphella fusca,* but it is much less neat and regular, particularly in the secondary twisting of the egg string. The outer part of the jelly is striated, and encloses the narrow egg string, which is frequently interrupted by areas without capsules. The capsules are neatly and closely arranged, each being oval and someimes partially collapsed. Each contains 1, 2, 3 or up to 6 eggs per capsule in a number of specimens examined. Capsule and egg size do

Figure 17a

Small Portion of the Egg Mass of *Dirona aurantia*
ae – attached edge of egg mass cf – capsule-filled area
ca – capsule fe – free edge of egg mass
js – capsule-free jelly sheet

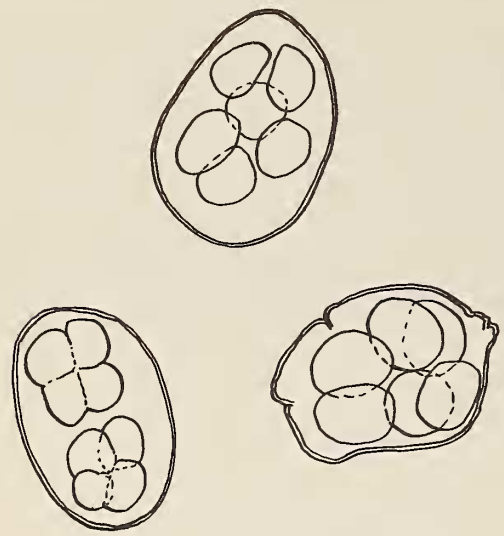

Figure 17b

Three Capsules from Three Different Egg Masses of *Dirona aurantia*

not vary in direct proportion to the number of eggs per capsule. The eggs are rounded, smooth and brownish, reaching the 2-cell stage some 24 hours after laying.

Hermissenda crassicornis, Text figure 4a; Plate 31, Fig. 22

The masses of this species are common on blades of *Zostera.* The egg mass is a flat pink coil (when laid on a plane surface) similar to those of *Coryphella fusca* and *Dirona aurantia,* but generally laid in a tighter coil than either. The jelly has longitudinal striations and some slight sculpturing and encloses a secondarily twisted egg string with larger, more irregular twistings than in *C. fusca* (Text figure 12a). There are frequent constrictions in the egg string, so that it looks like a series of pink sausages raised above the substratum in loops, due to the fairly wide capsule-free attaching jelly sheet. The mass has been described and photographed by O'Donoghue & O'Donoghue (1922) and capsule sizes agree with those of the present account. The smooth, oval capsule walls and enclosed round eggs are pinkish, becoming more yellow with age. In most masses there is one egg per capsule but in some 2 per capsule is also frequent, while in masses from exceptionally large adults 3 to 4 eggs per capsule also occur.

Olea hansineensis, Plate 31, Figure 23

The masses are found in proximity to those of *Haminoea* and probably to those of *Chelidonura,* on the eggs of which adult *Olea* feed. This species, like most sacoglossans, lays a simple, very close coil in which the attaching sheet is very narrow and the egg string not secondarily twisted. The small white mass thus appears flush with the substratum and usually consists of 3 to 6 turns. The capsule walls are smooth and thin, in contact with each other but not squashed together.

Tritonia exsulans, Text figs. 18a, b, c, d; Plate 31, Fig. 24

The cream egg mass of *Tritonia* is laid in a long straggling string, randomly twisted or straight and often more than 70 cm long. The colourless capsule-free sheet is rather wide and its attaching edge is white and thickened (Text figure 18c). The sheet is not folded except at its outer edge where it is considerably longer and thrown into folds as a consequence (Text figures 18b, d). At

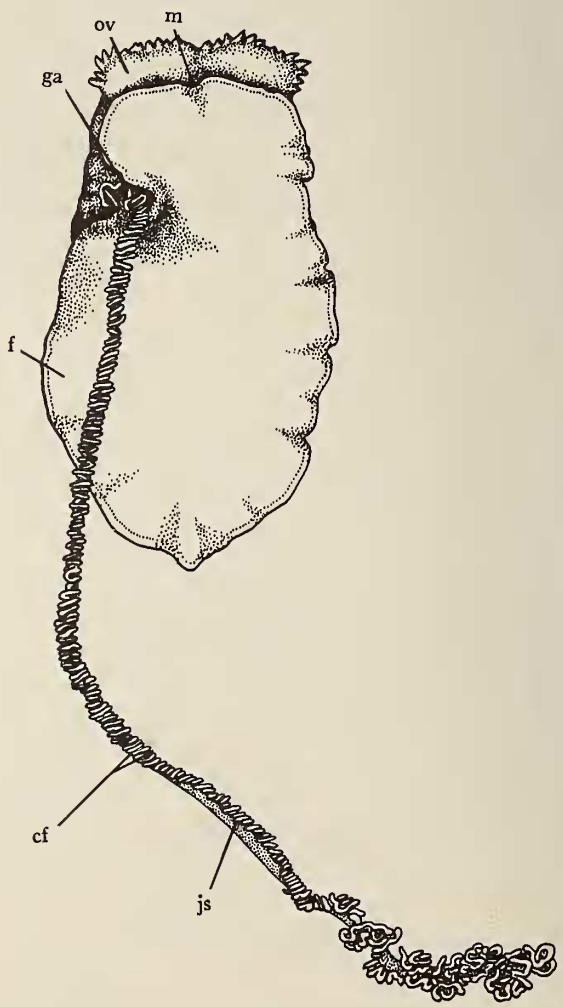

Figure 18a

Ventral View of *Tritonia exsulans* laying an Egg Mass

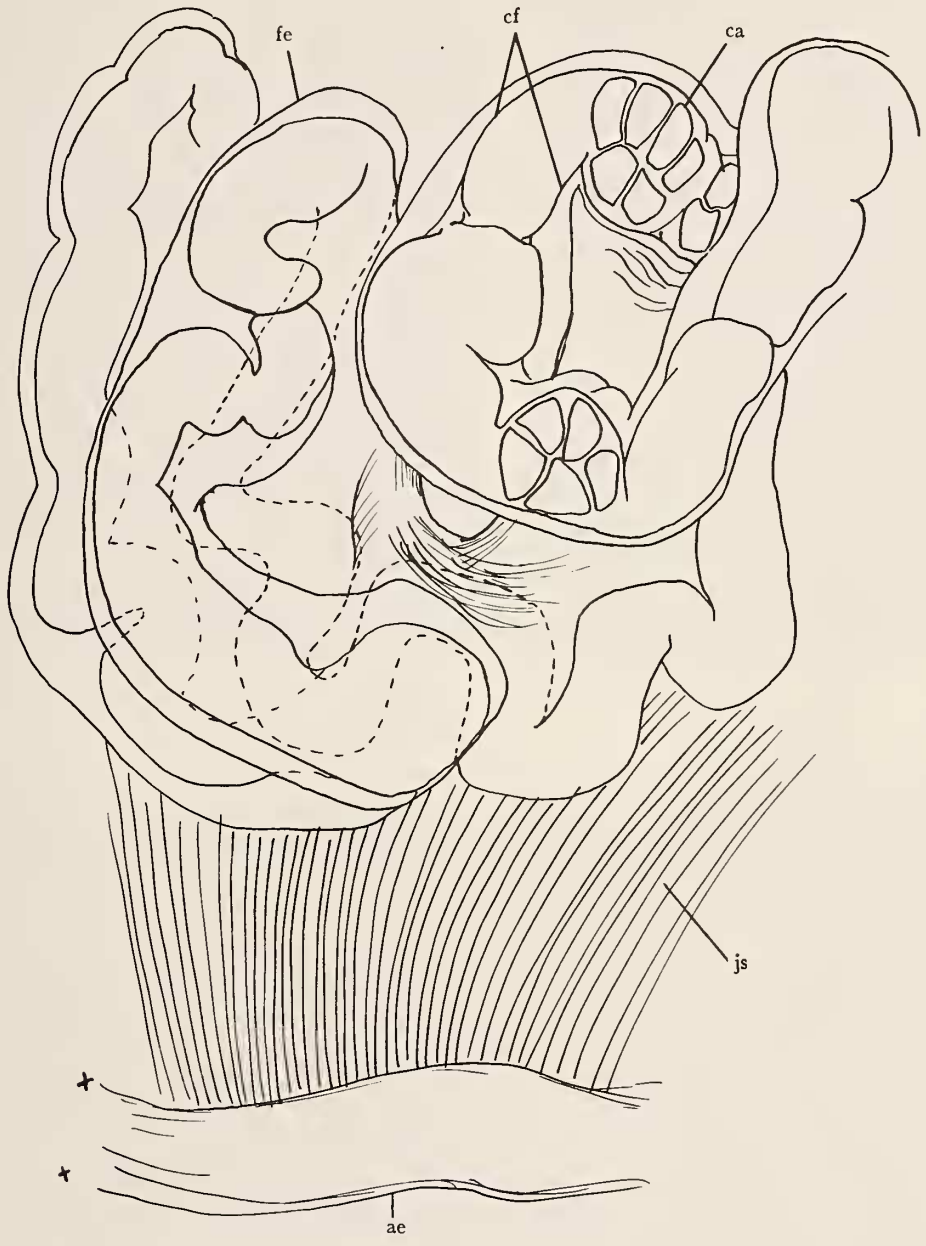

Figure 18 b

Small Portion of the Egg Mass of *Tritonia exsulans*

ae – attached edge of egg mass
ca – capsule
cf – capsule-filled area
f – foot
fe – free edge of egg mass
ga – genital aperture
js – capsule-free jelly sheet
m – mouth
ov – oral veil

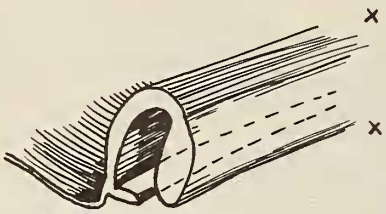

Figure 18c

Detail of the Attached Edge of the Egg Mass of *Tritonia exsulans*

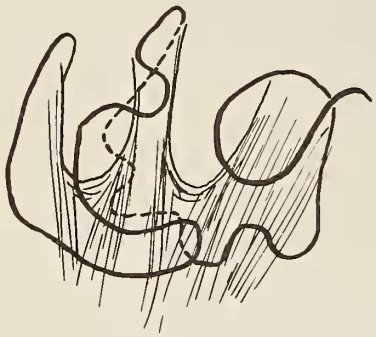

Figure 18d

Diagrammatic Representation of the Coils of the Capsule-Filled Area of the Portion of the Egg Mass shown in Figure 18b

the outer edge is the egg string which may twist in a regular or irregular fashion, greatly affecting the appearance of the egg mass. Sometimes both occur in one mass, as in Text figure 18a. In most masses the folding of the whole outer part of the ribbon and the egg string within it is irregular, as in the earliest part of the mass figured. The large capsules are usually polygonal due to flattening of their sides by contact between adjacent capsules. Each contains many small eggs.

Egg Masses of Type C

Egg masses of this type laid by cephalaspids, are usually attached by burrowing into the sand with the jelly string from the apex of the mass, as described by GUIART (1901) in *Philine* and FRETTER & GRAHAM (1954) in *Acteon*. The animals whose egg masses are described here also burrow and usually attach their jelly-bags similarly.

Aglaja diomedea

The ovoid egg masses are found in large numbers in spring and summer, attached to weed or below the sand's surface, the mass itself not being buried. The sandy colour provides good camouflage. The egg string is obvious and some capsules are mutually attached by a narrow string between their respective walls, running from the narrower end of the oval shape. Information on *Aglaja* in Table 5 refers to local animals, but some smaller specimens from a more distant area (within the same region) laid smaller masses (0.3 by 0.4 cm) with no obvious egg string. The specimens may represent another species or subspecies. Capsule size lay within the range of that of undoubted *Aglaja diomedea* but veliger size did not and the veliger shells were distinguishable (discussed further below). The adult animals showed some slight external differences from local specimens.

Chelidonura phocae

This animal lays a cylindrical egg mass with rounded ends, in which the coils of the egg string are very obvious. The colour is white and the capsules are egg shaped with stout smooth walls. Each contains a slightly oval, centrally placed single egg.

Gastropteron pacificum

The egg mass is almost globular and of clear jelly. It contains widely separated rounded capsules containing spherical pink eggs. The smooth-walled capsules each have a short string-like protrusion from one point on their surfaces and this does not appear to be attached elsewhere. As the eggs develop to form a ball of cells, the pink colour becomes concentrated and at one side of it is a group of yellowish cells, the whole being surrounded by a narrow layer of greenish cells.

Egg Masses of Type D

The small, often sac-like egg masses of this group are not morphologically uniform and are considered together for convenience.

Catriona aurantia, Text figure 19; Plate 32, Figure 25

The egg mass is whitish or colourless and is a small bag, gathered together at one end which is attached to a solid surface. The oval capsules within it are smooth-walled and closely packed, but are not squashed together.

Cratena albocrusta

In the laboratory, the egg masses were attached by one side to the surface film of the water, or occasionally to the aquarium wall. It is unlikely that the egg mass would be attached to the surface film in the natural habitat. Each pinkish egg mass was less than 1 cm long and was sausage shaped. The capsules are closely arranged but not pressed out of shape. They are oval and often joined together by a small region of their walls, frequently at the narrow end of the oval.

Figure 25: Egg Mass of *Catriona aurantia*

Figure 26: Egg Mass of *Eubranchus olivaceus*

Figure 27: Veliger of *Acanthodoris brunnea*

Figure 28: Veliger of *Acanthodoris hudsoni*

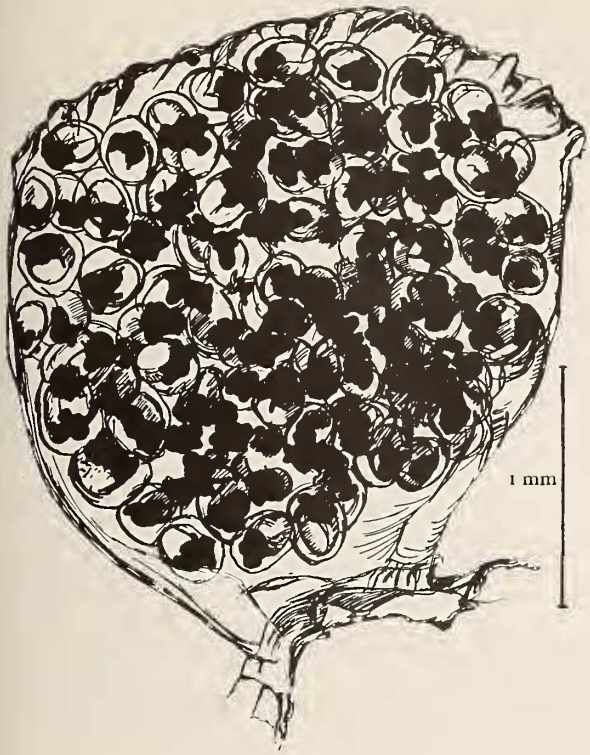

Figure 19

Egg Mass of *Catriona aurantia*

Eubranchus olivaceus, Text figure 20; Plate 32, Figure 26

The rather uniform and characteristic masses are found on the hydroid prey of the adults, present specimens laying eggs earlier than those of O'Donoghue & O'Donoghue (1922). The egg mass is like a small section of a Type B mass, without secondary twisting of the egg string. Eggs occupy a crescent-shaped area and the mass is attached by a small area at the base of a capsule-free attaching sheet. The whole is approximately triangular, with a convex free edge. The oval capsules are closely arranged and each contains a single egg. Their size overlaps with that measured by the O'Donoghues, being a little larger. The description given by these authors otherwise agrees with present observations.

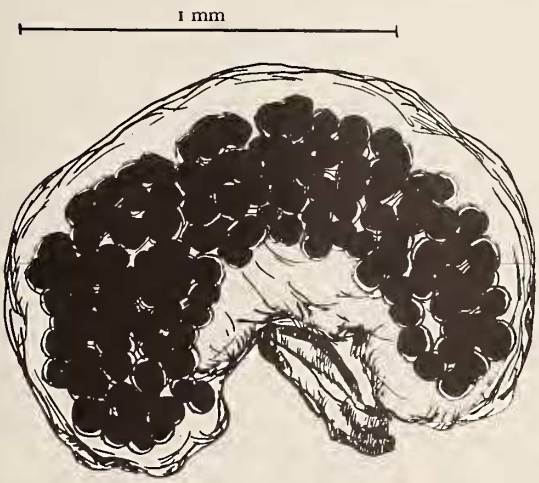

Figure 20

Egg Mass of *Eubranchus olivaceus*

VELIGER SHELLS

To some extent it is possible to identify the veligers of opisthobranchs by examination of their shells, especially when these are freshly empty. As Thompson (1961) has noted, the shells are of two main types: firstly coiled, uninflated shells of $\frac{3}{4}$ to 1 whorl only; secondly somewhat egg-shaped, inflated shells. All are typically sinistral as mentioned by Fretter & Graham (1962). Thorson (1946) also recognized a third group of cap-like shells,

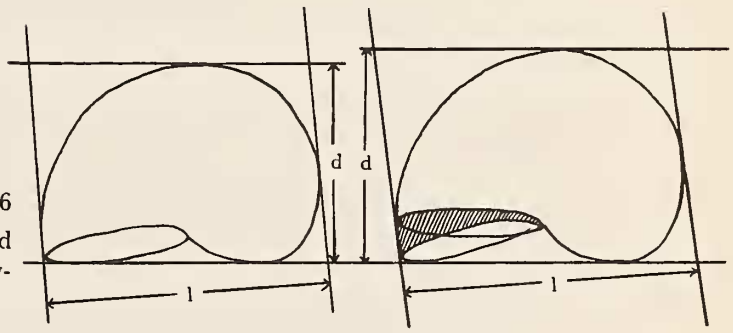

Figure 21

Length and Depth Measurements of a Veliger Shell of Type 1 a – before Growth; b – after Growth. The Effect of Growth is greater in Depth Measurement than in Length Measurement.

which is not here regarded as a separate type. It has been observed that damaged shells of Type 1 and less inflated shells of Type 2 may be cap-like, also prematurely hatched veligers of some species e. g. *Dendronotus* may have cap-shaped cells (Text figure 30: [sh]) – as also occurs in *Tritonia* (Thompson, 1961). The veligers mentioned in this paper have thus been divided into Types 1 and 2, following Thompson.

The average measurements given (Tables 9, 11) are derived from standard samples of empty shells, each collected from a healthy population of seemingly normal veligers hatched in the laboratory. In some cases the

Table 1

Characteristics of the Egg Masses of Species of Type A

	Months found											
	January	February	March	April	May	June	July	August	September	October	November	December
Acanthodoris brunnea:					×	×						
Acanthodoris hudsoni:				×	×							
Acanthodoris nanaimoensis:		×			×					×	×	
Archidoris montereyensis:	×	×	×	×	×	×				×	×	×
Austrodoris odhneri:				×	×	×						
Diaulula sandiegensis:		×	×	×	×							
Haminoea virescens:		×			×	×	×	×		×	×	×
Melibe leonina:	×	×	×	×	×	×	×	×	×	×	×	×
Onchidoris bilamellata:		×	×							×	×	×
Onchidoris muricata:	×	×	×									
Rostanga pulchra:			×	×	×	×				×		
Triopha carpenteri:				×	×	×						

Table 2

Characteristics of the Egg Masses of Species of Type A

	Eggs per Capsule									Capsules Touching			Capsule Wall	
	1	2	3	4	5 - 7	8 - 12	12 - 15	15 - 30	30 - 60	Majority	Fairly frequent	Rarely or none	Sculptured	Smooth
Acanthodoris brunnea:	×											×		×
Acanthodoris hudsoni:	×											×		×
Acanthodoris nanaimoensis:	×											×		×
Archidoris montereyensis:	×	×	×								×		×	
Austrodoris odhneri:			×	×	×	×					×	×		×
Diaulula sandiegensis:	×	×								×				×
Haminoea virescens:	×	×								×	×			×
Melibe leonina:					×	×		×			×			×
Onchidoris bilamellata:	×	×	×								×			×
Onchidoris muricata:	×											×		×
Rostanga pulchra:	×	×									×	×		×
Triopha carpenteri:	×	×			×					×				×

Table 1

Characteristics of the Egg Masses of Species of Type A

Colour					Ribbon Width							Length Free Edge			Egg String	
White	Cream	Yellow	Pink	Other	< 2 mm	2 and < 4 mm	4 and < 7 mm	7 and < 10 mm	10 and < 15 mm	15 and < 25 mm	25 mm and up	Longer than attached	Similar to attached	Shorter than attached	Extremely obvious	Not extremely obvious (see text)
×	×					×							×			×
×	×						×					×				×
×	×						×						×			×
	×	×								×		×				×
×											×	×				×
×		×					×					×	×		×	×
×	×	×						×	×			×	×		×	
×								×	×	×	×	×				×
×					×							×				×
×					×								×			×
×	×								×			×			×	

Table 2

Characteristics of the Egg Masses of Species of Type A

Capsule Dimensions in μ																					Veliger Type		Days Taken	
. minimum maximum . < average of least diameter > average of greatest diameter																								
- 80	81 - 100	101 - 120	121 - 140	141 - 160	161 - 180	181 - 200	201 - 220	221 - 240	241 - 260	261 - 280	281 - 300	301 - 320	321 - 340	341 - 360	361 - 380	381 - 400	401 and up				1: uninflated	2: inflated	time to hatch	appearance of veliger
	.<	.>																			×		9	7
	.	<.>																			×		16	12
		.<	.>																		×		9	6
			.	<.>																	×		23-28	13-22
								.	<	.>											×		22-33	13-16
			.<	.>																	×		22-28	17
			.<	>		.															×		9-18	7-12
									.						<		> 443 .567				×		8-15	7-12
		.		<>		.															×		12-13	7-10
	.<	.>																			×		7-14	4-13
		.<>	.																		×		30	26
																					×		18	17

Table 3

Characteristics of the Egg Masses of Species of Type B

	Months found												Colour				
	January	February	March	April	May	June	July	August	September	October	November	December	White	Cream	Yellow	Pink	Other
Aeolidia papillosa:	×	×										×	×			×	
Armina californica:	×	×			×	×		×				×	×	×	×		
Coryphella fusca:		×						×			×	×				×	
Coryphella ?rufibranchialis:		×	×							×			×				
Cumanotus beaumonti:					×								×			×	
Dendronotus frondosus:			×			×										×	
Dendronotus iris:						×							×				
Dirona albolineata:	×					×						×	×				
Dirona aurantia:	×	×	×													×	
Hermissenda crassicornis:		×	×		×		×	×			×	×				×	
Olea hansineensis:							×						×				
Tritonia exsulans:	×	×	×				×	×	×		×	×		×			

Table 4

Egg Capsule Dimensions of Species of Type B

Capsule Dimensions in μ

. minimum < average of least diameter

	- 80	81 - 100	101 - 120	121 - 140	141 - 160	161 - 180	181 - 200	201 - 220	221 - 240	241 - 260	261 - 280	281 - 300	301 - 320	321 - 340	341 - 360	361 - 380	381 - 400	361 - 380	381 - 400	401 - 420	421 - 440	441 - 460
Aeolidia papillosa:									.	<		>		.								
Armina californica:							.			<					>							
Coryphella fusca:		.<		>	.																	
Coryphella ?rufibranchialis:		.<>	.																			
Cumanotus beaumonti:									.		<			>.								
Dendronotus frondosus:				.<>.																		
Dendronotus iris:																						
Dirona albolineata:				.	<			>.														
Dirona aurantia:			.		<		>			.												
Hermissenda crassicornis:		.<		>.																		
Olea hansineensis:		.<	>	.																		
Tritonia exsulans:	.																					

Table 3

Characteristics of the Egg Masses of Species of Type B

Width Egg String		Attachment		2ndy Twisting		Eggs per Capsule									Veliger Type		Days Taken	
< 1 mm	> 1 mm	Most of length	Other	Present	Not present	1	2	3	4	5 - 7	8 - 12	13 - 19	20 - 30	30 - 60	1: uninflated	2: inflated	time to hatch	appearance of veliger
	×	×		×				×	×	×	×	×			×		10–24	8 – 15
	×		×	×							×	×			×		17–23	12 – 15
×		×		×		×	×								×		7 - 8	6
×		×			×	×									×		23	
	×		×		×				×	×	×	×			×		10	8
×		×		×		×										×	7–15	2 – 7
	×		×	×										×		×		
	×	×		×			×		×	×	×				×			8 – 9
×		×		×		×	×	×		×					×		13	9–10
×		×		×		×	×	×	×						×		7 – 8	5
×		×			×	×									×		5 – 7	3
	×	×		×										×	×		12–16	8

Table 4

Egg Capsule Dimensions of Species of Type B

	Capsule Dimensions in μ																																
	> average of greatest diameter																	maximum .															
	461 - 480	481 - 500	501 - 520	521 - 540	541 - 560	561 - 580	581 - 600	601 - 620	621 - 640	641 - 660	661 - 680	681 - 700	701 - 720	721 - 740	741 - 760	761 - 780	781 - 800	801 - 820	821 - 840	841 - 860	861 - 880	881 - 900	901 - 920	921 - 940	941 - 960	961 - 980	981 - 1000
.																																	
.																			<					>		.							
.<					>	.																											

Table 5

Characteristics of the Egg Masses of Species of Type C

	Months found											
	January	February	March	April	May	June	July	August	September	October	November	December
Aglaja diomedea:			×			×						
Chelidonura phocae:			×	×	×	×						
Gastropteron pacificum:	×	×	×		×	×						

Table 6

Characteristics of the Egg Masses of Species of Type C

	Capsule Dimensions in μ . minimum < average of least diameter maximum . > average of greatest diameter												Veliger Type		Days Taken	
	- 80	81 - 100	101 - 120	121 - 140	141 - 160	161 - 180	181 - 200	201 - 220	221 - 240	241 - 260	261 - 280	281 - 300	1: uninflated	2: inflated	time to hatch	appearance of veliger
Aglaja diomedea:				.		<					> .		×		8-20	18
Chelidonura phocae:				.<		> .							×		7-12	11
Gastropteron pacificum:							.<	> .					×		14-15	9-10

Table 7

Characteristics of the Egg Masses of Species of Type D

	Months found											
	January	February	March	April	May	June	July	August	September	October	November	December
Catriona aurantia:			×									
Cratena albocrusta:								×				×
Eubranchus olivaceus:					×		×	×				