The invasion ecology of *Tricellaria inopinata* into the lagoon of Venice: morphological notes on larva and ancestrula

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Abstract

The invasion ecology of *Tricellaria inopinata* in the lagoon of Venice is evaluated by adding the description of the larva and the ancestrula. The larva is similar to all columnar cheilostomate larvae, corresponding to type V of d'Hondt (1977a) = AEO/ps of Zimmer & Woollacott (1977). Observations in aquaria revealed that larvae settle a few hours after having been released. The ancestrula is rapidly fixed with two short rhizoids and is decorated by many long spines, bearing a certain resemblance to other Scrupocellariidae.

The hypothesis of human introduction of *T. inopinata* in the lagoon of Venice is considered in the light of some criteria established for other estuarine organisms, concerning the ecological, evolutionary and geographical attributes of introduced species. Special attention is paid to reproduction and dispersal mechanisms. The nomenclatural position of *T. inopinata* and *Menipea porteri* in relation to *T. occidentalis* is discussed; provisionally a species complex is postulated, whose biogeographical distribution is strongly influenced by human transport.

Keywords: Bryozoa, invasive species, ecology, larvae, biogeography.

Introduction

The invasion of *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi into the lagoon of Venice was previously described by d'Hondt & Occhipinti Ambrogi (1985) and by Occhipinti Ambrogi (1991). Some interesting ecological questions are raised by this kind of phenomenon, which is widespread in the plant and animal kingdoms all over the world (Carlton 1989).

In this paper we focus upon some relationships between the morphological attributes of the larval stage (and the ancestrula) and the ecological attributes that are generally assigned to invasive species. The aim of this study is to put together morphological, taxonomic, biogeographic and ecological knowledge in order to elucidate a case which may be a good example of human responsibility for recent changes in the distribution of bryozoans.

Material and methods

Colonies of *Tricellaria inopinata* were collected in the lagoon of Venice in July 1991 near the Hydrobiological Station of the University of Padua, at Chioggia. Selected colonies having ovicells with embryos were placed in aquaria with running sea water and kept sheltered from light overnight. The following morning water circulation was stopped, colonies were exposed to ambient light and released larvae were collected and transferred to a Petri dish with a minimum amount of sea water. The dish was then filled with a buffered fixative composed of 2 parts of 6 % glutaraldehyde and 1 part of sodium cacodylate plus 1 part of 7 % NaCl. Later the larvae were transferred to 70 % ethyl alcohol. For scanning electron microscope examination the larvae were critical point dried with liquid nitrogen, coated with gold, and examined with a scanning electron microscope (Jeol).

A control survey on the distribution of *T. inopinata* was conducted in July 1992 in a smaller number of stations (total 20 stations over the entire lagoon); samples were taken from the fouling community on the wooden piles defining the navigable canals in the northern and central sectors of the lagoon (see Occhipinti Ambrogi 1991). Colonies from fouling experimental plates were collected in the southern sector.

Results

Morphological study of the larva

The larva of *Tricellaria inopinata* is cylindrical in shape, measuring 115 to 120 μm in width. The larval diameter is smaller in the equatorial region in comparison with polar regions; the entire surface is uniformly covered by cilia; almost all its external visible part is made up by the ciliated cells of the corona; each cell is 10 to 12 μm wide at its largest part (equatorial).

An apical circular prominence ('calotte') is also covered by cilia radiating outwards with the exception of a small central region. The calotte, whose diameter is 60 μm, is separated from the cells of the corona by a marked pallial sinus. The cilia at the centre of the apical organ complex are stouter than peripheral cilia, delimiting a small non-ciliated area. The latter most probably corresponds to the non-ciliated 'cellules du centre de la calotte' described by d'Hondt (1973) in *Alcyonidium polyoum* (Hassall) (= *A. gelatinosum* (Linn.)), having a sensory function and being connected basally to a nerve ganglion. These sensory cells have been found, though with a different number of cilia (Stricker 1987), in the same place and with the same features in the larval types of several bryozoans: e.g. in the Ctenostomatida *Bowerbankia imbricata* (Adams) and *Flustrellidra hispida* (Fabricius), in the Cyclostomatida *Crisia denticulata* (Lamk.) (cf. d'Hondt 1977b, c & d), in columniform and cyphonautes cheilostomate larvae (Woollacott & Zimmer 1971, d'Hondt 1976). The two rings of ciliated cells located between the centre of the apical organ and the pallial sinus need to be studied from a cytological point of view to determine if the differences in the cilia correspond to a different cellular organization. The terms used by various authors suggest that different ultrastructures (morphology of cells, number of cilia) have been observed (Zimmer & Woollacott 1977, Stricker 1987).

A tuft of cilia, perhaps joined along a part of their length, is observable in a distal-axial position, in a depressed region of the larval surface; it is interpreted as the vibratile plume of the pyriform organ (Woollacott & Zimmer 1971, 1972).

In lateral view, the larva is asymmetric; the posterior region is higher and more rounded than the anterior. The internal sac occupies almost all the volume of the inferior region and its opening is situated in the rounded part. The neck cells of the internal sac are not ciliated as in all other bryozoan larvae (d'Hondt 1979). The opening of the internal sac appears as a bare area with a diameter of about 50 µm, encompassing a transverse elongated groove, 35 µm long, corresponding to the opening through which the evagination of the larval sac occurs at the onset of metamorphosis.

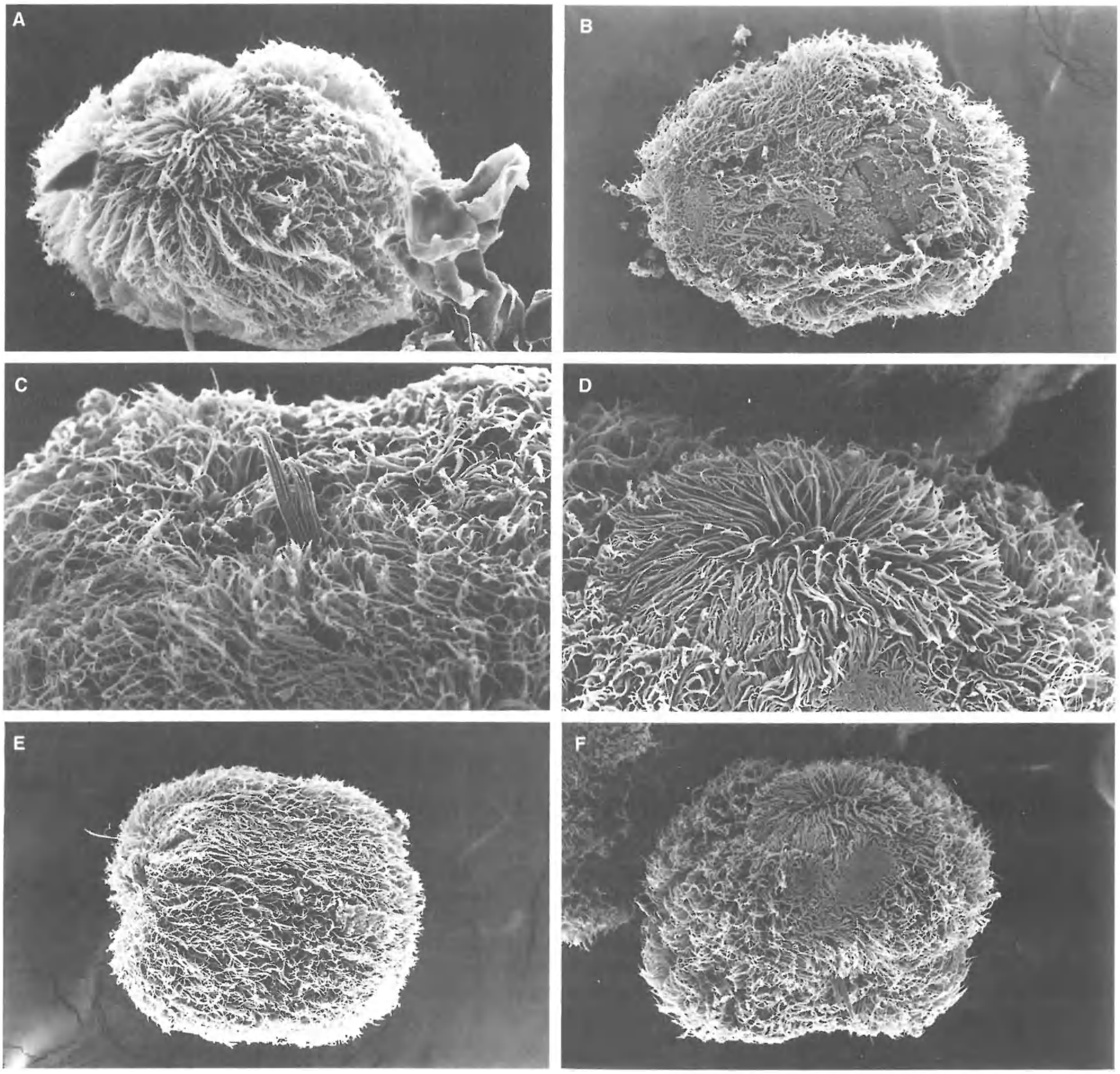

Figure 1.
Scanning electron microscopy of larvae of *Tricellaria inopinata*.
A, view from above, showing the apical circular prominence ('calotte'), ×850;
B, frontal view, opening of the internal sac, ×670;
C, pyriform organ, ×1950;
D, details of the apical circular prominence, ×1830;
E, lateral view, ×610;
F, larva in toto, showing the pyriform organ and the 'calotte', ×730.

In conclusion, the larva of *T. inopinata* corresponds to the larval type described for all Cheilostomatida Neocheilostomina with an erect colony = type Va of the classification by d'Hondt (1977a) ('larves de Cheilostomes de type columniforme, à sillon palléal symétrique et superficiel') and is equivalent to type AEO/ps of Zimmer & Woollacott (1977) ('coronate larvae with expanded coronas that are aboral equatorial and oral (AEO) in position and with small pallial sinuses (ps)').

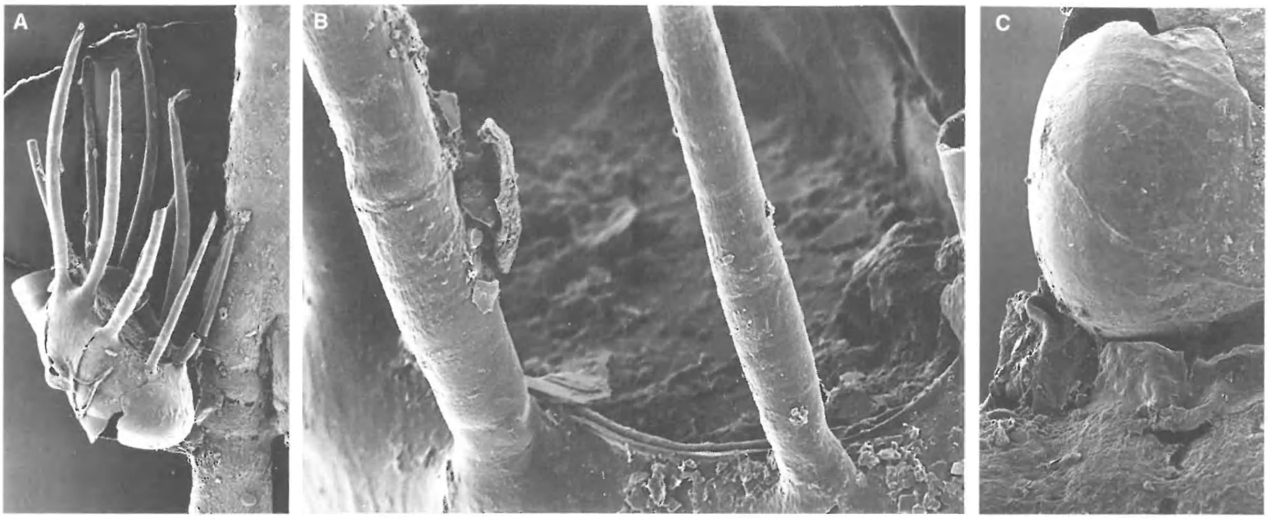

Figure 2.
Scanning electron microscopy of ancestrula of *Tricellaria inopinata*.
A, in toto, ×200;
B, details of spines, ×1275;
C, fixation peduncle, ×650.

The ancestrula

The ancestrula is attached to the substrate by means of two short rhizoids 40-45 µm thick and 45-55 µm long; it is cylindrical in shape, flattened on the frontal face, rounded proximally, truncated distally, 280 µm long, and with a diameter of 100 µm. Its frontal face bears a membranous area 175 µm in length limited by a thin cryptocyst (20 µm wide). The opesia is surrounded by ten long slender spines: one distal, one proximal and four lateral pairs. The latter have unequal diameters, the three distal being thicker with a basal section of 20 µm versus 10-12 µm for the proximal pair. All of them are finely annulate, with some marked growth rings. The maximum length of spines is 320 µm. The proximal, rounded portion of the ancestrula has a thin transverse suture, dividing it into two half-cylinders, one in the upper part and one in the lower. The rhizoids originate from the most convex part of the inferior face of the ancestrula, whereas the first zooidal bud is from the superior blunt face in the distal portion.

Larval behaviour

From observations of the material placed in aquaria we can assert that the liberation of larvae was enhanced by stopping the water current. In still water, the larvae swim actively for a few hours and tend to attach themselves onto the aquaria glass walls where metamorphosis occurs within a few minutes.

Present-day distribution in the lagoon of Venice

The distribution of *T. inopinata* in the lagoon, in July 1992, suggests that it is still in a state of vigorous colonization, having been found in 80 % of the stations examined, with colonies densely ovicellate.

The species is still absent from the inner northern part of the lagoon, which receives large freshwater inputs from the river Dese and is also scantily represented in the vicinity of the lagoon mouth at the Malamocco opening to the Adriatic Sea. Outside the dyke protecting the mouth, it is totally absent. In this open sea situation, on the same substratum at the same tidal level, it is replaced by *Scrupocellaria reptans* (Linn.) and *S. bertholletii* (Audouin).

As far as competition with other species is concerned, we confirm that *T. inopinata* prefers an intertidal position among clumps of mussels, or under a canopy of green algae (*Ulva* and *Enteromorpha*), whereas other species, such as *Bugula neritina* (Linn.), are abundant at the lower tidal level. Moreover, in many stations *T. inopinata* was the only bryozoan species found, overgrowing other organisms present, e.g. sponges, hydroids, muddy tubes of amphipods, ascidians. When present with other Bryozoa, it was growing on a *Bugula neritina* colony in one case, on *Cryptosula pallasiana* (Moll) in another.

The ability of *T. inopinata* to colonize is shown by the presence of colonies in all stages of development: dense aggregations of ancestrulae on dead branches of the hydrozoan *Tubularia crocea* (Agassiz), young colonies growing on other organism (sponges, ascidians and other Bryozoa), and dense, mature colonies with ovicells and embryos.

Discussion

Larval development traits are fundamental in determining life-history strategies of marine invertebrates (Roughgarden *et al.* 1988, Boero 1990), and this is particularly true for invasive species, whose ability to occupy space largely depends on the availability of their propagules. The larvae of *Tricellaria inopinata*, like those of most Cheilostomatida, are lecithotrophic with a short pelagic existence, with some degree of brood protection in the ovicells and are produced in high numbers by each brooding zooid. The low dispersal potential of lecithotrophic larvae is thus not very effective in long-range transportation of the species. On the other hand, species colonizing brackish environments commonly have a short pelagic larval period, which indicates that there must be alternative explanations for their dispersal from one lagoon to the other (Strathmann 1982, Scheltema 1986).

The production of larvae occurs over a long period of time and this could help the species maintain a continuously recruiting population in the lagoon, compared to other Bryozoa, known to settle only during a shorter period.

The hypothesis of human introduction of *T. inopinata* into the lagoon of Venice was originally proposed by d'Hondt & Occhipinti Ambrogi (1985). We can now test this hypothesis against some criteria recently proposed for recognizing introduced species in an estuarine area, using also information on larval type. Chapman & Carlton (1991) examined the case of the peracaridan crustacean *Synidotea laevidorsalis* (Miers) in San Francisco Bay, where the species was described as early as the last century (Benedict 1897), and concluded that it was introduced into the bay from Asia.

The ecological, geographical, and evolutionary attributes defined for an introduced peracaridan crustacean can be examined to see if they match the characters of the invasive bryozoan *T. inopinata*. This can help in deriving some general statements about human introductions and also to elucidate some questions about the origin of *T. inopinata*.

These attributes can be either provincial (within a biogeographic realm) or global (characteristic of the species over the entire geographical range).

Provincial

Criterion 1: *Appearance in local regions where not previously found*: this criterion fits precisely the case of *T. inopinata* in the lagoon of Venice, where the species first appeared in 1982.

Criterion 2: *Initial expansion of local range subsequent to introduction*: this criterion was satisfied by the rapid spread of the species from a few stations into virtually all the lagoon, in the years 1982-1992.

Criterion 3: *Association with human mechanisms of dispersal*: individual colonies of *T. inopinata* should have remained associated with the supposed means of introduction in the lagoon, e.g. ship hulls or oyster and clam cultivation, but this could not be investigated.

Criterion 4: *Association with other introduced species*: no such evidence has been gathered for our species. Although many introduced species are known in the lagoon of Venice, none seems to be directly associated with *T. inopinata*.

Criterion 5: *Prevalence or restriction to new or artificial environments*: this is a distinctive character of this fouling species.

Criterion 6: *Relatively restricted distribution on a continent compared to distribution of native species*: in effect, as far as we know, no *Tricellaria* species has been recorded from Mediterranean lagoons.

Global

Criterion 7: *Isolated populations on different continents or in isolated oceans; in other terms, widespread disjunct geographic distribution*: to discuss this point we must go through the nomenclatural discussion below.

Criterion 8: *Insufficient active dispersal capabilities to account for the observed distribution of the species*: as discussed above, the larvae of *Tricellaria* have a very limited potential for dispersal, not to mention the possibility of trans-oceanic transport.

Criterion 9: *Insufficient passive dispersal mechanisms to account for the observed distribution of the species*: it is extremely unlikely that any species of bryozoan could be transported by such a mechanism as far as Australia or to Venice from the northern Pacific coast.

Criterion 10: *Exotic evolutionary origin*: the species closest to *T. inopinata* occur in different biogeographic provinces.

The systematic status of Tricellaria inopinata

Gordon & Mawatari (1992) considered *T. inopinata* to be a junior synonym of *T. occidentalis* (Trask, 1853). This synonymy was not evident from comparison of our material with that of unknown origin loaned in 1983 by John and Dorothy Soule (Allan Hancock Foundation) (cf. d'Hondt & Occhipinti Ambrogi 1985). The photograph published by Gordon & Mawatari (1992) cannot lead us to reject the hypothesis of synonymy, although a direct comparison of a larger number of specimens should be performed to settle the question. According to Gordon & Mawatari (1992) and to Mawatari (1951), *T. occidentalis* has a wide variability in the morphology of the scutum, and the ovicells seem to have a proportionately more elongated shape compared to specimens mentioned. The lateral avicularia are larger in *T. inopinata* than in *T. occidentalis* and the pores of the ovicells are placed somewhat differently in the two species: in an arc that is convex toward the distal part in *T. inopinata*, convex toward the proximal part in *T. occidentalis*. Moreover in *T. inopinata* lateral pores are present very close to the orifice, but not in *T. occidentalis*.

Mawatari (1951) illustrates the larva of *T. occidentalis*, which corresponds also to the typical cheilostomate larva, without any specialization.

McGillivray (1889) briefly described a new species of Scrupocellariidae from Australia, as *Menipea porteri*. Its generic status is not determinable from his description and perhaps for this reason it was not included in Harmer's (1923) monograph of Cellularines. According to P.L. Cook (pers. comm.), this species, which has been found again in Australia, has been synonymized with *T. occidentalis* by Gordon & Mawatari (1992). An illustration of *M. porteri* McGillivray, coupled with a redescription of the type, would be welcome to confirm the stated synonymy.

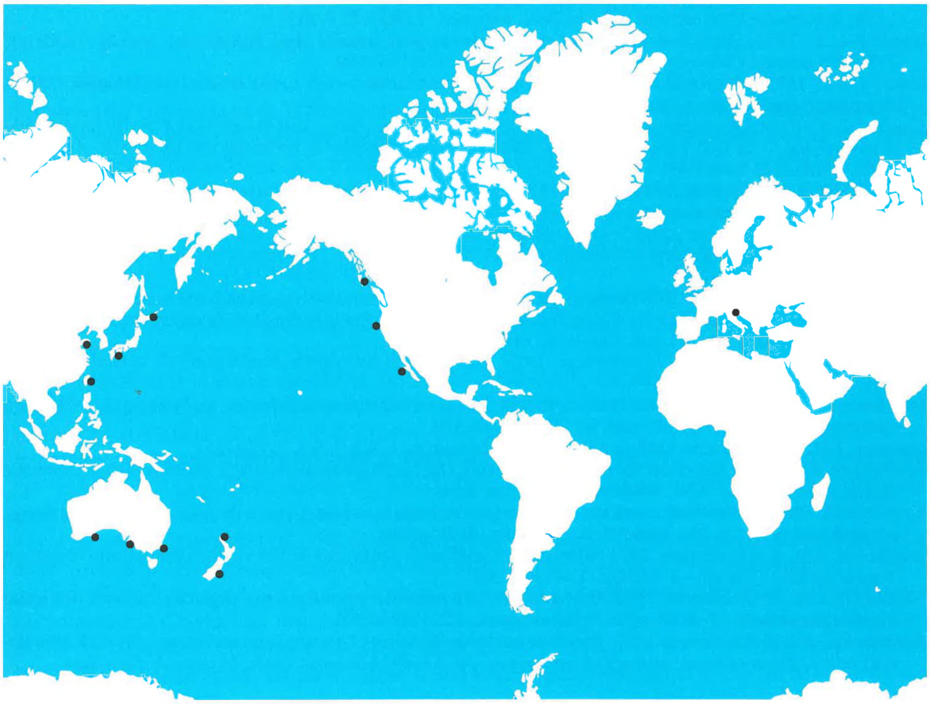

Figure 3.
Distribution of the *Tricellaria occidentalis* complex.

While waiting for more evidence on the taxonomic status of the three species, we can provisionally accept the idea that the *T. occidentalis* complex has a very puzzling distribution. Starting from that indicated by Mawatari (1951), it ranges from British Columbia to Southern California and from the North of Japan to Taiwan. It was later documented in Auckland (New Zealand) fouling communities (Harger 1964), and most likely at Lyttelton (New Zealand) (Skerman 1958). It is also present in Australia (Brock 1985). The known distribution is shown in Figure 3.

Gordon & Mawatari (1992) concluded that *T. occidentalis* was probably transported from the Pacific coasts of the US to Asia and Australasia and are surprised by its late arrival to Europe, where it is known only from the lagoon of Venice. In our opinion it might have been transported here together with some fisheries products (e.g. oysters or clam spat) whose cultivation is widespread in the lagoon.

Another particular feature of the Venice populations is their restriction to the lagoon environment, whereas no indication of preference for brackish or fully saline waters is reported in literature. We conclude that better knowledge of the ecology of the species could help to elucidate the taxonomic position of the species complex.

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