

Groups travel further: pelagic metamorphosis and polyp clustering allow higher dispersal potential in sun coral propagules

Damián Mizrahi · Sergio A. Navarrete ·
Augusto A. V. Flores

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Abstract We report that planulae produced by *Tubastraea coccinea* can metamorphose and aggregate in groups of up to eight polyps in the water column, without previous settlement on benthic substrate. We also evaluated the survival of propagules to test whether different levels of aggregation allowed for longer planktonic life and, therefore, higher dispersal potential. Our results show that pelagic polyps live longer than planulae, probably because they can feed and meet the presumably high-energy demands of swimming. Clusters of two or more individuals lived longer than solitary polyps. However, mortality did not differ between small (2–3 polyps) and large (4–8 polyps) clusters, suggesting the existence of an upper limit to cluster size. Most swimming clusters (80 %) remained alive after 6 months, suggesting that pelagic metamorphosis and cluster formation can be a key life-history feature increasing dispersal potential, population connectivity, and the colonization of new habitats in this invasive species.

Keywords Larvae · Planktonic metamorphosis · Pelagic clusters · Invasive species · Propagule dispersal

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D. Mizrahi · A. A. V. Flores (✉)
Centro de Biologia Marinha (CEBIMar/USP), Universidade de
São Paulo, Rod. Manoel Hipólito do Rego, km 131.5,
São Sebastião, São Paulo 11600-000, Brazil
e-mail: guca@usp.br

S. A. Navarrete
Estación Costera de Investigaciones Marinas, Las Cruces, and
Center for Marine Conservation, Pontificia Universidad Católica
de Chile, Casilla 114-D, Santiago, Chile

Introduction

The sun coral *Tubastraea coccinea* is an invasive species that rapidly colonizes large extents of benthic habitat, causing substantial change of the structure of native benthic communities (Lages et al. 2011). In recent decades, its range distribution has increased, and today, the species is considered pantropical (Cairns 1994). It has been suggested that its remarkable capacity to colonize bare artificial surfaces like oil rigs, together with increased maritime traffic, have facilitated the establishment of this species over its non-native range (Ferreira 2003). Undoubtedly, increased traffic has played a major role in long-distance dispersal, especially across oceans, but early development attributes of the sun coral may facilitate dispersal of colonies, and thus be very important in the spread of colonies within regions and into natural habitat.

It is assumed that this brooding coral species follows the typical scleractinian life cycle, in which pelagic, lecithotrophic larvae metamorphose into founder polyps at settlement and develop into colonies through cloning. In fact, planulae usually settle and metamorphose within a relatively brief period of time, around 3 d (Glynn et al. 2008), probably favoring self-recruitment and promoting the gregarious spatial pattern often reported for this species (e.g., Paula and Creed 2005; Glynn et al. 2008). However, we observed that alternative developmental pathways are possible in *T. coccinea*. More specifically, we report in this paper that larvae released from laboratory-held colonies, during conspicuous planulation events, can metamorphose to polyps while still in the plankton and that swimming polyps can attach to each other, forming pelagic clusters of different sizes. We hypothesize that larvae, swimming solitary polyps, and clusters may play different functional roles in the population dynamics of this invasive species by altering their dispersal capacity.

Besides corals, numerous benthic invertebrates spanning different phyla exhibit gregarious settlement patterns. Larval behavior is thought to be critical in setting these spatial patterns, including conditional swimming activity and responses to conspecific chemical cues (reviewed by Burke 1986; Qian 1999; Clare and Matsumura 2000; Müller and Leitz 2002). However, it is known that many gregarious invertebrate species can follow a bet-hedging strategy and produce descendants with contrasting dispersal potential, even among siblings. This is the case, for instance, of poecilogonous polychaete and opisthobranch species (Chia et al. 1996), whose egg masses give rise to both crawling juveniles and dispersive swimming larvae, sometimes within the same egg batch, originating siblings with contrasting dispersal potential (Gibson and Chia 1989, 1995). Non-poecilogonous gregarious polychaetes, which usually produce short-living larvae settling in nearby habitat in response to conspecific cues (“aggregators”), may simultaneously release a small subset of larvae following an alternative behavioral pattern, in which individuals favor dispersal away from their parents and the eventual foundation of new colonies (“founders”; Toonen and Pawlik 2001a, b).

Species producing lecithotrophic offspring can apparently also control the pelagic larval duration, and thus dispersal potential, by manipulating resource allocation to individuals (Wendt 2000; Krug 2001; Marshall and Keough 2003; Gribben et al. 2006; Stamps 2006). This regulation, however, is obviously limited by the constraints on the amount of resources that parents can transfer to eggs. Richmond (1985) and Vermeij (2009) suggested that coral planktonic polyps can feed because they have fully developed mouth and tentacles. If so, pelagic polyps, or polyp clusters, are not solely dependent on paternal resource allocation, but also capable of obtaining food resources from the surrounding environment. Because pelagic propagule duration is a reasonable proxy for dispersal potential, especially for long-lasting propagules (Shanks et al. 2003; Shanks 2009), we hypothesize that metamorphosis to free-living polyps in *T. coccinea*, and the formation of polyp clusters, may prolong planktonic life, increasing dispersal potential and thus the temporal window for substrate selection and settlement. To test this, we conducted an experiment to compare survival time, and hence dispersal potential, among the different types of propagules that can be produced by this coral.

We were particularly interested in three different comparisons to clarify the potential adaptive value of alternative propagule types. First, we compared survival rates between planulae and single polyps to test two alternative hypotheses. The occurrence of pelagic polyps could be an outcome of a desperate strategy (sensu Knight-Jones 1953), in which planulae could no longer delay metamorphosis. In

this case, polyps would perform poorly in the water column and die shortly in the absence of proper settlement habitat. Alternatively, single polyps may actually consist of functional pelagic organisms, capable of oriented swimming and feeding. In this case, polyps could indeed capture and ingest planktonic particles and endure longer than non-feeding larvae. Second, we compare survival of single polyps and polyp clusters. If polyp mortality does not differ between single and clustered individuals, clusters would last longer based on chance alone. However, colonies may not live longer if, for instance, energetic costs to maintain swimming in the water column are excessive, or competition for food resources among clustered polyps is too high, leading to massive mortality within the cluster. The third comparison was therefore the survival among clusters with a different number of polyps.

Methods

Observations of alternative propagule types

During April 2012, we collected 150 adult colonies, with a number of polyps ranging from 19 to 78, at Búzios Island (23°48'11"S; 45°08'21"W), 25 km off the coast of São Paulo state, Brazil, which were brought to the Center for Marine Biology, University of São Paulo (CEBIMar), São Sebastião, and held for 2 months in two indoor 500-l tanks with running seawater. During a massive larval release observed from June 9 to 11, we removed all larvae from the tanks and transferred them to two 6.5-l plastic aquaria with transparent plastic walls and filled with unfiltered seawater without aeration. Water temperature ranged between 20 and 25 °C.

Just after transfer, larvae rose to the surface and could be easily counted. We photographed the surface of aquaria from above and counted the larvae in the photographs. Three days after transferring larvae (day 3), metamorphosis and polyp aggregation had already begun. At this time, we counted all swimming planula larvae, swimming solitary polyps, and polyp clusters, and carefully selected propagules from each of these conditions to set up the survival experiment described below. At day 7, we realized that no further clustering or metamorphosis occurred and made detailed observations on over 100 polyps and polyp clusters to determine whether complete metamorphosis and production of skeletal tissue, respectively, had taken place.

Survival of propagule types

Between three and four days after larval release, we sorted pelagic *T. coccinea* propagules into four different categories: (a) planula larvae, (b) solitary polyps, (c) clusters

formed by 2–3 polyps, and (d) clusters formed by 4–8 polyps. Since there were approximately equal numbers of 2–3 and 4–8 polyp colonies, grouping in these size categories allowed us to maximize replication in a balanced design. A total of 120 propagules of each condition were randomly selected and transferred in groups of 30 to each of four replicate 0.5-l plastic tanks ($14 \times 14 \times 8$ cm), maintained with running unfiltered seawater pumped directly from the nearshore. The number of living, swimming propagules (in the case of clusters, those that had at least one living polyp) was recorded every 3–8 d (mean = 4.3 d) for 6 months. Seawater temperature during this period ranged between 23 and 27 °C. Survivors at each observation were transferred to new clean tanks filled with fresh seawater using pipettes. To avoid settlement, only clean and smooth tank surfaces were provided as hard substrates throughout the experiment.

Separate survival curves for each replicate tank were examined, and independent estimates of per capita mortality rates (m) for each tank were obtained by fitting a simple exponential decline model, $\ln(N_t/N_0) = mt$, using OLS regression, where N_t is the number of propagules alive at time t (in days), and N_0 is the number of initial propagules in the replicate tank ($n = 30$). Per capita mortality rates were then compared among the four propagule conditions using a one-way analysis of variance, followed by specific planned comparisons to test the predictions presented above: (1) larvae versus single polyps, (2) single polyps versus clusters, and (3) 2–3 versus 4–8 polyp clusters. Data were transformed to $\arcsin \sqrt{m}$ previous to analysis to achieve homoscedasticity.

Results and discussion

Natural history of propagule formation

During the massive planulation event reported in this study, 2,710 planulae were released. At day 3, planulae comprised 58 % of all propagules, and the remaining 42 % either metamorphosed into single polyps which remained solitary (5 %) or further aggregated into swimming colonies (37 %). At day 7, both solitary and clustered polyps were fully metamorphosed individuals (Fig. 1), with oral openings, tentacles, and a ciliated epidermis covering their body, which assists in swimming. At this time, we noticed an incipient formation of the carbonate exoskeleton in clustered polyps, which was not associated with any noticeable behavioral change since clusters remained actively swimming and feeding in the water column. Calcification was not observed in solitary polyps (Fig. 1).

Pelagic metamorphosis of planulae into polyps is apparently rare in corals (Edmondson 1929; Richmond

1985; Vermeij 2009) and has never been described for this species. Unlike the previous report by Richmond (1985), we did not observe post-settlement reversal of metamorphosis into a secondary larval stage (as it has also been proposed for mussel larvae; Baker and Mann 1997), since calcareous remains were never observed on tank walls and we never observed larvae exploring the bottom. Thus, both metamorphosis and clustering occurred in individuals that had never settled before. As in Richmond (1985), we observed water-column metamorphosis under conditions of high larval density. This aggregation behavior is therefore likely to be a dose-dependent response to conspecific water-borne cues, but this possibility needs to be further explored.

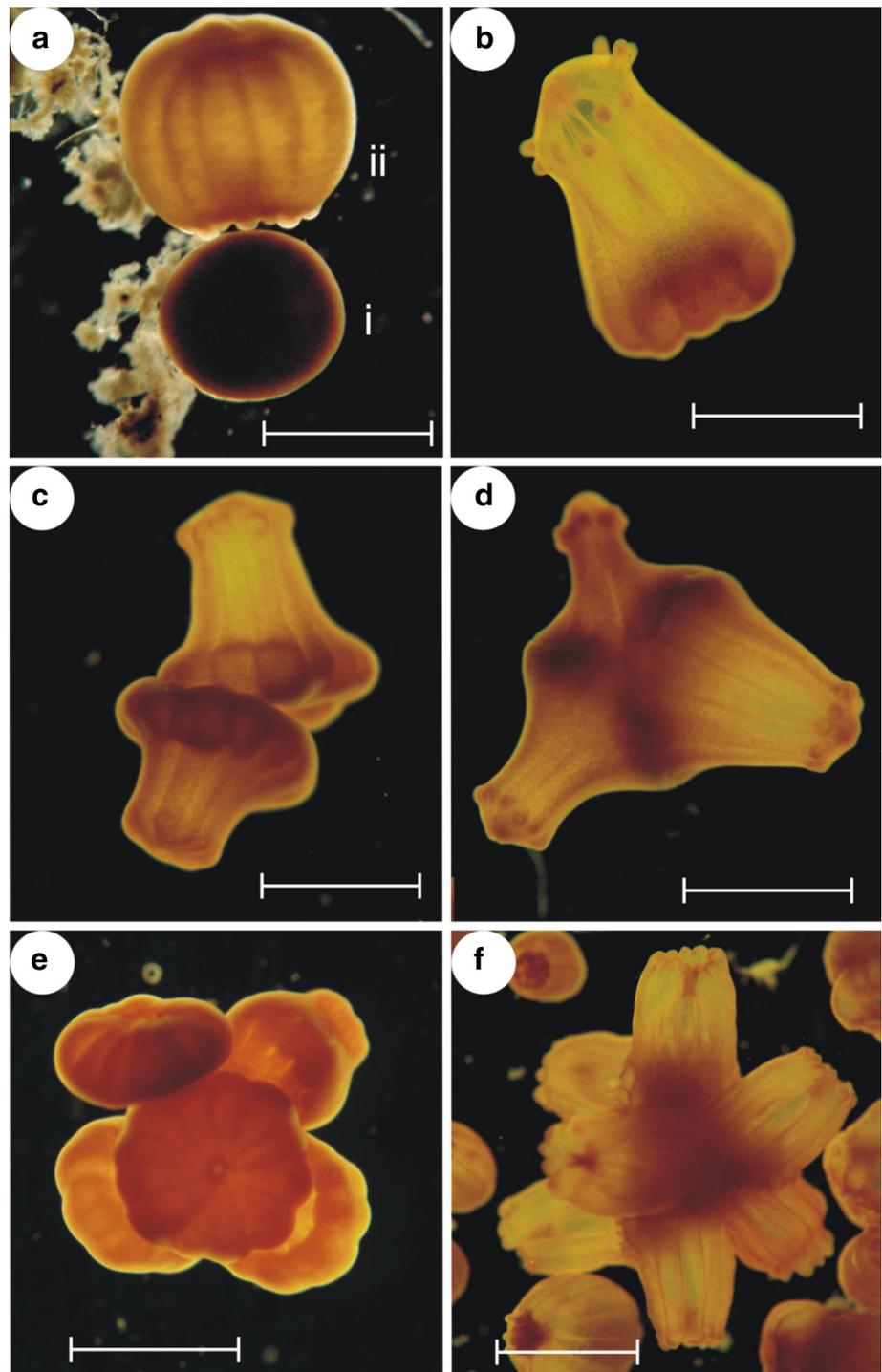
Propagule survival

Mortality rate differed strongly among propagule types (Fig. 2; $F = 333.2$, $p < 0.0001$). Planned contrasts supported that survival was: (1) higher for planktonic polyps than for larvae ($F = 17.2$, $p = 0.0013$), and (2) higher for multiple-polyp than single-polyp propagules ($F = 28.2$, $p < 0.0001$), while (3) no differences were detected between the two sizes of multiple-polyp propagules ($F = 0.86$, $p = 0.37$).

We conclude that swimming polyps are functional pelagic organisms, capable of directional swimming and lasting significantly longer in the water column compared with planulae. Unlike larvae, which depend on parental allocation of resources (Wendt 1996, 2000; Pechenik et al. 1998; Qian and Pechenik 1998), fully metamorphosed polyps are able to feed and sustain the presumably high-energy demands associated with swimming in the plankton. Therefore, their competency window, an important factor affecting the spatial distribution of settlers and their dispersal potential (Richmond and Hunter 1990; Vermeij et al. 2006), may be greatly extended. It is therefore conceivable that these swimming polyps, and other pelagic polyps that eventually detach from benthic colonies (as in *Seriatopora hystrix*; Sammarco 1982) or directly from the substrate (Vermeij 2009), could travel from a few to even tens of kilometers in the plankton depending on hydrographic conditions, which can greatly expand the spread of this species within invaded regions of the world.

Our results also demonstrate that clustering of polyps can significantly and greatly extend pelagic life over solitary polyps. Assuming that these clusters become viable colonies immediately after settling, increased dispersal potential could be an important selective force favoring pelagic polyp clustering. However, there appears to be a limit to this potential benefit, since we found no differences in survival between small (2–3 polyps) and large (4–8 polyps) clusters. It is unclear what factors can be setting

Fig. 1 Types of pelagic propagules in *T. coccinea*. **a** Planula larva (*i*) as released and during metamorphosis, with (*ii*) incipient septation and developing tentacles in the oral opening. **b** A fully developed swimming planktonic polyp propelled by cilia covering their entire body. **c** Coupling of two free-living polyps. **d** A cluster of three polyps, showing the accumulation of skeletal tissue. **e** Metamorphosing larvae and its coupling to a multiple-polyp propagule. **f** Consolidated cluster of eight polyps. Scale bars 1 mm



this apparent size threshold for plankton survival. We can speculate that polyps in larger colonies may compete for food and that a relatively higher proportion of skeletal tissue in large clusters may carry exceedingly high swimming energetic costs (Okamura 1984, 1985; Sebens et al. 1997; Pratt 2004). But even if pelagic life is not further extended in larger clusters, these may be favored after

settlement because they could be less vulnerable to predation (Carr and Hixon 1995; Allen 2008), and provide higher genetic variability in newly colonized areas, assuming that aggregations are formed by polyps originating from different parental colonies. It is important to state, however, that we do not know whether swimming polyps or colonies are able to settle in natural conditions,

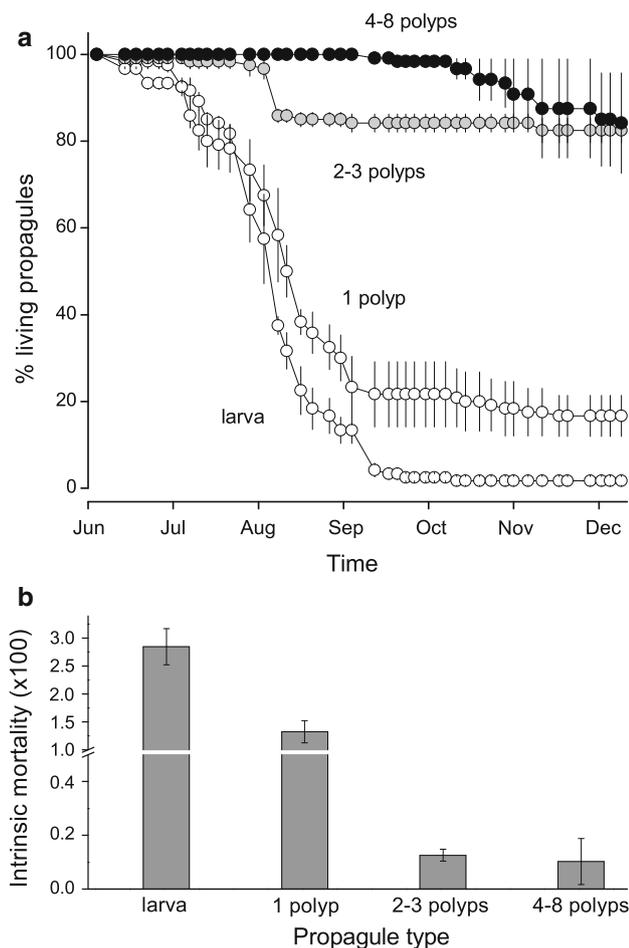


Fig. 2 **a** Survival of different propagule types in time. **b** Intrinsic mortality for the different types of propagules of *T. coccinea*. Whiskers indicate \pm SE in both plots

because settlement was prevented in our experiment by not providing any substrates that could be used for fixation. In the case that swimming colonies are actually capable to settle, it would be interesting to investigate whether colonies are formed by random clustering or kin aggregation, as shown by colonial ascidians (Grosberg and Quinn 1986), since this would determine genetic variability, and perhaps the fitness of adult colonies.

In conclusion, we suggest that metamorphosis to swimming polyps and the formation of pelagic clusters is an important mechanism to expand pelagic life and achieve long-distance dispersal, at least on scales of tens of kilometers, which can be orders of magnitude higher than expected dispersal of short-living planula larvae. Although not measured in this contribution, the occurrence of pelagic metamorphosis and clustering may respond to density of larvae in the plankton and, therefore, indirectly to the abundance of adult benthic colonies in the area. A similar facultative dispersal mechanism has been documented for

Bugula neritina, a bryozoan which produces larger larvae, with longer pelagic duration when adult density is high and intra-specific competition very likely (Allen et al. 2008). Our experimental conditions, in which larval densities were very high and turbulent diffusion absent, may lead to much higher concentrations of any adult and larval cues that might eventually trigger the formation of long-lasting propagules under average natural conditions. However, along the invaded range of *T. coccinea* in Southeastern Brazil, colonies cover large rocky extensions (i.e., Mantelatto et al. 2011) and concentrate reproduction in two annual maxima (Mizrahi 2008). If intense planulation is timed with exceptional slack-water conditions, favorable conditions for the formation of alternative propagules might eventually take place. Even rare, such events could suffice to greatly increase the chances of spread to a new habitat within a given invaded region. Further experiments are needed to evaluate density effects on the formation of dispersal propagules and also to compare the performance of founder settlers, originating from different types of propagules. If density-dependent dispersal strategies are confirmed, reductions in colony density, instead of complete eradication, could be a feasible strategy to stem expansion to new areas. In any case, efforts to control the spread of this invasive exotic species along the southeastern Brazilian coast should take into consideration a much higher pelagic dispersal potential than currently estimated, and the likely occurrence of considerable genetic variability within single benthic adult colonies.

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References

- Allen JD (2008) Size-specific predation on marine invertebrate larvae. *Biol Bull* 214:42–49
- Allen RM, Buckley YM, Marshall DJ (2008) Offspring size plasticity in response to intraspecific competition: An adaptive maternal effect across life-history stages. *Am Nat* 171:225–237
- Baker P, Mann R (1997) The postlarval phase of bivalve mollusks: a review of functional ecology and new records of postlarval drifting of Chesapeake Bay bivalves. *Bull Mar Sci* 61:409–430
- Burke RD (1986) Pheromones and the gregarious settlement of marine invertebrate larvae. *Bull Mar Sci* 39:323–331

- Cairns SD (1994) Scleractinia of the temperate North Pacific. *Smithson Contrib Zool* 557:1–150
- Carr MH, Hixon MA (1995) Predation effects on early postsettlement survivorship of coral-reef fishes. *Mar Ecol Prog Ser* 124:31–42
- Chia FS, Gibson GD, Qian PY (1996) Poecilogony as a reproductive strategy of marine invertebrates. *Oceanol Acta* 19:203–208
- Clare AS, Matsumura K (2000) Nature and perception of barnacle settlement pheromones. *Biofouling* 15:57–71
- Edmondson CH (1929) Growth of Hawaiian corals. *Bull Bernice P Bishop Museum* 58:1–38
- Ferreira CEL (2003) Non-indigenous corals at marginal sites. *Coral Reefs* 22:498
- Gibson GD, Chia FS (1989) Developmental variability (pelagic and benthic) in *Haminaea callidegenita* (Opisthobranchia: Cephalaspidea) is influenced by egg mass jelly. *Biol Bull* 176:103–110
- Gibson GD, Chia FS (1995) Developmental variability in the poecilogonous opisthobranch *Haminaea callidegenita*: life-history traits and effects of environmental parameters. *Mar Ecol Prog Ser* 121:139–156
- Glynn PW, Colley SB, Maté JL, Cortés J, Guzman HM, Bailey RL, Feingold JS, Enochs IC (2008) Reproductive ecology of the azooxanthellate coral *Tubastraea coccinea* in the Equatorial Eastern Pacific: Part V. *Dentrophylliidae*. *Mar Biol* 153:529–544
- Gribben PE, Marshall DJ, Steinberg PD (2006) Less inhibited with age? larval age modifies responses to natural settlement inhibitors. *Biofouling* 22:101–106
- Grosberg RK, Quinn JF (1986) The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature* 332:456–459
- Knight-Jones EW (1953) Laboratory experiments on gregariousness during setting in *Balanus balanoides* and other barnacles. *J Exp Biol* 30:584–599
- Krug PJ (2001) Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Adalaria modesta*. *Mar Ecol Prog Ser* 213:177–192
- Lages BG, Fleury BG, Menegola C, Creed JC (2011) Change in tropical rocky shore communities due to an alien coral invasion. *Mar Ecol Prog Ser* 438:85–96
- Mantelatto MC, Mourão GG, Migotto AE, Creed JC (2011) Range expansion of the invasive corals *Tubastraea coccinea* and *Tubastraea tagusensis* in the Southwest Atlantic. *Coral Reefs* 30:397
- Marshall DJ, Keough MJ (2003) Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. *Mar Ecol Prog Ser* 255:145–153
- Mizrahi D (2008) Influência da temperatura e luminosidade na distribuição da espécie invasora *Tubastraea coccinea* na região de ressurgência de Arraial do Cabo, RJ, Brasil. MSc. thesis, Universidade Federal do Estado de Rio de Janeiro, p 88
- Müller W, Leitz T (2002) Metamorphosis in the Cnidaria. *Can J Zool* 80:1755–1771
- Okamura B (1984) The effects of ambient flow velocity, colony size and upstream colonies on the feeding success of Bryozoa: 1. *Bugula stolonifera*, an arborescent species. *J Exp Mar Biol Ecol* 83:179–194
- Okamura B (1985) The effects of ambient flow velocity, colony size and upstream colonies on the feeding success of Bryozoa: 2. *Conopeum reticulum*, an encrusting species. *J Exp Mar Biol Ecol* 89:69–80
- Paula A, Creed JC (2005) Spatial distribution and abundance of non indigenous coral genus *Tubastraea* (Cnidaria, Scleractinia) around Ilha Grande, Brazil. *Braz J Biol* 65:661–673
- Pechenik JA, Wendt DE, Jarrett JN (1998) Metamorphosis is not a new beginning. *Bioscience* 48:901–910
- Pratt M (2004) Effect of zooid spacing on Bryozoan feeding success: Is competition or facilitation more important? *Biol Bull* 207:17–27
- Qian PY (1999) Larval settlement of polychaetes. *Hydrobiologia* 402:239–253
- Qian PY, Pechenik JA (1998) Effects of larval starvation and delayed metamorphosis on juvenile survival and growth of the tube-dwelling polychaete *Hydroides elegans* (Haswell). *J Exp Mar Biol Ecol* 227:169–185
- Richmond RH (1985) Reversible metamorphosis in coral planula larvae. *Mar Ecol Prog Ser* 22:181–185
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific, and the Red Sea. *Mar Ecol Prog Ser* 60:185–203
- Sammarco PW (1982) Polyp bail out: an escape response to environmental stress and a new means of reproduction in corals. *Mar Ecol Prog Ser* 10:57–65
- Sebens KP, Witting J, Helmuth B (1997) Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). *J Exp Mar Biol Ecol* 211:1–28
- Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. *Biol Bull* 216:373–385
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecol Appl* 13:S159–S169
- Stamps JA (2006) The silver spoon effect and habitat selection by natal dispersers. *Ecol Lett* 9:1179–1185
- Toonen RJ, Pawlik JR (2001a) Foundations of gregariousness: a dispersal polymorphism among the planktonic larvae of a marine invertebrate. *Evolution* 55:2439–2454
- Toonen RJ, Pawlik JR (2001b) Settlement of the gregarious tube worm *Hydroides dianthus* (Polychaeta: Serpulidae) II: testing the desperate larvae hypothesis. *Mar Ecol Prog Ser* 224:115–131
- Vermeij MJA (2009) Floating corallites: a new ecophenotype in scleractinian corals. *Coral Reefs* 28:987
- Vermeij MJA, Fogarty ND, Miller MW (2006) Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral *Montastraea faveolata*. *Mar Ecol Prog Ser* 310:119–128
- Wendt DE (1996) Effect of larval swimming duration on success of metamorphosis and size of the ancestral lophophore in *Bugula neritina* (Bryozoa). *Biol Bull* 191:224–233
- Wendt DE (2000) Energetics of larval swimming and metamorphosis in four species of *Bugula* (Bryozoa). *Biol Bull* 198:346–356