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Asexually Generated Propagules from Subtidal Sessile Benthic Organisms

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Abstract

A morphological study of planktonic propagules of sessile benthos is presented. In an available collection of material collected by sediment traps along the Salento coast of Gulf of Taranto, asexually generated propagules were the 80.2% of collected items (with 11.5% of specialised propagules and 88.5% of simple fragments), suggesting an unexpected prominent role of asexual reproduction in propagule supply for benthic communities. The morphology of "specialised propagules" shows a body plan that is present in both algae and animals: a central body with radiating projections. This design probably improves both flotation and settling. Unspecialised asexual propagules (simple fragments, viable) of colonial organisms are the bulk of collected material. They are usually overlooked as “detritus” in most plankton ecology research, with loss of potentially important information for benthos ecology.

Keywords: Benthos Dispersal; Community Dynamics; Propagules; Meroplankton

Introduction

The distribution of benthic species is influenced by the mobility of their planktonic stages, acting as propagules. Wide distributions, thus, should be correlated with great larval mobility, usually achieved by swimming structures such as cilia or appendages, and/or with the duration of larval life (the teleplanic strategy proposed by Scheltema) [1]. However, high vagility of larvae and wide distribution of species are not correlated (see [2]) for a case study on the Hydrozoa). An explanation might be that most subtidal benthic organisms are modular and tend to “lose pieces” in consequence of wave hydro-dynamism. The fragmentation represents a damage for individual organisms, but it has not evident consequences for a colony. These fragments could be responsible of the species dispersal and genetic flow more than the tiny and short living larvae. Jackson [3], Jackson & Coates [4], Van Den Hoek [5], Jokiel [6], Maldonato & Uriz, Bavestrello et al. [7], Walters et al. [8] and Fraser et al. [9] among others, demonstrated that dispersal and recruitment might occur also throughout ways alternative to larvae.

Marine benthic, modular organisms (animal colonies and algal thalli) produce several types of morphs adapted to a pelagic life for varied periods before settlement on proper substrata. These propagules are originated either sexually (e.g., seeds, zygotes, embryos, larvae) or asexually (e.g., spores, fragments, gemmules, statoblasts and even medusae, these last being sexual individuals deriving by the asexual budding of colonial polyps).

Fanelli and Moscatello & Belmonte [10,11] evaluated as predominant the presence of asexually produced propagules in the whole plankton community sampled with a sediment trap and respectively a common net in subtidal sites. Bavestrello, et al. [7] described clearly the birth of a new colony of *Hydractinia pruvoti* originating by the settlement of fragments detached from a mother colony subjected to wave action. Activities that cause fragmentation can significantly facilitate the spread of invasive Non Indigenous Species as *Didemnum vexillum* [12]. In-water cleaning of biofouling and dredging are likely expediting the spread of this invasive species unless biofouling can be contained and removed from the water. Studies on planktonic asexual propagules are, however, so rare and not generalised that a long distance island hopping of the isopod *Septemserolis septemcarinata* (without "dispersal stages") has been treated as a sort of mystery [13]. It is possible, unfortunately, that this lacking of information could be due to both the low interest that these forms have for plankton specialists and to the low interest that benthos specialists have for plankton.

The present study stems from the PhD thesis of Fanelli [10] devoted to quantify the importance of asexually generated propagules in the coastal benthos. We used that collected material to describe morphological details of specialized asexual propagules, and those useful to consider as propagules also fragments.

Material and Methods

Meroplankton was collected at two sites [10] about 15 km apart from each other, at shallow depth (about 5 m) along the Apulia coast (Salento Peninsula, Gulf of Taranto, Southern Italy, Mediterranean Sea; Figure 1), from 1992 to 1993. Samples were taken by sediment traps (2 for each site, arranged according to Yund, et al.) [14], for 28 two-week collecting-periods. The typical meroplankton (i.e., eggs and larvae), plus any other fragment of colonies or thalli (i.e., the propagules of sessile benthic organisms), were separated and counted under a stereomicroscope. Specialised and simple fragments were distinguished; not all simple fragments, however, were labelled as propagules; in fact, some of them were in an evident state of decomposition or were damaged, thus being considered as not viable ("detritus"). Propagule identification at species level was difficult in some cases; unidentified propagules were given descriptive names. Photographs of propagule types were realized under a compound microscope.

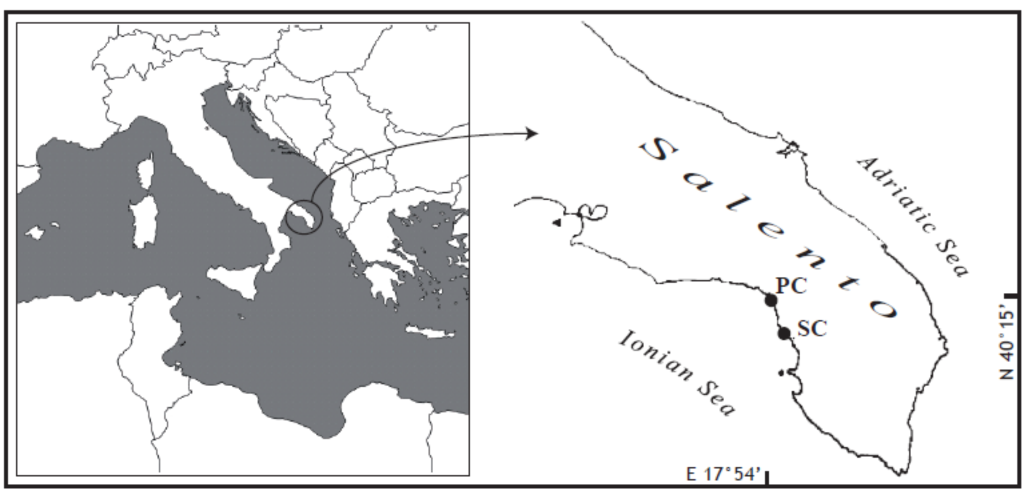

Figure 1: Area of investigation. Sampling sites (PC= Porto Cesareo, SC=Santa Caterina) along the Salento Peninsula coast of Gulf of Taranto (North Ionian Sea, Mediterranean).

Some specialised propagules were analysed by SEM to study in detail the morphology of their appendage tips. For this scope, propagules were pre-fixed in 5% neutralised (pH 7.3) formalin for 3-5 days. After pre-fixation, propagules were rinsed in filtered (0.45 μm) sea water for 24 h, dehydrated in an ethanol series, slowly dried at 38°C for 48 h, mounted on stubs and sputtered with gold. Procedure is reported in Belmonte [15].

Results

Sediment traps of the two considered sites collected organisms belonging to a total of 19 different Phyla (Table 1). Only the 19.2% of total collected propagules of sessile organisms were of sexual origin (eggs or larvae). The remaining 80.8% were composed by forms asexually generated by modular animals and algae, represented by a wide array of both simple (88.5%) and specialised (11.5%) forms (Table 1).

Sexual Propagules		
... of colonial animals	**... of individual animals**	
Hydrozoa planulae	Polychaeta larvae	
Bryozoa cyphonautes	Bivalvia veliger	
Ascidiacea juveniles	Cirripedia nauplius	
Asexual Propagules		
Chlorophyceae Fragments	**Hydroid Fragments**	**Specialized Propagules**
Anadyomene stellata	*Aglaophenia octodonta*	*Sphacelaria fusca* (brown alga)
Caulerpa sp.	*Aglaophenia* sp.	*Sphacelaria cirrhosa* (brown alga)
Cladophora prolifera	*Amphinema* sp.	*Jania* cfr. *adherens* (red alga)
Cladophora sp.	Campanularidae sp.	*Alectona millari* (sponge)
Enteromorpha prolifera	*Clytia haemispherica*	*Halecium pusillum* (hydroid)
Valonia sp.	*Clytia linearis*	*Perophora* sp. ? (ascidian)
	Clytia sp.	Undetermined Rhodophyta
Phaeophyceae Fragments	*Coryne pusilla*	
Cystoseira sp.	*Dynamena* sp.	
Dictyota dichotoma	*Eudendrium* sp.	
Ectocarpus sp.	Haleciidae sp.	
Halopteris filicina	*Halecium pusillum*	
	Halecium sp.1	
Rhodophyceae Fragments	*Halecium* sp.2	
Borgeseniella fruticulosa	*Kirchempaueria echinulata*	
Callithamnion corymbosum	*Kirchempaueria* sp.	
Callithamnion tenuissimum	*Obelia* sp.	
Callithamnion cordatum	*Orthopyxis* sp.	
Ceramium ciliatum var. *ciliatum*	*Plumularia setacea*	
Ceramium ordinatum	Plumularidae sp.	
Ceramium sp.	*Scandia gigas*	
Chondria capillaris	*Sertularella* sp.	
Chondria sp.	*Ventromma halecioides*	
Crouania attenuata	Undeterm. fragment (polyps)	
Gelidiacea ind.	Undeterm. fragment (hydrorhizae)	
Gryffithsia sp.		
Hypoglossum hypoglossoides	**Bryozoan Fragments**	
Laurencia obtusa	*Amathia lendigera*	
Laurencia sp.	*Amathia semiconvoluta*	
Polysiphonia scopulorum	*Beania hirtissima*	
Polysiphonia sp.	*Beania mirabilis*	
Stylonema alsidii	*Beania* sp.	
Wrangelia penicillata	*Chorizopora brongniarti*	
	Crisia sp.	
	Rosseliana rosselii	
	Undetermined fragments	

Table 1: Sexual and asexual propagules collected by sediment traps at two sites of Salento coast of Gulf of Taranto (North Ionian Sea, Mediterranean) [10].

Sexually-Generated Propagules

Both larvae of individual and modular sessile organisms were present all year round. Larvae of solitary species were collected with an annual average of 162 specimens dm^{-2} day^{-1}. The most abundant were Bivalvia veligers that were present all year round; Cirripedia nauplii were present only during summer, and larvae of sessile Polychaeta (e.g., Serpulidae) were present only in June [10]. Larvae of colonial species were sensibly less abundant than those of solitary species. Both Hydrozoa planulae and Bryozoa cyphonautes seldom were found.

Asexually-Generated Propagules

Both specialised and unspecialised fragments were present (Table 1).

Specialised propagules: Specialised asexual propagules were present throughout the year, with lower concentrations in autumn-winter, and maximal in June. The annual flow average numbered 80 items dm^{-2} day^{-1}.

Specialised propagules were referred to seven species of both algae and animals. They had similar morphologies (a more or less developed central body, with appendages), but they can be distinguished in spherical and flattened:

- **Spherical with Appendages** (Figure 2): This category comprises two Phaeophyceae, [15,16] (Figure 2a), one Porifera [17] (Figure 2b), one Hydrozoa [18] (Figure 2c) and an undetermined Rhodophycea (Figure 2e). The Rhodophycea propagule was found also on attached thalli and is similar to the adhesive, flattened holdfasts of *Jania* (a red alga) (see below, point b). Specialised propagules of *Sphacelaria* spp. were present all year round, but particularly in spring-summer period (from April to August). *A. millari* propagules were present from August to December. Propagules of *H. pusillum* were found from October to December. Some propagules of undetermined Rhodophyta were found only in September.

- **Flattened with Appendages**: The adhesive holdfast of *Jania* cfr. *adhaerens* (Figure 2d), found in the water column only while still attached to thallus fragments, could be included in this category. Also in this case, some propagules were found in September.

Scanning Electron Microscopy (SEM) analysis revealed that the tips of the appendages of specialised propagules were not similar to the other parts of their bodies. Surface expansions (Figure 3a), swollen structures probably corresponding to glandular prominences (Figure 3b), and double-lamina expansions resembling sucker-like structures (Figure 3c), were typical features of propagule tips.

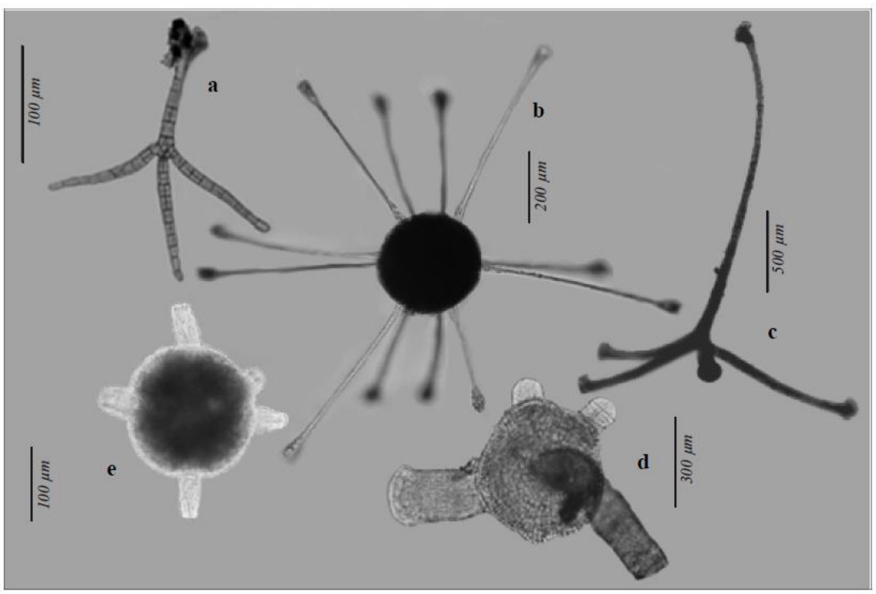

Figure 2: Asexual specialised planktonic propagules with convergent architectures: spherical with appendages: a) *Sphacelaria fusca* and *S. cirrhosa*, (Phaeophyta); b) *Alectona millari* (Porifera); c) *Halecium pusillum* (Cnidaria); d) undetermined Rhodophyta ;- flattened with appendages: e) *Jania* cfr *adhaerens* (Rhodophyta).

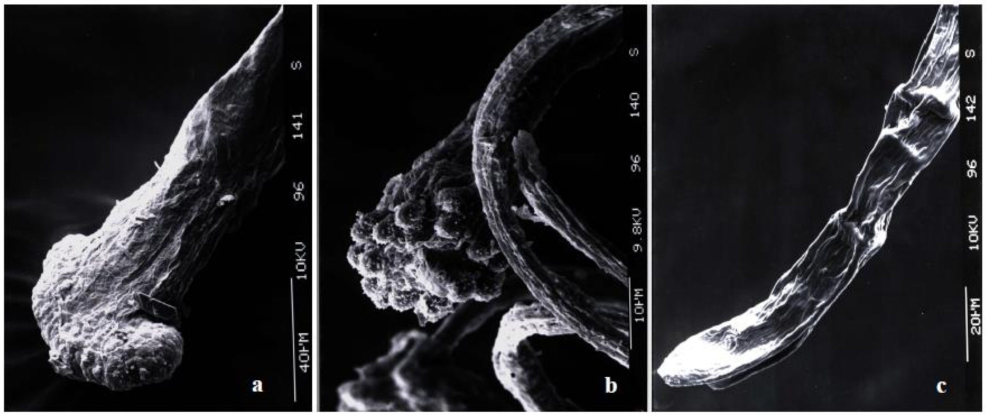

Figure 3: Observations by SE Microscopy of appendage tips of: a) *Halecium pusillum* (Cnidaria), b) *Alectona millari* (Porifera), c) *Sphacelaria* sp. (Phaeophyta).

Unspecialised propagules (fragments): Unspecialised fragments of colonial (modular) organisms were very abundant with an annual average of 617 units dm^{-2} day^{-1}. They were classified (Tab. 1) as Hydrozoa (25 species), Bryozoa (9 species), Rhodophyceae (19 species), Chlorophyceae (6 species), and Phaeophyceae (4 species). Hydrozoa fragments (Figure 4) were found all year round, Bryozoa fragments were limited to the summer. Algae fragments were present all year round.

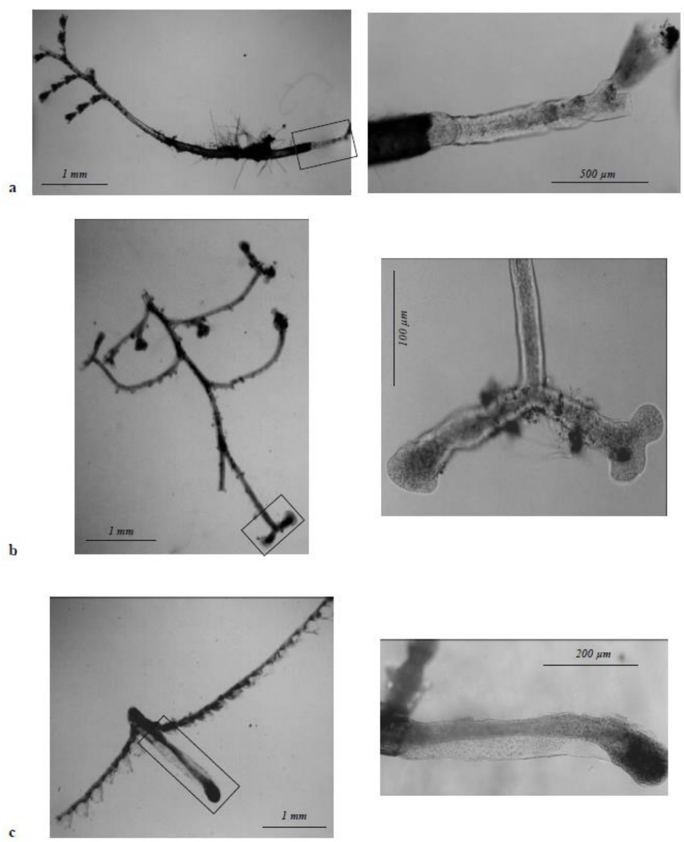

Figure 4: Examples of simple fragments having regeneration: a) *Aglaophaenia tubiformis*, b) *Plumularia setacea*, c) *Aglaophenia* sp. In a) regeneration occurs in breaking-zone from the mother colony, in b) and c) regeneration occurs in a different part.

Discussion

Yund, et al. [14] warned about the efficiency of tubular sediment-traps which, in fact, can be selective for certain propagule sizes and/or types. In spite of the possibly partial picture of propagule diversity and abundance, however, the sampling technique here considered allowed a continuous collection that is not possible by net tows. This led to the collection of a vast array of propagule types. The small size of larvae (sexual propagules) of modular organisms, could also affect the result of a sediment trap collection since they could have been lost during sample filtration through 50 µm meshes. In any case, the study of Moscatello & Belmonte [11] confirms that also in collections performed with plankton net, larvae are less abundant than asexually generated propagules.

Even if (due to methodology) the diversity and abundance of sexual propagules were underestimated, it is evident from the study that asexual propagules are a quantitatively important component in near bottom water column and, possibly, in life history dynamics of benthos.

The comparison between sexual and asexual propagule abundance in the water column, the wide diffusion of asexual propagule production in many species, and their dispersal and settlement ability (see Tab. 2), suggest that probably the distribution of many species could heavily rely upon strategies alternative to larvae. In this frame, colonial organisms appear as favourite, against individual organisms, in loosing pieces without negative consequences, simply for architectural reasons.

Phylum - Species	Specialised propagules	Dispersal range	Sources
Phaeophyta			
Sphacelaria fusca	Floating radiate fragments	L	Santelices [16]
Sphacelaria cirrosa	" " "	L	" "
Rhodophyta			
Acanthophora najadiformis	Sinking elongate	S	Cecere, et al. [19]
Alsidium corallinum	" "	S	Cecere, et al. [20]
Centroceras clavulatum	" "	S	Lipkin [21]
Polysiphonia ferulacea	" "	S	Kapraun [22]
Chondria crassicaulis	Detatchable buds/knobs	L	Okamura [23]
Decaulion levringii	" "	L	Huisman & Kraft [24]
Anisoschizus propaguli	" "	L	"
Jania sp.	Floating radiate fragments	L	present paper
Porifera			
Tethya spp.	Detatchable buds/knobs	L	Bergquist [25]
Aaptos aaptos	" "		"
Polymastia granulosa	" "	L	Battershill & Bergquist [26]
Polymastia sp.	" "	L	" "
Chondrilla nucula	Rolling spheres	L	Boero, et al. [27]
Polymastia spp.	" "	L	Battershill & Bergquist, [26]
Alectona millari	Floating radiate fragments	L	Garrone [17]
Thoosa spp.	" " "	L	Bergquist [25]
Cnidaria			
Acropora cervicornis	Sinking radiate	S	Highsmith [28]
Sarsia tubulosa	Rolling spheres	L	Clare, et al., [29]
Tubularia larynx	" "	L	" "
Goniopora stokesy	" "	L	Rosen & Taylor [30]
Halecium pusillum	Floating radiate fragments	L	Huvé, [18]
Halecium sessile	" " "	L	Billard, [31]
Ventromma halecioides	" " "	L	" "
Obelia longissima	" " "	L	Allman (1871)
Obelia geniculata	" " "	L	Billard [31]
Obelia dichotoma	" " "	L	Leloup [32]
Obelia spinulosa	" " "	L	" "

Campanulina hincksi	" " "	L	Leloup [33]
Leptoscyphus tenuis	" " "	L	Billard [31]
Tubularia crocea	Autotomized parts	L	Rungger [34]
Zelounies estrambordi	" "	L	Gravier-Bonnet [35]
Campanulariidae sp.	" "	L	PATI, unpublished
Favia favus	" "	L	Silen, et al. [36]
Oculina patagonica	" "	L	" "
Phoronida			
Phoronis sp.	Autotomized parts	L	Silen [37]
Bryozoa			
Electra pilosa	Rolling spheres	L	Ryland & Hayward [38]
Urochordata			
Polyzoa vesiculiphora	Detatchable buds/knobs	L	MUKAI, et al. [39]
Perophora japonica	Floating radiate fragments	L	MUKAI, et al. [39]
L: long range dispersal			
S: short range dispersal			

Table 2: Specialised asexual meroplankton produced by colonial benthic organisms (literature data).

Specialised asexual propagules are different from simple colonial fragments. Fragments, in fact, are just pieces that detach from mother colonies. Specialised asexual propagules, on the contrary, appear as the result of a specific adaptation to the pelagic life; they break off in a predetermined way and disperse in the pelagos before to settle. According to the literature almost every group of algae and modular animals has some members known to produce specialised asexual propagules, whose ability settlement is widely demonstrated (Table 2).

Asexual specialised propagules can have different morphologies (rounded, elongate, radiate, etc.) and, as a consequence, different dispersal possibilities (Table 2). Those ones that tend to sink, for example, settle within or near the source population, whereas an enhanced floating ability due to an adaptation to pelagic life, could correspond to a long-range dispersal. The floatability (and the dispersal) is favoured by radial appendages branching from a central body (Figure 2); in addition this particular morphology, enriched with adhesive terminations, enables an efficient positioning when touching the substratum and seems to be a compromise between optimal floating and efficient settling, apparently two contradictory requirements. Morphologically similar propagules are produced by species referred to both algae and animals: this suggests that the selective pressure (that is, the necessity of both effective dispersal and settlement) acting on sessile modular benthic organisms is so strict that propagules have the same basic architecture in representatives of different kingdoms [40].

The microstructures of the tips of radial appendages, observed by SEM, probably represent adhesive devices when they touch a substrate, so increasing the recruitment success of specialised propagules in respect to that of unspecialised ones (Figure 2). However, histological studies on propagule tips, to our knowledge, are missing, and this hypothesis is still to be tested, even if the importance of this adhesive device has been already demonstrated [41].

Also simple fragments (pieces of animal colonies or algal thalli which detach randomly) can have an important ecological role for species dispersal via water column. Their role in recruitment patterns and processes was quantified *in situ* for some species only [26,28,42].

The re-settlement ability of fragments from modular organisms is well known: in laboratory experiments, colonies and thalli can be reared by simply breaking pieces and have they settled on experimental surfaces [43]. Furthermore, the presence of regenerating parts in many of the fragments collected in this study made evident their ability to survive also during floating and before successive settlement (Figure 4).

Conclusion

Supply-side ecology [44] has been a successful interpretation of recruitment and connectivity between adjacent benthic populations. However, this aspect of community dynamics refers exclusively to sexually originated propagules (larvae) of individual organisms. Larvae of colonial organisms are generally not considered as fundamental in this framework. Some indications in agreement with such a point of view, show that for modular organisms, larvae are greatly outnumbered in importance by both simple and specialised asexual propagules. Larvae, in fact, are usually produced during limited periods, are tiny, and are not able to cross long distances. Colonial fragments, on the contrary, could detach during most of the year, and can persist in the pelagos. In addition, some colonial organisms evolved the possibility to produce specialized asexual propagules, thus demonstrating how the large scale dispersal relies also on specially evolved adaptations.

The present study wants to encourage further investigations about the ecology and biology of planktonic propagules, especially regarding:

- Seasonality of propagule production and hydrodynamics affectivity on their dispersal. Abundances of both sexually- and asexually-originated propagules of clonal organisms seem to be lower in winter than in summer. This can be the result of lower colony fragmentation, notwithstanding the strong wave movements, due to reduced growth, and/or to lower sexual reproduction in the cold season. The higher turbulence of winter months, however, might interfere with propagule capture by sediment traps, keeping them in the water column;
- Role of resting stages as planktonic asexual propagules during hard environmental conditions; being resting forms [45,46] they might represent, therefore, a further escape strategy of benthic species from benthos to plankton;
- Possible interactions of asexual propagule on planktonic communities, for example in terms of competition for food. It is reported that some propagules are able also to feed during their planktonic life.

It has been highlighted that propagule dispersal of marine organisms occurs at a wide range of spatial scales. This phenomenon has important implication for marine community processes [47] and consequentially, for their management and conservation [48].

The disregarding of asexually generated propagules probably causes a great loss in the explanatory power of studies on the processes leading to community persistence and development, connectivity, and on the relevant parameters considered in life-history studies.

References

1. Scheltema RS (1986) On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. Bull Mar Sci 39(2): 290-322.
2. Boero F, Bouillon J (1993) Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria). Biol J Linn Soc 48(3): 239-266.
3. Jackson JBC (1986) Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. Bull Mar Sci 39(2): 588-606.
4. Jackson JBC, Coates AG (1986) Life cycles and evolution of clonal (modular) animals. Phil Trans R Soc B 313(1159): 7-22.
5. Van Den Hoek C (1987) The possible significance of long-range dispersal for the biogeography of seaweeds. Helgol Wiss Meeresunters 41: 261-272.
6. Jokiel PL (1989) Rafting of reef corals and other organisms at Kwajalein Atoll. Mar Biol 101(4): 483-493.
7. Bavestrello G, Puce S, Cerrano C, Castellano L, Arillo A (2000) Water movement activating fragmentation: a new dispersal strategy for hydractiniid hydroids. J Mar Biol Ass 80: 361-362.
8. Walters LJ, Smith CM, Coyer JA, Hunter CL, Beach KS, et al. (2002) Asexual propagation in the coral reef macroalga Halimeda (Chlorophyta, Bryopsidales): production, dispersal and attachment of small fragments. J Exp Mar Biol Ecol 278: 47-65.
9. Fraser CI, Nikula R, Waters JM (2011) Oceanic rafting by a coastal community. Proc Biol Sci 278(1706): 649-655.
10. Fanelli G (1995) Development of hard substrate biocenosis in highly stressed marine environments. PhD Thesis, University of Lecce, pp: 170.
11. Moscatello S, Belmonte G (2007) The plankton of a shallow submarine cave ('Grotta di Ciolo', Salento Peninsula, SE Italy). Mar Ecol 28(S1): 47-59.
12. Morris JA, Carman MR (2012) Fragment reattachment, reproductive status, and health indicators of the invasive colonial tunicate Didemnum vexillum with implications for dispersal. Biological Invasions 14(10): 2133-2140.
13. Leese F, Agrawal S, Held C (2010) Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. Naturwissenschaften 97(6): 583-594.
14. Yund PO, Gaines SD, Bertness MD (1991) Cylindrical tube traps for larval sampling. Limnol Oceanogr 36(6): 1167-1177.

15. Belmonte G (1998) The egg morphology of 7 Acartiidae species: a preliminary survey of the ootaxonomy of calanoids. J Mar Sys 15(1-4): 35-39.

16. Santelices B (1990) Patterns of reproduction, dispersal, and recruitment in seaweeds. Oceanogr Mar Biol Ann Rev 28: 177-276.

17. Garrone R (1974) Ultrastructure of a planktonic "gemmule army" of Clionidae sponge. Arch Anat Microsc 63: 163-182.

18. Huvé P (1955) Sur des propagules planctoniques de l'hydroide Halecium pusillum (Sars). Bull Inst Océanogr Monaco 1064: 1-11.

19. Cecere E, Perrone C, Petrocelli A (1994) Acanthophora najadiformis (Ceramiales, Rhodophyta) in the Gulf of Taranto. Giorn Bot It 128: 1082-1084.

20. Cecere E, Petrocelli A, Saracino OD (1995) Observations on the biological cycle of Alsidium corallinum (Rhodophyta, Ceramiales) in the Mar Grande of Taranto. Giorn Bot It 129: 1267-1269.

21. Lipkin Y (1977) Centroceras, the 'missile'-launching marine red alga. Nature 270: 48-49.

22. Kapraun DF (1977) Asexual propagules in the life history of Polysiphonia ferulacea (Rhodophyta, Ceramiales). Phycologia 16(4): 417-426.

23. Okamura K (1902) On the vegetative multiplication of Chondria crassicaulis Harv. and its systematic position. Bot Mag 17: 1-5.

24. Huisman JM, Kraft GT (1982) Decaulion gen. nov. And Anisoschizus gentile nov. (Ceramiaceae, Ceramiales), two new propagule-forming red algae from Southern Australia. J Phycol 18(2): 177-192.

25. Bergquist PR (1978) Sponges. University of California Press, pp: 268.

26. Battershill CN, Bergquist PR (1985) The influence of storms on asexual reproduction, recruitment, and survivorship of sponges. 3rd Internat. Sponge Conf. Paris, pp: 397-403.

27. Boero F, Fanelli G, Geraci S (1993) Desertification and decolonization in coastal environment: a model of development of biocenosis. Mem Soc Tic Sci Nat 4: 219-228.

28. Highsmith RC (1982) Reproduction by fragmentation in corals. Mar Ecol Prog Ser 7: 207-226.

29. Clare J, Jones D, O'sullivan AJ (1971) On the occurrence of detached spherical colonies of the hydroids Sarsia tubulosa and Tubularia larynx in Morecambe Bay. J Mar Biol Assoc UK 51(2): 495-503.

30. Rosen BR, Taylor JD (1969) Reef coral from Aldabra: new mode of reproduction. Science 166(3901): 119-121.

31. Billard A (1904) Contribution a l'étude des hydroides. Ann Sci Nat Zool 20: 1-251.

32. Leloup E (1932a) Temporary pelagic life in some hydropolypes of the genus Obelia. Bull Mus Roy Hist Nat Belgique 8: 1-7.

33. Leloup E (1932b) L'hydraire Campanulina hincksi Hartlaub. Bull Mus Roy Hist Nat Belgique 8: 8-9.

34. Rungger D (1969) Autotomy in Tubularia crocea and its ecological and physiological significance. Marine Biology 37: 95-139.

35. Gravier-Bonnet N (1992) Cloning and dispersal by buoyant autotomised hydranths of a Thecate hydroid (Cnidaria, Hydrozoa). Sci Mar 56: 229-236.

36. Kramarsky-Winter E, Fine M, Loya Y (1997) Coral polyp expulsion. Nature 387: 137.

37. Silen L (1955) Automized tentacle crowns as reproductive bodies in Phoronis. Acta Zool 36: 159-165.

38. Ryland JS, Hayward PJ (1977) British anascan bryozoans. Academic Press, London, pp: 180.

39. Mukai H Koyama H, Watanabe H (1983) Studies of the reproduction of three species of Perophora (Ascidiacea). Bio Bull (Woods Hole) 164(2): 251-266.

40. Pati AC, Belmonte G, Fanelli G, Giangrande A, Gravili C, et al. (1998) Interkingdom convergence in the architecture of asexual propagules. Biol Mar Med 5: 365-366.

41. Abelson A, Weihs D, Loya Y (1994) Hydrodynamic impediments to settlement of marine propagules, and adhesive-filament solutions. Limnol Oceanogr 39(1): 164-169.

42. Fong P, Lirman D (1995) Hurricanes cause population expansion of the branching coral Acropora palmata (Scleractinia): wound healing and growth patterns of asexual recruits. Mar Ecol 16(4): 317-335.

43. Hughes RN (1990) A functional biology of clonal animals. Chapman and Hall, New York, pp: 331.

44. Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc Nat Acad Sci 82(11): 3707-3711.

45. Ryland JS (1981) Colonies, growth and reproduction. In: Larwood GP, Nielsen C (Eds.), Recent and fossil Bryozoa. Olsen & Olsen, Fredensborg, pp: 221-226.

46. Fell PE (1985) Tolerances of the dormant forms of some estuarine sponges, notably Microciona prolifera. 3rd Internat Sponge Conf., Paris, pp: 497-503.

47. Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. Diversity Distrib 11(2): 139-148.

48. Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13(S1): 159-169.