

13. Ecology and systematics of the ascidian fauna in the Gulf of Eilat (Aqaba)

(color plates pp. 235-237)

Shenkar N. and Loya Y.

Introduction

Ascidians (Phylum Chordata, Class Ascidiacea), or sea squirts, are the largest and most diverse class of the sub-phylum Tunicata (also known as Urochordata). They comprise approximately 3,000 species found in all marine habitats. Adult ascidians bear little resemblance to typical chordates; their larvae (tadpole larvae) clearly exhibit the four fundamental characteristics of the phylum: a dorsal tubular nerve cord, notochord, pharyngeal gill slits and a post-anal tail. The larvae also possess a sensory vesicle containing two darkly-pigmented sense organs - a light sensitive ocellus and a statolith. Following settlement, the lecithotrophic larvae undergo retrograde metamorphosis during which they lose all of these characteristics except for the pharyngeal gill slits (Millar, 1971). The name “tunicate” (sub-phylum Tunicata) comes from the polysaccharide-containing tunic that envelops the animal and forms a somewhat flexible skeleton. Various proteins, some blood cells and spicules occur in the tunic (Monniot et al., 1991). All ascidians are hermaphrodites, having both male and female organs. They generally avoid self-fertilization by developing only eggs or only sperm at any one time (Newlon et al., 2003). Most solitary ascidians release their eggs and sperm into the water for external fertilization. Under natural conditions, ascidian larvae do not normally disperse very far, often just a few meters or less (Ayre, 1997). The majority of ascidians filter their food from the water-column via an oral siphon that brings water into the pharyngeal chamber; a cloacal siphon then expels the water. Particles suspended in the current are trapped in a mucous net on the gill slits. The net pores range from 0.1 to 0.3, μm allowing ascidians to filter even very small particulate matter, primarily in the range of 0.5 to 2 μm diameter (Bak et al., 1998; Bone et al., 2003). The substances caught in the mucous net are later transported to the stomach for digestion. Ascidian larvae and juveniles are known to be preyed on by various gastropods (Young and Chia, 1984), oysters that are able to trap the larvae (Dalby and Young, 1992), polychaetes (Goodbody, 1962), crabs (Davis, 1988) and fish (Olson and McPherson, 1987; Hurlbut, 1991), especially during their early life stages (Osman and Whitlatch, 1995; 2004). Adult ascidians are preyed on by prosobranch and

nudibranch gastropods (Thompson, 1964; Dalby, 1989). Several solitary ascidians, such as *Halocynthia roretzi* (von Drasche, 1884) and *Microcosmoum sabatieri* (Roule, 1885) provide a human food source in Japan, Korea, Europe and Chile (Lambert, 2005). In the contribution below, we review the major fields of interest in this group, ecological aspects of coral reef ascidians and present new data on the ascidian fauna in the Gulf of Eilat with suggestions for future research.

Significance

As stated by Pourquié (2001) “Ascidians are back in the limelight, with a good chance of staying there.” During the past two decades enormous progress has been achieved in the fields of development, evolution, immunology, natural products and ecology of ascidians. The small ascidian genome, small cell numbers and a short life-cycle make it an attractive model system for developmental biologists (Nishida and Sawada, 2001; Pourquié, 2001). Investigating the phylogenetic position of the subphylum Tunicata (Urochordata) in relation to the other subphyla in the phylum Chordata is crucial to the understanding of possible mechanisms of chordate evolution (Swalla et al., 2000; Zeng and Swalla, 2005). Moreover, the study of self/non-self recognition in ascidians provides important information regarding the evolutionary origin of the vertebrate immune system (Khalturin and Bosch, 2007).

Some species, mainly from the order Phlebobranchia, are known to accumulate vanadium (Lambert, 2005) and store it in specialized blood cells called vanadocytes, reaching a concentration of 10^7 -fold higher than the concentration of vanadium in seawater (Yamaguchi et al., 2006). Since some ascidian species can survive in highly polluted areas, and accumulate arsenic, cadmium, chromium, cobalt, copper, iron, lead, mercury, selenium, tin (as tributyltin) and zinc (Papadopoulou and Kanias, 1977; Philip et al., 2003), they can be used in bioassays for pollutants (Monniot et al., 1986) and as bioindicators (Naranjo et al., 1996).

Ascidians provide a fertile ground for studies in the field of natural products. Similar to sponges and bryozoans, many ascidians avoid predation or fouling by producing noxious secondary metabolites (Teo and Ryland, 1994; 1995; Davis, 1998; Pisut and Pawlik, 2002; McClintock et al., 2004). In addition, ascidians serve as a potential source of new anti-cancer compounds (Wright et al., 1990; Scotto, 2002). Ecteinascidin 743, a highly promising, exceedingly potent antitumor agent, isolated from extracts of the ascidian *Ecteinascidia turbinata* (Herdman, 1880) is currently in phase II/III clinical trials (Liu et al., 2006). Recently, antimalarial compounds have been isolated from the solitary ascidians *Microcosmus goanus* (Michaelsen, 1918), *Ascidia sydneyensis* (Stimpson, 1855) and *Phallusia nigra* (Savigny, 1816; Mendiola et al., 2006).

Introductions of non-indigenous ascidians into harbors in both tropical and temperate waters are now commonplace, with the rate of introductions increasing (Monniot et al., 1991; Lambert and Lambert, 1998; Coles et al., 1999; Lambert, 2002). Most of the

non-indigenous species tolerate wide fluctuations in temperature, salinity, and even pollution. They have a rapid growth rate, usually a short life span of a few months, reach sexual maturity when only a few weeks old, and produce large numbers of short-lived, non-feeding planktonic larvae (Lambert, 2002). These characters, combined with the lack of significant predators, make the ascidians very successful invaders and result in the establishment of huge populations that can significantly change the benthic community of a region (Castilla et al., 2004; Lambert, 2005).

The increasing evidence of the negative effects of non-indigenous ascidians on the natural fauna (Cohen et al., 2005), and the fact that some species have become a significant economic problem (Carver et al., 2003), highlight the need for additional research into the ecology, physiology and taxonomy of this group world-wide.

Systematics

Following the original classification of Lahille (1886), the class Ascidiacea is now divided into three orders based on the structure of the adult branchial sac: Aplousobranchia, Phlebobranchia and Stolidobranchia. This is the current classification used by ascidian taxonomists rather than Perrier's (1898) division that was based upon the position of the gonads and other morphological considerations. The number of families of ascidians is still uncertain, since there are many cases of synonymy and misidentification. For example, whereas the Monniot's counted 13 major families (Monniot et al., 1991), Kott (1992) described 23 families from Australian waters. The interesting peculiarity of ascidian classification is the relatively small number of genera in relation to the number of species. More than half of all known species belong to 10 very large genera, listed here in decreasing order of number of species: *Aplidium*, *Didemnum*, *Molgula*, *Polycarpa*, *Ascidia*, *Styela*, *Eudistoma*, *Pyura*, *Cnemidocarpa*, and *Synoicum*. Ascidian systematics is the domain of specialists, but a keen observer can recognize the well-described common species. Although you "cannot judge an ascidian by its cover," underwater photographs can provide much information and assist in distinguishing one species from another.

The local fauna

The ascidian fauna of the northern Gulf of Aqaba (Eilat) is relatively unknown. The published list of ascidians from Eilat contains 19 species (Pérès, 1962, Table I). This list is certainly incomplete considering the number of ascidian species (approximately 40) reported from the Red Sea (Michaelsen, 1918; 1920a, b). The coral reefs of this region and their associate fauna are well known for their extraordinarily high biodiversity and high number of endemic species (Loya, 1972; Goren, 1993). The relatively low numbers of ascidian species described from Eilat thus appear to be a result of less research and fewer sampling efforts. A new collection of ascidians of this region is

currently being established at the National Collections of Natural History, Tel Aviv University in order to provide an up-to-date species description for the region. This collection already houses several new species records from the region and three new endemic species (Shenkar and Monniot, 2006; N. Shenkar, unpublished data).

The dominant and most common species found along the Red Sea coast of Israel are shown in Plates 1 to 3. p. 235-237. These species are found on both artificial and natural substrates at a depth range of 0 - 30 meters.

Ecological aspects of coral reef ascidians

In general, ascidians constitute a minor benthic component on exposed surfaces of the natural coral reefs. They are often found in cryptic environments such as caves, crevices and the sides or undersides of rocks and corals. In exposed sites, solitary species frequently protect themselves better than colonial species from the dangers of predation, abrasion and physical damage. In such environments their rigid tunic is often covered by epibionts that provide camouflage and physical protection (Monniot et al., 1991). Some colonial species of the family Didemnidae that host the photosynthetic prokaryote symbiont *Prochloron* thrive on surfaces exposed to high irradiance on the reef flat (Kühl and Larkum, 2002). The *Prochloron* symbiont was originally described as unicellular algae (Zoochlorellae) hosted in *Trididemnum symbioticum* tissue collected at Marsa Abu-Zabad, Gulf of Aqaba (Pérès, 1962). Both colonial and solitary species successfully foul various artificial substrates such as jetties and other man-made substrata adjacent to the natural coral reef (Oren and Benayahu, 1998; Paulay et al., 2001).

The rapid spread of several ascidian species (native and non-indigenous) in various tropical regions of the world has been reported (Bak et al., 1996; Lambert, 2002). In a study conducted in Guam, it was noted that all the 15 known non-indigenous ascidian species in this area were found on artificial surfaces. On the natural reefs the three non-indigenous species were small, sparse, and formed only a negligible part of the reef fauna (Paulay et al., 2001; Lambert, 2002). Periodical surveys along the Red Sea coast of Israel have revealed that all the ascidian species recorded on artificial substrates are also found in the natural environment; therefore, there is no evidence for the arrival of non-indigenous species to this region as yet (N. Shenkar, unpublished data).

Recently, a new colonial ascidian, *Botryllus eilatensis* (Shenkar and Monniot, 2006), was observed overgrowing dead coral skeletons and rapidly colonizing artificial substrates in the coral reefs of Eilat. Monthly monitoring of more than 50 fixed ascidian-coral interactions revealed that this species has a seasonal appearance (Shenkar et al., 2008). During spring time (April - June) the average ascidian cover percentage over the available coral area reached approximately 30% and then decreased rapidly during the summer months (Figure 1). This may be a result of the vertical mixing phenomenon that occurs in Eilat every winter and results in higher nutrient levels in the water column (Genin et al., 1995; Lindell and Post, 1995). A significant association was found between visibility (measured as Secchi disk

depth) and ascidian cover percentage (Shenkar et al., 2008). As visibility decreased (which indicates particulate matter present in the water column) the ascidian cover percentage increased significantly due to the additional food supply. Gradually, as the water column became depleted, the percentage of ascidian cover declined until the following winter. Although year-round reproduction is typical to tropical coral reef ascidians (Goodbody, 1961; van Duyl et al., 1981) *B. eilatensis* only reproduces sexually from August to October. Therefore it is suggested that, in the case of *B. eilatensis*, there is first an investment in asexual growth during the winter months following the vertical mixing event, and then in sexual reproduction as the water

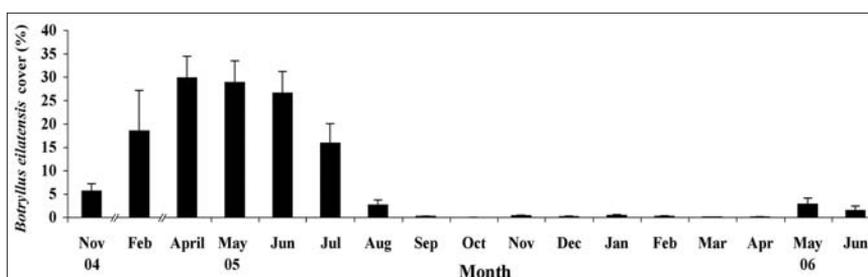


Figure 1. Seasonal variation of mean percentages of *Botryllus eilatensis* cover (+ SE) relative to available coral area from November 2004 to June 2005 (adapted from Shenkar et al., 2008).

temperature rises during the summer months.

Bak et al. (1996) reported a 9-fold increase in the density of *Trididemnum solidum* (van Name, 1902), a colonial ascidian, along the 84 km of fringing reef in Curaçao over a period of 15 years. They suggested that increased human activity had resulted in an environment less favorable to corals, but in which the ascidians would have a competitive advantage. Such conditions also seem to exist in the northern Gulf of Aqaba (Eilat). Due to a rise in anthropogenic activity the coral reefs in this region are experiencing increased eutrophication (Loya, 2007). This environment creates favorable conditions for filter-feeding organisms such as ascidians and sponges, providing an advantage in competition for space with reef-building corals and possibly eventuating in booming populations of native species (Smith et al., 1981; Wilkinson and Cheshire, 1990; Bak et al., 1998). In deteriorating environments, dead portions of corals exhibiting partial mortality, may be rapidly colonized by ascidians and other filter-feeding organisms, preventing both regeneration of the coral tissue and recruitment by coral planulae (Aronson et al., 2002).

Another interesting ecological aspect in the study of Red Sea ascidians is the opportunity that it offers to conduct comparative studies of the same species in the Mediterranean. This allows the study of ascidian distribution and introductions via the Suez Canal. The nearly tropical temperature and salinity conditions along

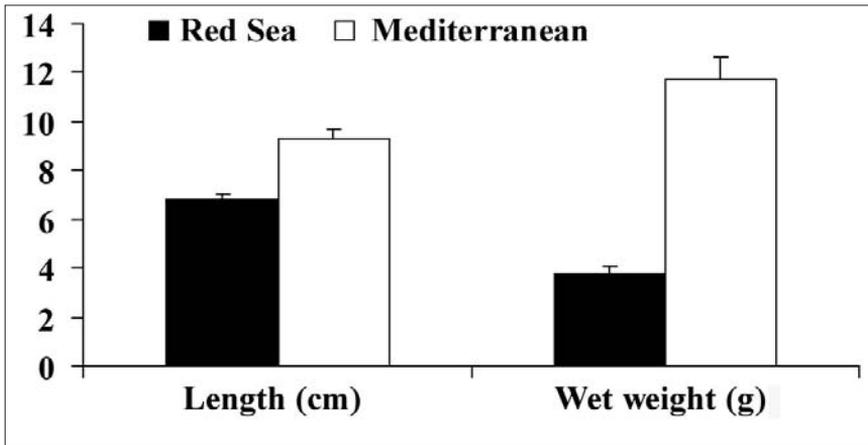


Figure 2. *Herdmania momus*. Size comparison- average (+ SE) length (cm) and weight (g) of individuals from the Red Sea (black bars, n = 104) and Mediterranean Sea (blank bars, n = 101) adapted from Shenkar and Loya, 2008

the Mediterranean coast of Israel measured during the summer, combined with the relatively low species diversity in this region (Spanier and Galil, 1991; Fishelson, 2000), results in thriving populations of Red Sea species along the Levantine coasts. For example, *Herdmania momus* (Savigny, 1816) is a common solitary ascidian found along the Mediterranean and Red Sea coasts of Israel. However, the findings show clear differences in *H. momus* populations between the two sites. For example, *H. momus* specimens collected from the Mediterranean (non-indigenous population) were significantly larger in size compared to those from the Red Sea (native population, Figure 2). This may be a result of the higher organic material ($\sim 0.35 \mu\text{g/l}$ chlorophyll *a*, IOLR database, <http://www.ocean.org.il>) in the coastal waters of the Mediterranean in contrast to the oligotrophic conditions in the coral reefs of Eilat ($\sim 0.16 \mu\text{g/l}$ chlorophyll *a*, NMP database, <http://www.ini-eilat.ac.il>). In addition, it was found that *H. momus* in the Mediterranean is restricted to artificial substrates, is found at greater depths, has different symbionts and has a limited reproduction season (Shenkar and Loya, 2008). These differences are attributed to both a-biotic factors, such as different temperature ranges and wave exposure, and biotic factors that inhibit the establishment of *H. momus* on the natural rocky substrate. Future results from molecular analysis may contribute to a better understanding of the arrival and dispersal modes of this species.

Summary

The Ascidiacea constitute a unique group of invertebrates that serves as an essential source for a variety of studies in fields ranging from development and evolution to immunology, natural products and ecology. Although in the past two decades

enormous progress has been achieved in these fields, ascidian ecology has barely been studied in coral reef environments. The ascidian fauna of the northern Gulf of Aqaba (Eilat) are relatively unknown. Only 19 ascidian species have been described from this region, a very low number considering the high number of ascidian species reported in the past from the Red Sea and the high rates of endemism reported for other groups from this region. In recent years a rise in anthropogenic activity, resulting in increased eutrophication in this area, has created favorable conditions for filter-feeding organisms such as ascidians. This environment may provide the ascidians with an advantage over reef-building corals in competition for settlement on newly available substrate. This is illustrated by a new species of colonial ascidians, *Botryllus eilatensis* (Shenkar and Monniot, 2006), observed overgrowing dead coral skeletons and rapidly colonizing artificial substrates (Shenkar et al., 2008). Recent reports from various tropical and temperate regions of the world have described the rapid spread of several ascidian species (native and non-indigenous), with negative effects on the local fauna. This has led to renewed interest in this group, particularly as indicators of disturbed environments. It is therefore imperative to continue monitoring the ascidian population, and to study further the ecological aspects of the ascidian fauna of the Gulf of Eilat.

Acknowledgements

We are grateful to R. Segal, O. Bronstein, Y. Zeldman, O. Barneah and N. Sokolover for their technical support in the field, to A. Gur for his kind assistance, to E. Kramarsky-Winter, N. Paz and V. Wexler for editorial assistance, and to F. Monniot and X. Turon for their assistance with taxonomic identification. N.S. would like to thank the JNF-Rieger Foundation for their financial support. This research was a part of N.S. PhD study and was supported by the Israel Science Foundation (ISF) and the Raynor Chair for Environmental Conservation Research to YL.

Family	Species
Polycitoridae	<i>Polycitor torensis</i> (Michaelson)
	<i>Distaplia stylifera</i> (Kowalevsky)
Polyclinidae	<i>Amaroucium lobatum</i> (Savigny)
Didemnidae	<i>Trididemnum savignyi</i> (Herdman)
	<i>Trididemnum symbioticum</i> (Pères)
	<i>Diplosoma listerianum</i> (Milne-Edw)
	<i>Didemnum candidum</i> (Savigny)
Perophoridae	<i>Ecteinascidia conklini</i> (Berrill)
Asciidiidae	<i>Ascidia savignyi</i> (Hertmeyer)
	<i>Phallusia arabica</i> (Savigny)
	<i>Phallusia nigra</i> (Savigny)
Corellidae	<i>Rhodosomea verecundum</i> (Ehrenberg)
Pyuridae	<i>Pyura gangelion</i> (Savigny)
	<i>Herdmania momus</i> (Savigny)
	<i>Halocynthia spinosa</i> (Sluiter)
Styelidae	<i>Styela canopus</i> (Savigny)
	<i>Polycarpa mytiligera</i> (Savigny)
Botryllidae	<i>Metrocarpa nigrum</i> (Herdman)
	<i>Metrocarpa magnicoecum</i> (Hartmeyer)

Table I. The published ascidian species list from the Gulf of Eilat (from Pères, 1962)

References

- Aronson, R.B., Precht, W.F., Toscano, M.A., and Koltes, K.H.** 2002. The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology* 141: 435-447.
- Ayre, D.J., Davis, A.R., Billingham, M., Llorens, T., and Styan, C.** 1997. Genetic evidence for contrasting patterns of dispersal in solitary and colonial ascidians. *Marine Biology* 130: 51-62.
- Bak, R.P.M., Lambrechts, D.Y.M., Joenje, M., Nieuwland, G., and Van Veghel, M.L.J.** 1996. Long-term changes on coral reefs in booming populations of a competitive colonial ascidian. *Marine Ecology Progress Series* 133: 303-306.
- Bak, R.P.M., Joenje, M., de Jong, I., Lambrechts, D.Y.M., and Nieuwland, G.** 1998. Bacterial suspension feeding by coral reef benthic organisms. *Marine Ecology Progress Series* 175: 285-288.
- Bone, Q., Carre, C., and Chang, P.** 2003. Tunicate feeding filters. *Journal Marine Biology Association U.K.* 83:907-919.
- Carver, C.E., Chisholm, A., and Mallett, A.L.** 2003. Strategies to mitigate the impact of *Ciona intestinalis* (L.) biofouling on shellfish production. *Journal of Shellfish Research* 22: 621-631.
- Castilla, J.C., Lagos, N.A., and Cerda, M.** 2004. Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a midintertidal rocky shore. *Marine Ecology Progress Series* 268: 119-130.
- Cohen, A.N., Harris, L.H., Bingham, B.L., Carlton, J.T., Chapman, J.W.,**

- Lambert, C.C., Lambert, G., Ljubenkov, J.C., Murray, S.N., Rao, L.C., Reardon, K., and Schwindt, E.** 2005. Rapid assessment survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. *Biological Invasions* 7 (6): 995-1002.
- Coles, S.L., DeFelice, R.C., Eldredge, L.G., and Carlton J.T.** 1999. Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian Islands. *Marine Biology* 135: 147-158.
- Dalby, J.E.** 1989. Predation of ascidians by *Melongena corona* (Neogastropoda: Melongenidae) in the northern Gulf of Mexico. *Bulletin of Marine Science* 45: 708-712.
- Dalby, J.E., and Young, C.M.,** 1992. Role of early post settlement mortality in setting the upper depth limit of ascidians in Florida epifaunal communities. *Marine Ecology Progress Series* 80: 221-228.
- Davis, A.R.** 1988. Colony regeneration following damage and size dependent mortality in the Australian ascidian *Podoclavella moluccensis* Sluiter. *Journal of Experimental Marine Biology and Ecology* 123: 269-286.
- Davis, A.R.** 1998. Antifouling defense in a sub tidal guild of temperate zone encrusting invertebrates. *Biofouling* 12: 305-320.
- Duyl, F.C., van, Bak, R.P.M., and Sybesma, J.** 1981. The ecology of the tropical compound *Trididemnum solidum* I. Reproductive strategy and larval behavior. *Marine Ecology Progress Series* 6: 35-42.
- Fishelson, L.** 2000. Marine animal assemblages along the littoral of the Israeli Mediterranean seashore: The Red-Med communities of species. *Italian Journal of Zoology* 67: 393-415.
- Genin, A., Lazar, B., and Brenner, S.** 1995. Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature* 377 (6549): 507-510.
- Goodbody, I.** 1961. Continuous breeding in three species of tropical ascidians. *Proceedings of the Zoological Society of London* 136: 403-409.
- Goodbody, I.** 1962. The biology of *Ascidia nigra* (Savigny). I. Survival and mortality in an adult population. *Biological Bulletin* 122: 40-51.
- Goren, M.** 1993. Statistical aspects of the Red Sea ichthyofauna. *Israel Journal of Zoology* 39: 293-298.
- Hurlbut, C.J.,** 1991. The effects of larval abundance, settlement and juvenile mortality on the depth distribution of a colonial ascidian. *Journal of Experimental Marine Biology and Ecology* 150: 183-202.
- Khalturin, K.,** and Bosch, T.C.G. 2007. Self/nonself discrimination at the basis of chordate evolution: limits on molecular conservation. *Current Opinion in Immunology* 19 (1): 4-9.
- Kott, P.,** 1992. The Australian Ascidiacea. Part 3: Aplousobranchia (2). *Memoirs of the Queensland Museum* 32 (2): 375-620.
- Kühl, M., and Larkum, A.W.D.** 2002. The microenvironment and photosynthetic performance of *Prochloron* sp. in symbiosis with didemnid ascidians. Chapter in: Seckbach, J. (ed.), *Cellular origin and life in extreme habitats* Vol. 3: *Symbiosis, mechanisms and model systems*. Kluwer Acad. Publ., Dordrecht (2002), pp. 273-290.

- Lahille, F.** 1886. Sur la classification des tuniciers. *CR Academic Science Paris* 102: 446-448.
- Lambert, C.C., and Lambert, G.** 1998. Non-indigenous ascidians in southern California harbors and marinas. *Marine Biology* 130: 675-688.
- Lambert, G.,** 2002. Nonindigenous ascidians in tropical waters. *Pacific Science* 56: 291-298.
- Lambert, G.,** 2005. Ecology and natural history of the protochordates. *Canadian Journal of Zoology* 83: 34-50.
- Lindell, D.,** and Post, A.F. 1995. Ultraphytoplankton succession is triggered by deep winter mixing in the Gulf of Aqaba (Eilat), Red Sea. *Limnology and Oceanography* 40 (6): 1130-1141.
- Liu, Z.Z., Wang, Y., Tang, Y.F., Chen, S.Z., Chen, X.G.,** and Li, H.Y. 2006. Synthesis and antitumor activity of simplified ecteinascid in saframycin analogs. *Bioorganic & Medicinal Chemistry Letters* 16 (5): 1282-1285.
- Loya, Y.** 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Marine Biology* 13: 100-123.
- Loya, Y.** 2007. How to influence environmental decision makers? The case of Eilat (Red Sea) coral reefs. *Journal of Experimental Marine Biology and Ecology* 344 (1): 35-53.
- McClintock, J.B., Amsler, M.O., Amsler, C.D., Southworth, K.J., Petrie, C., and Baker, B.J.** 2004. Biochemical composition, energy content and chemical antifeedant and antifoulant defenses of the colonial Antarctic ascidian *Distaplia cylindrica*. *Marine Biology* 145: 885-894.
- Mendiola, J., Hernández, H., Sariego, I., Rojas, L., Otero, A., Ramírez, Chávez, M.D.L.A., Payrol, J.A., and Hernández, A.** 2006. Antimalarial activity from three ascidians: an exploration of different marine invertebrate phyla. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 100 (10): 909-916.
- Millar, R.H.,** 1971. The biology of ascidians. *Advances in Marine Biology* 9: 1-100
- Michaelsen, W.** 1918. Ascidia Ptychobranchia und Dictyobranchia des Roten Meeres. Expedition Schiff Pola in das Rote Meer, nördliche und südliche Hälfte 1895 1896 1897/1898. *Zoologische Ergebnisse* 32: 1-120, 3 pls.
- Michaelsen, W.** 1920a. Die Ascidae Krikobranchiae des Roten Meeres: Clavelinidae und Synoicidae. In: Expedition S.M. Schiff *Pola* in das Rote Meer, nördliche und südliche Hälfte 1895/1896 – 1897/1898. *Zoologische Ergebnisse* 33. Denkschriften der Akademie der Wissenschaften in Wien 97: 1-38.
- Michaelsen, W.** 1920b. Die Krikobranchien Ascidien des westlichen Indischen Ozeans: Didemniden. *Jahrbuch der Hamburgischen wissenschaftlichen Anstalten* 37: 1-76.
- Monniot, F., Giannesini, P.J., Oudot, J., and Richard, M.L.** 1986. Ascidiées: “salissures” marines et indicateurs biologiques (métaux, hydrocarbures). *Bulletin du Museum D'Histoire Naturelle, Paris* 8: 215-245.
- Monniot, C., Monniot, F., and Laboute, P.** 1991. *Coral reef ascidians of New Caledonia*. Orstom, Paris.

- Naranjo, S.A., Carballo, J.L., and Garcia-Gomez, J.C.** 1996. Effects of environmental stress on ascidian populations in Algeciras Bay (southern Spain). Possible marine bioindicators? *Marine Ecology Progress Series* 144: 119–131.
- Newlon, A.W.I., Yund, P.O., and Stewart-Savage, J.** 2003. Phenotypic plasticity of reproductive effort in a colonial ascidian, *Botryllus schlosseri*. *Journal of Experimental Zoology Part A: Comparative Experimental Biology* 297 (2): 180–188.
- Nishida, H., and Sawada, K.** 2001. Macho-1 encodes a localized mRNA in ascidian eggs that specifies muscle fate during embryogenesis. *Nature* 409: 724–729.
- Olson, R.R., and McPherson, R.** 1987. Potential vs. realized larval dispersal: fish predation on larvae of the ascidian *Lissoclinum patella* (Gottschaldt). *Journal of Experimental Marine Biology and Ecology* 110: 245–256.
- Oren, U., and Benayahu, Y.** 1998. Didemnid ascidians: rapid colonizers of artificial reefs in Eilat (Red Sea). *Bulletin of Marine Science* 63: 199–206.
- Osman, R.W., and Whitlatch, R.B.** 1995. Predation on early ontogenetic life stages and its effect on recruitment into marine epifaunal community. *Marine Ecology Progress Series* 117: 111–126.
- Osman, R.W., and Whitlatch, R.B.** 2004. The control of development of a marine benthic community by predation on recruits. *Journal of Experimental Marine Biology and Ecology* 311: 117–145.
- Papadopoulou, C., and Kanias, G.D.** 1977. Tunicate species as marine pollution indicators. *Marine Pollution Bulletin* 8: 229–231.
- Paulay, G., Kirkendale, L., Lambert, G., and Starmer, J.** 2001. The marine invertebrate biodiversity of Apra Harbor: Significant areas and introduced species, with focus on sponges echinoderms and ascidians. Prepared for Naval Activities Guam, under Cooperative Agreement N68711-97-LT-70001.
- Pérès, J. M.** 1962. Sur une collection d'ascidies de la côte israélienne de la Mer Rouge et de la péninsule du Sinai. *Bulletin of Sea Fisheries Research Station, Haifa* 30: 39–47.
- Perrier, J.O.E.** 1898. Note sur la classification des Tuniciers. *CR Academic Science Paris* 126: 1758–1762.
- Philip, R.B., Leung, F.Y., and Bradley, C.** 2003. A comparison of the metal content of some benthic species from coastal waters of the Florida panhandle using high-resolution inductively coupled plasma mass spectrometry (ICP–MS) analysis. *Archives of Environmental Contamination and Toxicology* 44: 218–223.
- Pisut, D.P., and Pawlik, J.R.** 2002. Anti-predatory chemical defenses of ascidians: secondary metabolites or inorganic acids? *Journal of Experimental Marine Biology and Ecology* 270: 203–214.
- Pourquié, O.** 2001. A macho way to make muscles. *Nature* 409: 679–680.
- Scotto, K.W.** 2002. ET-743: a novel marine-derived anti-tumor agent. *Anti Cancer Drugs* 13:3–6.
- Shenkar, N., and Monniot, F.** 2006. A new species of the genus *Botryllus* (Asciacea) from the Red Sea. *Zootaxa* 1256: 11–19.
- Shenkar N., and Loya, Y.** 2008. Ecology of the ascidian *Herdmania momus*

(Savigny, 1816) in the Mediterranean and Red Sea. *Biological Invasions* published online 30 January 2008

Shenkar N., Bronstein O. and Loya, Y. in press. Population dynamics of a coral reef ascidian in a deteriorating environment. Submitted to *Marine Ecology Progress Series*.

Smith, S. V., Kummerer, W. J., Laws, E. A., Brock, R. E., and Walsh, T. W. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35: 279-402.

Spanier, E., and Galil, B.S. 1991. Lessepsian migration - a continuous biogeographical process. *Endeavour* 15: 102 – 106.

Swalla, B.J., Cameron, C.B., Corley, L.S., and Garey, J.R. 2000. Urochordates are monophyletic within the deuterostomes. *Systematic Biology* 49: 52-64.

Teo, S.L.M., and Ryland, J.S. 1994. Toxicity and palatability of some British ascidians. *Marine Biology* 120: 297–303.

Teo, S.L.M., and Ryland, J.S. 1995. Potential antifouling mechanisms using toxic chemicals in some British ascidians. *Journal of Experimental Marine Biology and Ecology* 188: 49–62.

Thompson, T.E. 1964. Grazing and the life cycles of British nudibranchs. *British Ecological Society Symposium* 4: 275–297.

Wilkinson, C.R., and Cheshire, C. 1990. Comparisons of sponge populations across the Barner Reefs of Australia and Belize. Evidence for higher productivity in the Caribbean. *Marine Ecology Progress Series* 67: 285-294.

Wright, A.E., Forleo, D.A., Gunawardana, G.P., Gunasekera, S.P., Koehn, F.E., and McConnell, O.J. 1990. Antitumor tetrahydroisoquinoline alkaloids from the colonial ascidian *Ecteinascidia turbinata*. *Journal of Organic Chemistry* 55: 4508–4512.

Yamaguchi, N., Amakawa, Y., Yamada, H., Ueki, T., and Michibata, H. 2006. Localization of Vanabins, vanadium-binding proteins, in the blood cells of the vanadium-rich ascidian, *Ascidia sydneiensis samea*. *Zoological Science* 23 (10): 909-915.

Young, C.M., and Chia, F.S. 1984. Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. *Marine Biology* 81: 61–68.

Zeng, L., and Swalla, B.J. 2005. Molecular phylogeny of the protochordates: Chordate evolution. *Canadian Journal of Zoology* 83(1): 24–33.

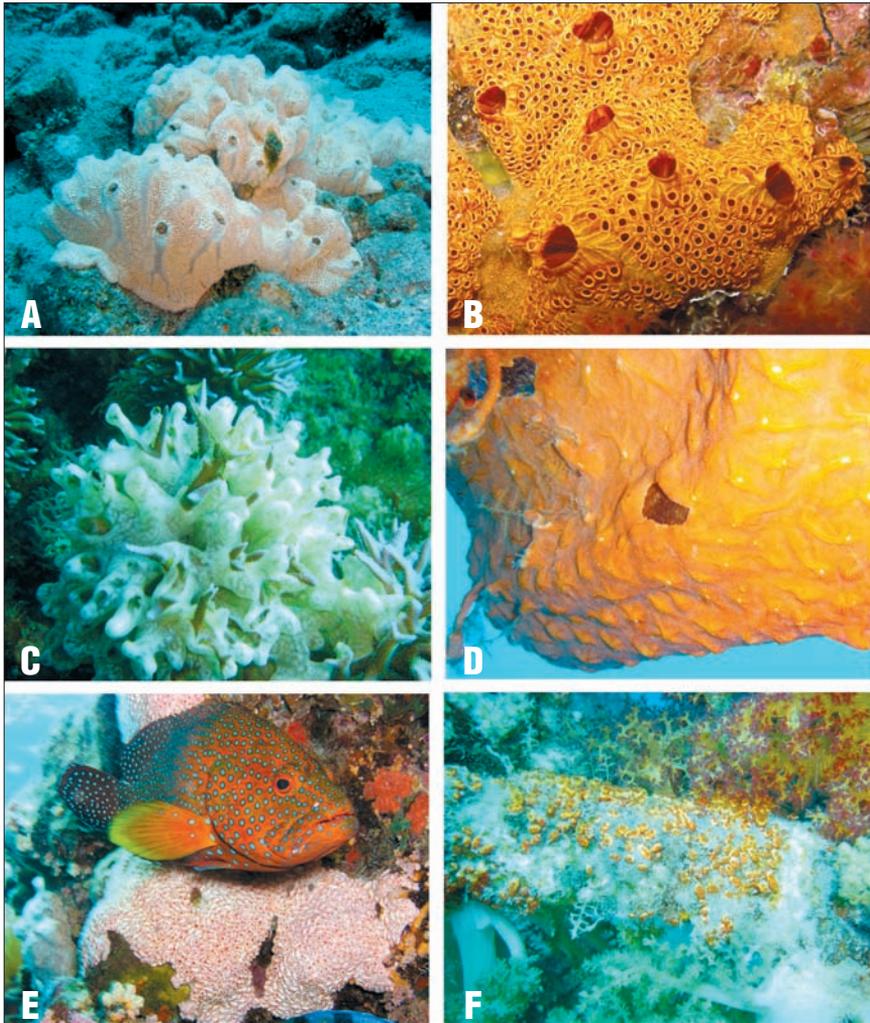


Plate 1. Common colonial ascidian species found along the Red Sea coast of Israel at a depth range of 0 – 30 meters. a, b) Both color morphs of *Botryllus eilatensis* (Shenkar and Monniot, 2006) c) *Didemnum candidum* (Savigny, 1816) d) *Didemnum granulatum* (Tokioka, 1954) e) *Eusynstyela latericius* (Sluiter, 1904) morph I (photo: A. Gur) f) *Eusynstyela latericius* morph II.

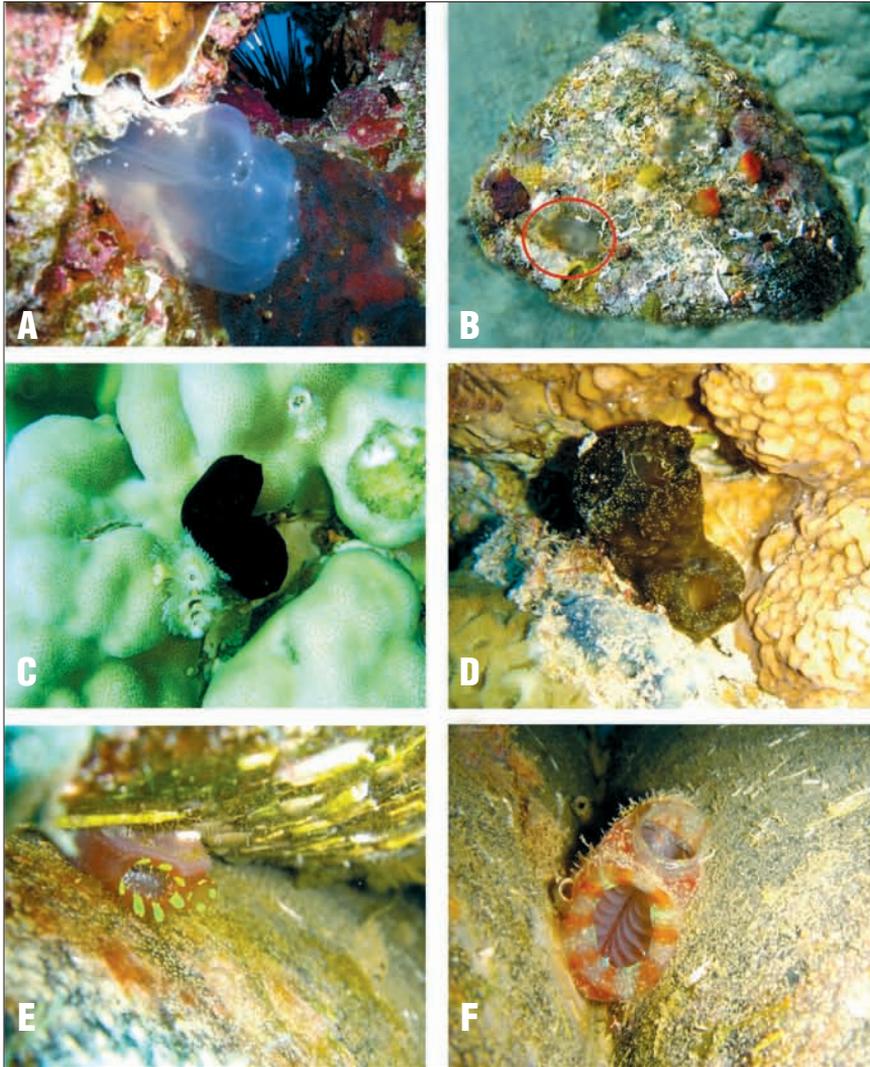


Plate 2. Common solitary ascidian species found along the Red Sea coast of Israel at a depth range of 0–30 meters. a) *Rhopalaea* sp., b) *Ascidia cannelata* (Oken, 1820, circled in red), c) *Phallusia nigra* (Savigny, 1816), d) *Phallusia arabica* (Savigny, 1816), e) *Rhodosoma turcicum* (Savigny, 1816), f) *Herdmania momus* (Savigny, 1816).

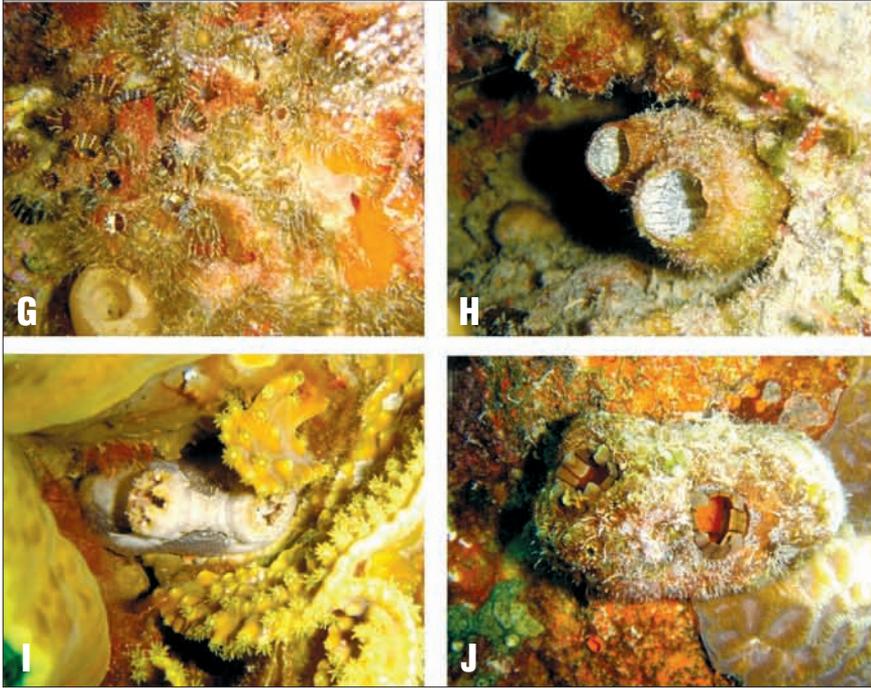


Plate 3. Common solitary ascidian species found along the Red Sea coast of Israel at a depth range of 0 – 30 meters. g) *Boltenia sp.*, h) *Polycarpa mytiligera* (Savigny, 1816), i) *Halocynthia spinosa* (Sloiter, 1905), j) *Pyura gangelion* (Savigny, 1816).