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Research Article

Floating docks in tropical environments - a reservoir for the opportunistic ascidian *Herdmania momus*

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Abstract

The solitary ascidian *Herdmania momus* is considered native to the Red Sea, and invasive in the Mediterranean. Periodic surveys have revealed high recruitment and growth rates of this species on floating docks in the Gulf of Aqaba, Red Sea, following the annual vertical mixing event. In order to ascertain the length of time taken by *H. momus* individuals to settle on new artificial substrates, and the pace at which they grow and reach the reproductive stage, we monitored a newly-deployed floating dock for two years following its deployment. The number of individuals and their sizes were recorded weekly in March-June 2013 (spring-early summer), in June-August (summer), and re-visited each spring (April 2014, 2015). In addition, seven fixed quadrates were artificially cleaned and monitored in summer 2013. Ascidians were visible after eight weeks in the spring and five weeks in the summer. Growth rate in spring was twice as fast as in summer (0.275 and 0.106 cm/week respectively). Recruitment was higher during spring, reaching a density of 34.3 ± 7.1 in June, with fully reproductive individuals, dropping to 0.86 ± 0.46 individuals per quadrate in August. Field surveys of additional floating docks revealed significantly higher densities at the northern sites during spring. Following a nutrient enrichment event such an opportunistic filter-feeder can potentially release and distribute propagules to natural reefs, inducing a shift in community assemblage. In addition, its ability to colonize artificial substrates within its native range sheds light on its success as an invasive species in the Mediterranean.

Key words: tunicates, coral-reef conservation, fouling, reproduction, artificial substrates, invasive species

Introduction

Floating docks or jetties are man-made structures that rise and fall with the tide. They are usually supported by plastic or metal pontoons which can be easily assembled and deployed. In tropical environments they are often used as platforms for recreational sports, in pleasure-craft marinas, and in order to prevent tourists from treading directly on the reef. Floating structures are well-known for their ability to create novel habitats for benthic organisms (Holloway and Connell 2002; Perkol-Finkel et al. 2006), and to establish favorable conditions for filter-feeding organisms in particular (Connell 2000). While the management and monitoring of floating docks is commonly

carried out nowadays in high-latitude environments in order to control the spread of invasive species (e.g., Gittenberger and van Stelt 2011; Pederson 2005), in tropical coral-reef environments this aspect has rarely been addressed.

Ascidians (Chordata, Ascidiacea) are sessile filter-feeder organisms that inhabit a variety of substrates among coral reefs around the world (Kott 1985; Monniot et al. 1991; Rocha et al. 2005; Shenkar 2012). Although they usually constitute a minor benthic component on exposed surfaces of the natural coral reefs (Goodbody 1995; Monniot et al. 1991) they thrive on nearby artificial substrates such as floats, buoys, and jetties (Lambert 2002; Shenkar et al. 2008a). As a well-known component of fouling communities worldwide (Lambert 2005)

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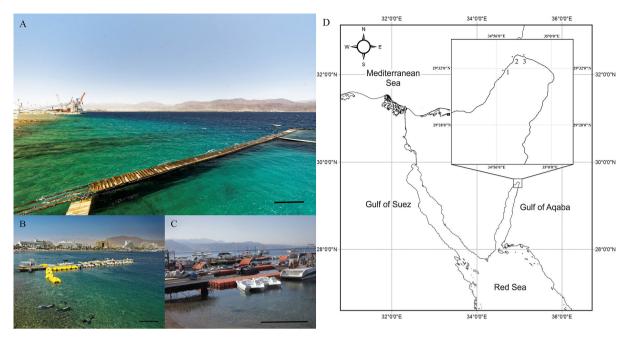


Figure 1. A) The Dolphin-Reef's floating dock, scale bar 10m; B) The newly deployed monitored floating dock at "Kisuski", scale bar 10m; C) North-beach sports jetty, scale bar 5m; D) Map of the study sites, numbers correspond to table 1. Photos: G. Koplovitz, Y. Shmuel.

ascidians can be found on many artificial substrates in tropical environments (Burt et al. 2009; Fukunaga and Bailey-Brock 2008).

Ascidians are able to filter minute particulate matter, primarily in the range of 0.2 to 2 µm diameter (Bak et al. 1998; Ribes and Atkinson 2007), and play an important role in benthopelagic coupling and coral-reef carbon and nitrogen cycling (Bak et al. 1998; Ribes et al. 2005; Yahel et al. 2005). They are all hermaphroditic, displaying either a solitary or a colonial life-style. Most solitary species release gametes into the water, while colonial species retain and brood their eggs (Lambert 2005). The lecithotrophic tadpole larvae have a short pelagic larval stage and do not disperse far (Ayre et al. 1997; Olson 1985). Some solitary and colonial species are known for their ability to form large aggregations on both natural and artificial substrates (Castilla et al. 2004; Lambert 2002, 2009; Minchin and Sides 2006; Rius et al. 2010). All the above traits play a significant role in competition for space in tropical environments. Indeed, in recent years several episodes of ascidian outbreaks in coral reefs around the world have drawn the attention of scientists to their potential negative influence on hermatypic corals (Bak et al. 1996; Littler and Littler 1995; Shenkar et al. 2008a; Sommer et al.

2010; Vargas-Ángel et al. 2009). Their potential to outcompete corals for space, and their unknown impact on the natural benthic fauna, raise the need to further monitor and study this unique group of invertebrates (Shenkar 2012; Sommer et al. 2010).

The solitary ascidian Herdmania momus (Savigny, 1816) is a common Indo-Pacific species, with a wide global distribution (Gewing et al. 2014; Rius and Shenkar 2012). In the Red Sea, which is considered to be its native range, it can be found on both artificial substrates and the natural coral reef, underneath rocks and at the base of stony corals (Shenkar and Loya 2008). In the northern Red Sea (Eilat, Israel) it reproduces year-round (Shenkar and Loya 2008; Shenkar et al. 2008b). Following recent reports of high densities of H. momus on artificial substrates among the coral reefs of Eilat, we investigated this species' density on floating docks in the Gulf of Agaba, and followed its growth, development, and recruitment rate on a newly-deployed floating dock. The acquisition of such data is crucial to our understanding of the ecological role that ascidians play in these environments, in particular in view of the increasing deployment of artificial structures in such areas, and contributes to our understanding of the characterizing traits of non-indigenous ascidians.

Materials and methods

Newly-deployed dock monitoring

The recruitment and growth rate study was conducted from March 2013 to April 2014 on an artificial floating dock in Eilat ("Kisuski" sports jetty, 29°32'51.93"N 34°57'13.47"E, Figure 1B, D). The submerged area is between 0-50 cm depth, allowing observations using both snorkeling and SCUBA diving. Ambient sea-surface temperature, chlorophyll-a levels, and visibility data (Secchi depth), which indicate the timing of the annual vertical mixing event, were obtained from the Israel National Monitoring Program (NMP, http://www.iuieilat.ac.il). Sea surface temperatures, as recorded by the NMP for this period were (mean \pm SD): Spring (March-May 2013): 22.88°C ±1.01; Summer (June-August 2013): 26.07° C \pm 1.07; Autumn (September-November 2013): 25.49°C ± 1.07; Winter (December 2013-February 2014): 22.57°C±0.87. The dock is constructed of a partially submerged metal frame and wooden plates and is ca. 60 m long, in a west-east orientation. The metal frame is constructed of paint-coated metal beams along the length of the pier, with metal rectangular plates $(2.4 \times 0.6 \text{ m})$ crossing its width. The metal plates are down-facing and permanently submerged. On February 18th, 2013 a portion of the pier was removed, cleaned of all foulants, repainted, and returned to the water. Monitoring of H. momus recruitment and development was conducted on the cleaned section by: 1) bi-weekly photographing of 13 marked locations on the external metal frames from March to June 2013 (vertical orientation); 2) weekly monitoring of seven fixed 0.25 m² quadrates on the underside of the metal rectangular plates from June to August 2013 (down-facing orientation); and 3) measurements of H. momus size and density in seven randomly chosen 0.25 m² quadrates located on the underside of the metal rectangular plates following seven months and 14 months of deployment (August 2013 and April 2014). Since the pier is used for recreational water sports, not every location on the external frame (vertical orientation) was available for photographing on each date. During the initial monitoring of the fixed quadrates, the density of H. momus was estimated, representing the density after 15 weeks in the water. The area beneath the quadrate was then completely scraped. Seven additional unscraped segments were randomly selected on the same metal plates, during August 2013 and April 2014, and the density of H. momus was estimated.

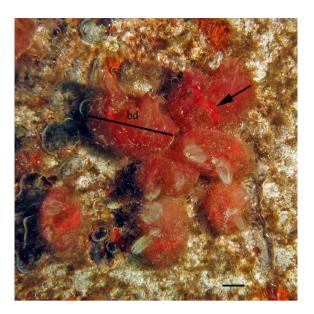


Figure 2. *Herdmania momus* individuals beneath the monitored floating dock. Scale bar: 1 cm. Arrow pointing to a developed gonad. bd: body diameter. Photo: G. Koplovitz.

Growth rate and reproductive state assessment

Growth and development of H. momus was estimated by analyzing the photos using ImageJ image analysis software (Schneider et al. 2012). Body size was estimated by measuring individual body diameters, excluding the siphons (illustrated in Figure 2). Growth rate was calculated from the mean ascidian size at the end of the monitoring period divided by the number of weeks since deployment/cleaning. To determine reproductive state following 15 weeks of deployment, the gonadal state of 20 dissected specimens which were randomly collected was assessed in the laboratory under a stereomicroscope, and Gonad Index (GI) was calculated following Pineda et al. (2013). The diameter of oocytes, sectioned at the nucleolus level, was measured using histological sections (Shenkar and Loya 2008), to a total of 100 oocytes from ten individuals. As the exact larval settlement dates could not be determined, H. momus growth rates were calculated from the day that the foulingfree surfaces were first exposed to sea water. Results were compared to a previous study that had investigated seasonal recruitment of ascidians on settlement plates (Shenkar et al. 2008b).

Periodic surveys of floating docks

Periodic surveys of three additional sites were conducted in September 2014 (autumn) and late March-April 2015 (spring) on several floating

Site No.	Site name	Location coordinates		Deck		No. of	No. of	Mean width ±SE
		Latitude, N	Longitude, E	material	Date	quadrates	individuals/ quadrate ±SE	(cm)
1	Dolphin-Reef	29.226944	34.936944	Foam	2 Dec 2014 26 March 2015	15 16	1.60±0.47 1.65±0.33	1.84±0.21 (24) 2.93±0.36 (24)
2	"Kisuski" sport jetty	29.547722	34.953972	Metal	16 Sept 2014 24 March 2015	16 18	0.06±0.06 3.83±0.76	3 (1) 1.54±0.2 (68)
3	North beach sport jetty	29.54825	34.962194	Plastic	17 Sept 2014 14 April 2015	24 26	0.08±0.0.08 3.92±0.79	2.8±0.37 (2) 3.09±0.19 (102)

Table 1. Floating dock survey in Eilat during Autumn 2014 and Spring 2015. Results are presented as average ± SE. In parentheses, total number of individuals observed. Site numbers correspond to Figure 1D.

docks in Eilat (Figure 1, data for each site is given in Table 1). At each site, between 15 to 26 (depending on the length of the dock) 0.25 m² quadrates were randomly placed on the submersed, down-facing surface of the floating dock, and the number of *H. momus* individuals and their diameter were recorded using SCUBA.

Statistical analysis

All statistical analyses were performed using R software for statistical computing (R Core Team 2013). Population densities were compared using the non-parametric Kruskal-Wallis test, while individuals' sizes were compared using a permutation ANOVA followed by Tukey's test. Results are presented as average ± standard errors, unless noted otherwise.

Results

Recruitment and growth rate to a newly-deployed floating dock

Periodic observations from spring to early summer documented the recruitment of individuals (approximately 0.5 cm in diameter) to a completely clean surface following a period of five weeks of submersion (for the down-facing orientation, at weekly intervals) and eight weeks of submersion (for the vertical orientation, at two-week intervals). Following 15 weeks of submersion, H. momus individuals had reached a maximum size of 7.5 cm and a mean (\pm s.e.) size of 4.4 ± 0.2 cm in diameter (n=47), with a normal population size distribution (Pearson's chi-squared test), indicating ongoing recruitment.

Laboratory observations of dissected specimens and histological sections documented the presence of both mature sperm and mature oocytes (>120 μ m, Figure 2), with a gonad index value averaging

 $11 \pm 0.8\%$ (n=20), and an average (\pm std) oocyte diameter of $190 \pm 18 \mu m$ (n=10). At this time the number of *H. momus* in the monitored quadrates ranged between 14 to 68 individuals with a mean of 34.3 ± 7.1 individuals per 0.25 m^2 quadrate. By the second period of observations, during the summer months (June-August), following a period of eight weeks from settlement-surface cleaning. individuals had reached a mean size of 0.85 ± 0.2 cm (n=6), indicating a much slower growth rate and recruitment rate during the summer months. The number of individuals was also considerably lower, with only 0.86 ± 0.46 per quadrate in mid-August. A similar phenomenon was also noted for the adjacent monitored area, in which H. momus density on the randomly chosen undisturbed quadrates was 1.29 ± 0.57 individuals per quadrate (n=7), with a mean size of 4.33 ± 0.40 cm (n=9), showing an overall reduction in H. momus abundance in the summer months. However, at 14 months postdeployment, in April 2014, the number of *H. momus* on randomly chosen quadrates ranged between 12 to 33 individuals, with a mean of 23.4 ± 2.7 per 0.25 m^2 quadrate (n=7), and a mean size of $2.2 \pm$ 0.1 cm (n=158). In September 2014, only one individual was observed from 16 randomly chosen quadrates, while in March 2015 the number of H. momus ranged between 0 to 12 individuals, with a mean of 3.83 ± 0.76 individuals per 0.25 m^2 quadrate (n=18), and a mean size of 1.54 ± 0.2 cm (n=68), emphasizing a seasonal trend in H. momus density and size (Table 1, Figure 3A, B).

Periodic surveys of floating docks

The periodic surveys at the north-beach sports jetties revealed a similar seasonal trend, with 0.08 ± 0.08 individuals per quadrate in September 2014 (n= 24), and a significantly higher (p < 0.01, Kruskal-Wallis) number of individuals in March 2015 (3.92 \pm 0.79, Table 1, Figure 3A,B).

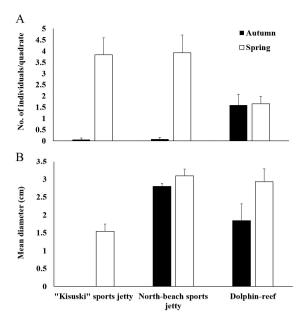


Figure 3. Periodic surveys of *Herdmania momus* on floating docks in Eilat, Red Sea. A) Number of individuals per 0.25 m² quadrate, and B) Mean diameter ± SE per 0.25 m² quadrate. In autumn (black bars), and spring (blank bars).

Field surveys of the dolphin-reef's floating dock revealed a different trend, with no significant difference in population density between the seasons (p >0.05, Kruskal-Wallis). However, during spring 2015 individual size was significantly larger in comparison to autumn (p < 0.01, t-test). This may be due to the survey being conducted in late autumn (December, Table 1) vs. September at the other sites. During spring, both the "Kisuski" sports jetty and the north-beach sports jetty had a significantly higher number of individuals in comparison to the dolphin-reef dock (p < 0.01). permutation ANOVA, followed by Tukey's test, Figure 3A, B). During spring, H. momus individuals in the "Kisuski" sports jetty were significantly smaller (p < 0.01, permutation ANOVA, followed by Tukey's test) in comparison to the two other sites, with the largest individuals measured at the north-beach sports jetty (Figure 3B).

Discussion

The current study aimed to monitor the density of the invasive ascidian *Herdmania momus* on floating docks in its native tropical habitat, to ascertain the length of time required for recruitment to newly-deployed docks, and to compare individual growth rates. These aspects are highly important in view of the potential of *H. momus* to affect

tropical ecosystems following environmental change, and taking into consideration its invasive status in the Eastern Mediterranean (Shenkar and Loya 2008). The results demonstrated that H. momus is a conspicuous member of the floating docks across the Gulf of Agaba (including Jordan, GK and YS personal observations), and is characterized by rapid recruitment and growth rates. Following a period of less than four months post-deployment. H. momus individuals on the newly-submerged floating dock were found with fully developed gonads. Other solitary invasive ascidians, such as Ciona intestinalis and Styela plicata, are also known to reach sexual maturity in only a few months (Yamaguchi 1975). The ability to reproduce at an early stage and to produce a large number of offspring is a known trait among invasive species, significantly contributing to their success in establishing sustainable populations at the introduced sites (Johnston et al. 2009). H. momus demonstrated a lower growth rate in the summer months (0.106 cm/week) than in the spring (0.275 cm/week). These findings reveal an opposite trend to those found for other solitary ascidians (Ciona intestinalis and Styela plicata) in temperate waters (Japan), which demonstrated roughly double the growth rates in the summer than in the winter (Yamaguchi 1975). The fast growth rate of H. momus during favorable conditions, coupled with its ability to reach sexual maturity within a few weeks, contribute to explaining its successful establishment in the Eastern Mediterranean, and strong potential to expand its distribution (Evans et al. 2013; Rius and Shenkar 2012).

Seasonal blooms of H. momus on artificial habitats as well as natural habitats in the Gulf of Agaba have been observed in other studies, with high recruitment rates during May 2012 and 2013 to settlement plates submerged at 10 m depth, and reaching even 47 m depth (G. Eyal and Y. Loya pers. comm.). Shenkar et al. (2008b) demonstrated a significant association between the number of H. momus individuals on recruitment plates throughout the year, and water visibility ($r^2 = 0.91$, y = -8.93 x + 280, p < 0.01, adapted results). Since this species reproduces year-round in this area (Shenkar and Loya 2008), ensuring a continuous larval supply, this strongly supports the hypothesis that seasonal blooms of ascidians are mostly related to food availability, i.e., nutrient levels (Shenkar et al. 2008a, b). Following the cooling of the surface water of the Gulf of Aqaba during the winter, a vertical mixing event occurs, resulting in high nutrient levels in the water column (Genin et al. 1995). Indeed, following this period we

anticipate a significant rise in ascidian number and coverage, as demonstrated in the current study (Figure 3A) and in Shenkar et al. (2008a,b). Recently, numerous (usually rare) winter floods in the region caused a coastal sediment runoff to the northern tip of the Gulf (Katz et al. 2015), which resulted in large densities of H. momus attached to the sea grass Halophila stipulacea, even on the sandy bottom (E. Gilad and N. Shenkar, unpublished data). This event may also explain the large size of *H. momus* measured during spring 2015 at the adjacent north-beach sports jetty. The increase in organic matter in the water column is thus a strong factor in determining ascidian appearance worldwide (Becerro and Turon 1992; Hunter et al. 2012; López-Legentil et al. 2005; Sahade et al. 2004). The oligotrophic tropical ecosystem is extremely vulnerable to any increase in organic matter in the water (Birkeland 1987). The accumulative effect is reflected in the increasing numbers of fast-growing filter feeders such as H. momus, suggesting their potential use as bioindicators of environmental change in tropical environments. Additionally, although H. momus is considered as a species native to the Red Sea, it is possible that a cryptic invasion of a nonnative genotype has occurred. Such cryptic invasions often go unnoticed until the invader is well established in the area (Saltonstall 2002). Applying molecular tools in future studies is thus essential.

Floating docks, such as that monitored in the current study, are abundant in tropical tourist areas. These relatively "harmless"-looking structures provide a unique protected habitat and favorable conditions for fast-growing organisms such as ascidians (Gittenberger and van Stelt 2011; Lambert 2002). Recent studies have shown that non-native species, especially ascidians, show a clear preference for settling on floating docks, compared with fixed structures (Dafforn et al. 2009; Gittenberger and van Stelt 2011), and studies have therefore strongly recommended the use of fixed docks over moving structures (Dafforn et al. 2009). Although floating docks are periodically cleaned, the fouling organisms can easily release and distribute propagules to the adjacent natural reefs. In the case of sudden environmental events forming new available niches, these year-round reproductive and fast-growing organisms on floating docks, such as H. momus, may present a threat to the natural ecosystem by competing with reefbuilding corals for recruitment and growth. Consequently, we strongly recommend that environmental agencies control the deployment of these artificial structures, and continuously monitor the appearance of ascidians on both artificial and natural substrates in tropical environments. Numerous case-studies from cold-water environments have demonstrated in the past the destructive nature of opportunistic ascidians overgrowing floating structures (Bullard et al. 2007; Coutts and Forrest 2007), and tropical coral reefs are no exception.

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References

- Ayre D, Davis A, Billingham M, Llorens T, Styan C (1997) Genetic evidence for contrasting patterns of dispersal in solitary and colonial ascidians. *Marine Biology* 130: 51–61, http://dx.doi.org/10.1007/s002270050224
- Bak R, Joenje M, De Jong I, Lambrechts D, Nieuwland G (1998) Bacterial suspension feeding by coral reef benthic organisms. *Marine Ecology Progress Series* 175: 285–288, http://dx.doi. org/10.3354/meps175285
- Bak R, Lambrechts D, Joenje M, Nieuwland G, Van Veghel M (1996) Long-term changes on coral reefs in booming populations of a competitive colonial ascidian. *Marine Ecology Progress Series* 133: 303–306, http://dx.doi.org/10. 3354/meps133303
- Becerro M, Turon X (1992) Reproductive cycles of the ascidians *Microcosmus sabatieri* and *Halocynthia papillosa* in the Northwestern Mediterranean. *Marine Ecology* 13: 363–373, http://dx.doi.org/10.1111/j.1439-0485.1992.tb00360.x
- Birkeland C (1987) Nutrient availability as a major determinant of differences among coastal hard-substratum communities in different regions of the tropics. UNESCO Reports in Marine Science, pp 45–125
- Bullard SG, Lambert G, Carman MR, Byrnes J, Whitlatch RB, Ruiz G, Miller RJ, Harris L, Valentine PC, Collie JS, Pederson J, McNaught DC, Cohen AN, Asch RG, Dijkstra J, Heinonen K (2007) The colonial ascidian *Didemnum* sp. A: Current distribution, basic biology and potential threat to marine communities of the northeast and west coasts of North America. *Journal of Experimental Marine Biology and Ecology* 342: 99–108, http://dx.doi.org/10.1016/j.jembe.2006.10.020
- Burt J, Bartholomew A, Bauman A, Saif A, Sale PF (2009) Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs and breakwaters. *Journal of Experimental Marine Biology* and Ecology 373: 72–78, http://dx.doi.org/10.1016/j.jembe.20 09.03.009
- Castilla JC, Lagos NA, Cerda M (2004) Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. *Marine Ecology Progress Series* 268: 119–130, http://dx.doi.org/10.3354/meps268119

- Connell SD (2000) Floating pontoons create novel habitats for subtidal epibiota. *Journal of Experimental Marine Biology* and Ecology 247: 183–194, http://dx.doi.org/10.1016/S0022-0981(00)00147-7
- Coutts AD, Forrest BM (2007) Development and application of tools for incursion response: Lessons learned from the management of the fouling pest *Didemnum vexillum. Journal of Experimental Marine Biology and Ecology* 342: 154–162, http://dx.doi.org/10.1016/j.jembe.2006.10.042
- Dafforn K, Johnston E, Glasby T (2009) Shallow moving structures promote marine invader dominance. *Biofouling* 25: 277–287, http://dx.doi.org/10.1080/08927010802710618
- Evans J, Borg JA, Schembri PJ (2013) First record of *Herdmania* momus (Ascidiacea: Pyuridae) from the central Mediterranean Sea. Marine Biodiversity Records 6: e134, http://dx.doi.org/10.1017/S1755267213001127
- Fukunaga A, Bailey-Brock JH (2008) Benthic infaunal communities around two artificial reefs in Mamala Bay, Oahu, Hawaii. *Marine Environmental Research* 65: 250–263, http://dx.doi.org/10.1016/j.marenvres.2007.11.003
- Genin A, Lazar B, Brenner S (1995) Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature* 377: 507–510, http://dx.doi.org/10.1038/377 507a0
- Gewing M-T, Rothman S, Nagar LR, Shenkar N (2014) Early stages of establishment of the non-indigenous ascidian *Herdmania momus* (Savigny, 1816) in shallow and deep water environments on natural substrates in the Mediterranean Sea. *BioInvasions Records* 3: 77–81, http://dx.doi.org/10.3391/bir.2014.3.2.04
- Gittenberger A, van Stelt RC (2011) Artificial structures in harbors and their associated ascidian fauna. *Aquatic Invasions* 6: 413–420, http://dx.doi.org/10.3391/ai.2011.6.4.06
- Goodbody I (1995) Ascidian communities in Southern Belize-a problem in diversity and conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 5: 355–358, http://dx.doi. org/10.1002/aqc.3270050407
- Holloway M, Connell SD (2002) Why do floating structures create novel habitats for subtidal epibiota? *Marine Ecology Progress Series* 235: 43–52, http://dx.doi.org/10.3354/meps23 5043
- Hunter W, Levin L, Kitazato H, Witte U (2012) Macrobenthic assemblage structure and organismal stoichiometry control faunal processing of particulate organic carbon and nitrogen in oxygen minimum zone sediments. *Biogeosciences* 9: 993– 1006, http://dx.doi.org/10.5194/bgd-8-10725-2011
- Johnston EL, Piola RF, Clark GF (2009) The role of propagule pressure in invasion success. In: Rilov G, Crooks JA (eds), Biological invasions in marine ecosystems. Ecological Studies. Berlin Heidelberg: Springer, pp 133–151, http://dx.doi.org/10.1007/978-3-540-79236-9_7
- Katz T, Ginat H, Eyal G, Steiner Z, Braun Y, Shalev S, Goodman-Tchernov B (2015) Desert flash floods form hyperpycnal flows in the coral-rich Gulf of Aqaba, Red Sea. Earth and Planetary Science Letters 417: 87–98, http://dx.doi. org/10.1016/j.epsl.2015.02.025
- Kott P (1985) The Australian Ascidiacea, Part 1. Phlebobranchia and Stolidobranchia. Memoirs of the Queensland Museum 23: 1–440
- Lambert G (2002) Nonindigenous ascidians in tropical waters. Pacific Science 56: 291–298, http://dx.doi.org/10.1353/psc.2002. 0026
- Lambert G (2005) Ecology and natural history of the protochordates. *Canadian Journal of Zoology* 83: 34–50. http://dx.doi.org/10.1139/z04-156
- Lambert G (2009) Adventures of a sea squirt sleuth: unraveling the identity of *Didemnum vexillum*, a global ascidian invader. *Aquatic Invasions* 4: 5–28, http://dx.doi.org/10.3391/ai.2009.4.1.2

- Littler MM, Littler DS (1995) A colonial tunicate smothers corals and coralline algae on the Great Astrolabe Reef, Fiji. *Coral Reefs* 14: 148–149, http://dx.doi.org/10.1007/BF00367232
- López-Legentil S, Ruchty M, Domenech A, Turon X (2005) Life cycles and growth rates of two morphotypes of *Cystodytes* (Ascidiacea) in the western Mediterranean. *Marine Ecology Progress Series* 296: 219–228, http://dx.doi.org/10.3354/meps 296219
- Minchin D, Sides E (2006) Appearance of a cryptogenic tunicate, a *Didemnum* sp. fouling marina pontoons and leisure craft in Ireland. *Aquatic Invasions* 1: 143–147, http://dx.doi.org/10.339 1/ai 2006 1 3 8
- Monniot C, Monniot F, Laboute P (1991) Coral reef ascidians of New Caledonia: IRD Editions, 247 pp
- Olson RR (1985) The consequences of short-distance larval dispersal in a sessile marine invertebrate. *Ecology*: 30–39, http://dx.doi.org/10.2307/1941304
- Pederson J (2005) Marine Invaders in the Northeast: Rapid Assessment Survey of Non-native and Native Marine Species of Floating Dock Communities: Report of the August 3-9, 2003 Survey: MIT Sea Grant College Program 46 pages, available online at http://hdl.handle.net/1721.1/97032
- Perkol-Finkel S, Zilman G, Sella I, Miloh T, Benayahu Y (2006) Floating and fixed artificial habitats: effects of substratum motion on benthic communities in a coral reef environment. *Marine Ecology Progress Series* 317: 9–20, http://dx.doi.org/ 10.1016/j.ecss.2007.10.005
- Pineda MC, López-Legentil S, Turon X (2013) Year-round reproduction in a seasonal sea: Biological cycle of the introduced ascidian Styela plicata in the Western Mediterranean. Marine Biology 160: 221–230, http://dx.doi.org/ 10.1007/s00227-012-2082-7
- Ribes M, Atkinson M (2007) Effects of water velocity on picoplankton uptake by coral reef communities. *Coral Reefs* 26: 413–421, http://dx.doi.org/10.1007/s00338-007-0211-4
- Ribes M, Coma R, Atkinson MJ, Kinzie RA (2005) Sponges and ascidians control removal of particulate organic nitrogen from coral reef water. *Limnology and Oceanography* 50: 1480–1489, http://dx.doi.org/10.4319/lo.2005.50.5.1480
- Rius M, Branch GM, Griffiths CL, Turon X (2010) Larval settlement behaviour in six gregarious ascidians in relation to adult distribution. *Marine Ecology Progress Series* 418: 151– 163, http://dx.doi.org/10.3354/meps08810
- Rius M, Shenkar N (2012) Ascidian introductions through the Suez Canal: The case study of an Indo-Pacific species. Marine Pollution Bulletin 64: 2060–2068, http://dx.doi.org/ 10.1016/j.marpolbul.2012.06.029
- Rocha RM, Faria SB, Moreno TR (2005) Ascidians from Bocas del Toro, Panama. I. Biodiversity. Caribbean Journal of Science 41: 600–612
- Sahade R, Stellfeldt A, Laudien J (2004) Macro-epibenthic communities and diversity of Arctic Kongsforden, Svalbard, in relation to depth and substrate. In: Wiencke C (ed), The coastal ecosystem of Kongsfjorden, Svalbard: synopsis of biological research performed at the Koldewey Station in the years 1991-2003/ [Alfred-Wegener-Institut fur Polar-und Meeresforschung]. Bremerhaven: Alfred-Wegener, 9 pp, available at http://epic.awi.de/10100/1/Sah2004a.pdf
- Saltonstall K (2002) Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences* 99: 2445–2449, http://dx.doi.org/10.1073/pnas.03247799
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671– 675, http://dx.doi.org/10.1038/nmeth.2089
- Shenkar N (2012) Ascidian (Chordata, Ascidiacea) diversity in the Red Sea. Marine Biodiversity 42: 459–469, http://dx.doi. org/10.1007/s12526-012-0124-5

- Shenkar N, Loya Y (2008) The solitary ascidian *Herdmania momus*: native (Red Sea) versus non-indigenous (Mediterranean) populations. *Biological Invasions* 10: 1431–1439, http://dx.doi.org/10.1007/s10530-008-9217-2
- Shenkar N, Bronstein O, Loya Y (2008a) Population dynamics of a coral reef ascidian in a deteriorating environment. *Marine Ecology Progress Series* 367: 163–171, http://dx.doi.org/10.335 4/meps07579
- Shenkar N, Zeldman Y, Loya Y (2008b) Ascidian recruitment patterns on an artificial reef in Eilat (Red Sea). *Biofouling* 24: 119–128, http://dx.doi.org/10.1080/08927010801902083
- Sommer B, Harrison P, Scheffers S (2010) Aggressive colonial ascidian impacting deep coral reefs at Bonaire, Netherlands Antilles. *Coral Reefs* 29: 245–245, http://dx.doi.org/10.1007/s00338-009-0579-4
- Vargas-Ángel B, Godwin L, Asher J, Brainard R (2009) Invasive didemnid tunicate spreading across coral reefs at remote Swains Island, American Sāmoa. Coral Reefs 28: 53–53, http://dx.doi.org/10.1007/s00338-008-0428-x
- Yahel G, Marie D, Genin A (2005) InEx—a direct in situ method to measure filtration rates, nutrition, and metabolism of active suspension feeders. *Limnology and Oceanography: Methods* 3: 46–58, http://dx.doi.org/10.4319/lom.2005.3.46
- Yamaguchi M (1975) Growth and reproductive cycles of the marine fouling ascidians *Ciona intestinalis*, *Styela plicata*, *Botrylloides violaceus* and *Leptoclinum mitsukurii* at Aburatsubo-Moroiso Inlet (central Japan). *Marine Biology* 29: 253–259, http://dx.doi.org/10.1007/BF00391851