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# Fouling reefal communities on artificial reefs: Does age matter?

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**Abstract**

Man-made submerged structures, including shipwrecks, offering substrata for fouling organisms and fish, have been classified secondarily as artificial reefs (ARs). The current approach in AR design is that of low-profile structures placed on the seabed and attempting to mimic natural reef (NR) communities with the aim of mitigating degraded marine ecosystems. To examine the validity of this concept, a long-term comparison of the developing AR fouling communities to those of nearby NRs is required. A survey of the fouling reefal organisms was conducted on seven shipwrecks (Red Sea, Egypt), comprising three young (*ca* 20 years old) and four old ( > 100 years old) unplanned ARs, in comparison to nearby NR communities. The hypothesis tested was that the age of the ARs shapes the structure of their fouling coral communities. The results demonstrated distinct differences between ARs and NRs and between young and old ARs. While the species composition on ARs may resemble that of NRs after approximately 20 years, obtaining a similar extent of coral cover may require a full century. Moreover, differences in structural features between ARs and NRs may lead to differences in species composition that persist even after 100 years.

**Keywords:** *Artificial reefs, community structure, coral reefs, shipwreck, Red Sea*

## Introduction

Man-made submerged structures, including shipwrecks, that offer substrata for settlement of fish and fouling assemblages, i.e. all biota that at any point in time develop on an artificial substratum (Svane & Petersen, 2001; Yan & Yan, 2003), have been classified secondarily as artificial reefs (ARs) (Seaman & Jensen, 2000). Such ARs are common worldwide and can be considered as a natural experiment in reef community development, accessible for monitoring (e.g. Wendt et al. 1989; Rilov & Benayahu, 2000; Perkol-Finkel & Benayahu, 2004). While using planned ARs for research purposes has many advantages, including the ability to design the structure according to the goals of the AR, and to control the experimental design in terms of tested variables, number of repetitions and controls, such ARs usually reflect the time-scale of a research study (a few years). In contrast, while studying unplanned ARs such as shipwrecks allows a lesser degree of control over the above factors, it does provide access to long-term processes of fouling community development on artificial substrata. Moreover, shipwrecks have been purposefully utilized worldwide, mainly for recreational diving or fishing (Baine, 2001), some of which have been studied following several years of submersion, at times in relation to NRs (Wilhelmsson et al. 1998). Although a few studies have dealt with the physical aspects of shipwrecks such as substratum orientation and structural complexity (Baynes & Szmant, 1989; Wendt et al. 1989), these were of wrecks submerged for less than two decades.

Over the years, ARs have been used for various economic and ecological applications, including the increase of fishery yield and production, as well as for recreational diving, prevention of trawling, control of beach erosion, conservation of biodiversity, and to test ecological theories (Seaman & Jensen, 2000; Baine, 2001). Since shipwrecks and designed ARs have a strong appeal for recreational divers, they also have a potential significance in diverting diving pressure away from natural reefs (NRs), and thus contributing to their conservation and, where applic-

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able, also to their restoration (Rilov & Benayahu, 1998; Wilhelmsson et al. 1998). However, despite the numerous studies conducted on ARs, there are still many knowledge gaps regarding their performance and potential applications. For example, the attraction *vs* production issue is still under debate (Pickering & Whitmarsh, 1997; Svane & Petersen, 2001), as is the feasibility of restoring degraded NRs using ARs (Spieler et al. 2001), and the need remains to determine the time frame necessary for the development of AR fouling communities beyond the initial successional phases (Wendt et al. 1989; Perkol-Finkel & Benayahu, 2005).

A widespread approach in AR design is to place on the seabed low profile structures with few or no projecting elements, attempting to mimic NR communities (Seaman & Jensen, 2000), with the aim of mitigating and enhancing damaged marine ecosystems (Svane & Petersen, 2001). In order to test the validity of this concept more fully, long-term comparisons of the developing benthic communities of the ARs to those of nearby NRs are required (Carr & Hixon, 1997). Only a few studies have followed the community development of an AR for a prolonged period of time, beyond its initial successional phases (Aseltine-Neilson et al. 1999; Clark & Edwards, 1999; Relini et al. 2000). Similarly, studies directly comparing ARs and NRs are relatively scarce (Chou & Lim, 1986; Wilhelmsson et al. 1998; Perkol-Finkel & Benayahu, 2004; 2005). Wendt et al. (1989) found that on shipwrecks in South Carolina, corals comprised a much greater proportion of the total biomass on older ARs (8 – 10 years) than on younger ones (3.5 – 4.5 years), and that the species composition of even the former differed from that of nearby NR.

Recently, Perkol-Finkel and Benayahu (2005) demonstrated that the time frame required for an AR community in a coral reef ecosystem (Eilat, Red Sea) to reach maturity might last well over a decade. In a study comparing 34- and 14-year-old ARs with adjacent NRs in Eilat, Perkol-Finkel and Benayahu (2004) revealed community differences between the two ARs and between them and their adjacent NRs. These differences resulted from the synergistic effect of an array of biotic and abiotic factors, such as life history traits of the recruited organisms, environmental variables and structural features of the ARs. Some structural features such as surface texture and complexity greatly influence the settlement of fouling organisms (Thomason et al. 2002), while others, such as the composition of the substratum may be of lesser importance (Glasby, 2000; Qiu et al. 2003).

Whether fouling communities on an AR will eventually mimic its neighboring NR communities, and if so, to what degree, has as yet to be determined. Therefore, it is imperative both to ascertain the time frame needed to achieve a well-developed AR community, in comparison to that of nearby NRs, and to define the environmental features that will shape its community structure. Studies that monitor experimentally designed ARs have by their nature been limited to a relatively short period of time. In the present study, advantage was taken of seven ARs in the form of shipwrecks, whose time of sinking was known, and a survey was conducted of their fouling reefal communities. The shipwrecks (termed hereon ARs), all located in close vicinity to each other in the northern Red Sea (Egypt), comprised two age categories, composed of three young (*ca* 20 years old) and four old ( > 100 years old) ARs. These unplanned ARs were utilized to test the hypothesis that the age of an AR shapes the structure of its fouling reefal communities and its degree of resemblance to its adjacent NR.

A comparative study of the benthic communities of the shipwrecks and of their surrounding NRs was conducted. Specifically, the authors i) compared the coral community structure of ARs with that of adjacent NRs, ii) compared the communities of young and old ARs, iii) examined possible correlations between the structural features of the ARs and their communities and iv) assessed the time frame required for establishing a well-developed AR fouling community, beyond the initial successional phases. This is the first survey in a coral reef environment to have adopted such an approach, examining shipwrecks submerged for over 15 years. The approach enabled the authors to elucidate the relationship between the time frame, scaled in decades, and the structural features of AR coral communities, in comparison to adjacent NR communities.

## Materials and methods

### *Study sites*

The study was conducted in the northern Red Sea (Egypt) during September 2000. Seven shipwrecks (ARs) and four of their adjacent NRs were examined. Four of the ARs were located at Sha'ab Abu Nuhas; one west of the Strait of Gubal and one at Sa'ab Ali (see Figure 1). The coordinates, year of sinking, dimensions and depth of all the ARs are presented in Table I. The latter data and the following descriptions of the various ARs were mainly derived from the authors' own observations and *via* http://www.touregypt.net. All the ships had similar structures and dimensions; all were composed of steel and were located at a similar depth range that was also comparable to the depth of their adjacent NRs (see Table I). There were four old ARs, over 100 years since submersion when surveyed, and three young ARs, *ca* 20 years old.

The oldest AR studied was the Carnatic (see Figure 1). It lay parallel to the reef on its port side, partly on the NR and partly on the sandy bottom. Its fore and aft sections were mostly intact, still linked by the damaged area where the ship had broken up. It offered vertical surfaces on the deck area and horizontal ones on the hulls. The adjacent NR was nearly vertical, facing west. The next oldest AR was the Dunraven (see Figure 1). It lay almost completely upside down, with its port side along the adjacent NR. Most of the surveyed surfaces comprised horizontal parts of the ship's bottom, as well as some vertical hull surfaces. The adjacent NR had a steep slope. The Kingston (aka Sarah H), lay right side up with its bow smashed into the reef, while the stern remained mostly intact (Figure 1). The hull of the ship offered vertical surfaces, while large metal plates, debris of the amidships section, offered horizontal ones. The adjacent NR had a moderate slope. The youngest of the old ARs studied was the Ulysses, which lay mostly on its port side on the reef (Figure 1). Most of its decking had rotted, revealing its metal framework. The bow of the ship was mostly broken up, its amidships opened up, but the hulls were held together by metallic cross bars, offering mainly vertical surfaces. The adjacent NR had a steep slope.

The three young ARs were all in the same location (see Figure 1). The Kimon M lay on the base of the NR on its starboard side, mostly on sandy bottom. While its front has been reduced to a scattered field of debris, its metal infrastructure has remained intact. Due to its position, the ship's hull was nearly horizontal and its deck vertical. The adjacent NR was mostly lifeless due to recent *Acanthaster planci* (crown-of-thorns starfish) attacks (see Hassan et al. 2002), and therefore was not surveyed. The Crisoula K, slightly younger than the Kimon M, had its main body positioned upright; its stern nearly separated from the main body, and the bow severely damaged by the impact and by wave action due to its shallow position (Figure 1). It also lay aground on a devastated NR severely affected by *A. planci*, and was therefore not surveyed. The youngest AR surveyed, the Giannis D, was broken into three sections: the bow rested nearly vertically, the amidships rested horizontally, and the stern, which was tilted at approximately 45°, lay nearly parallel to the NR. The adjacent NR was mostly horizontal. Since neither of the other young ARs (Kimon M and Crisoula K) had an adjacent living NR for comparison, the NR adjacent to the Giannis D was used as a reference NR for all three young ARs in all comparisons and statistical analyses.

*Data collection*

In order to study the community structure of the benthic fouling communities of both the shipwrecks (ARs) and the NRs, a series of 2 meter long and 0.1 meter wide transects were made, using SCUBA, following the methodology described in Perkol-Finkel and Benayahu (2004). This modification of Loya's (1972) line transect method was designed to increase the probability of recording data from complex artificial structures that include many gaps as well as protruding appendages. Transects were made on the two reef types at their respective depths. Transects on the ARs were performed on areas with rich fouling communities, and on the NRs on pristine reef areas. Within these areas, the location of the transects was chosen haphazardly on both reef types. Table I presents the total number of transects conducted on each AR and NR. Transects were

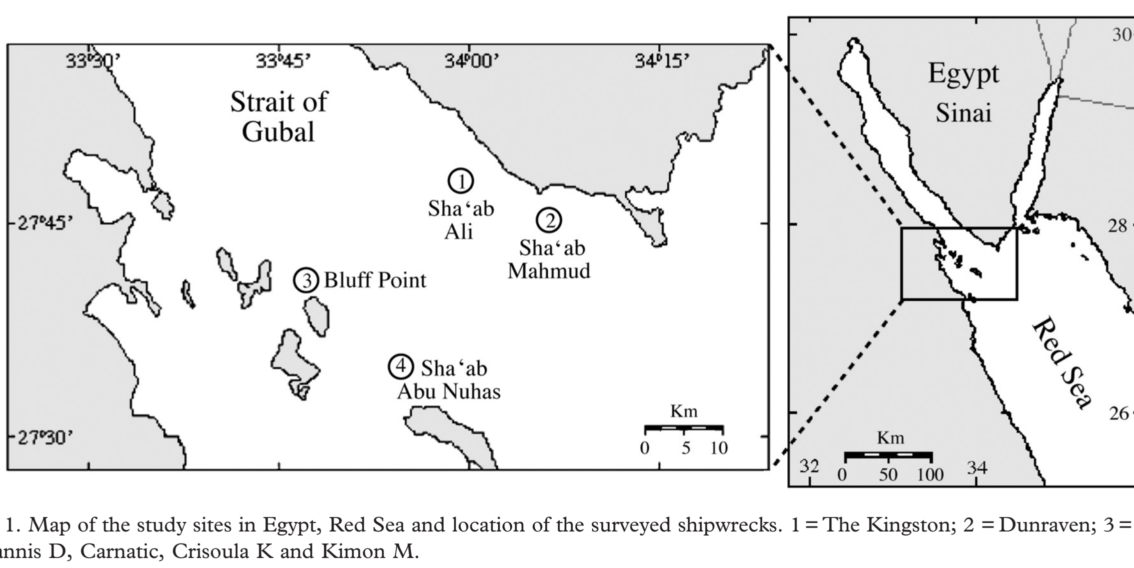



Figure 1. Map of the study sites in Egypt, Red Sea and location of the surveyed shipwrecks. 1 = The Kingston; 2 = Dunraven; 3 = Ulysses; 4 = Giannis D, Carnatic, Crisoula K and Kimon M.

Table I. Features of the studied shipwrecks: name, coordinates, year of sinking, age when surveyed (in brackets), dimensions (m), depth range in which transects were made (m) and number of 2-meter transects conducted at each.

| Wreck's name | Carnatic | Dunraven | The Kingston | Ulysses | Kimon M | Crisoula K | Giannis D |
|---|---|---|---|---|---|---|---|
| Coordinates | 27°34′53″N 33°55′32″E | 27°42′22″N 34°07′02″E | 27°46′42″N 33°52′36″E | 27°41′12″N 33°48′10″E | 27°34′48″N 33°56′00″E | 27°34′53″N 33°55′55″E | 27°34′42″N 33°55′24″E |
| Year of sinking (age) | 1869 (131) | 1876 (124) | 1881 (119) | 1877 (113) | 1978 (22) | 1981 (19) | 1983 (17) |
| Dimensions: length x width x height | 89.8 x 11.6 x 7.8 | 79.6 x 9.8 x 7.3 | 78 x 10 x 6 | 95.1 x 10.2 x 7.7 | 106.4 x 14.8 x 6.8 | 98 x 14.8 x 9 | 99.5 x 16 x 6.5 |
| Depth | 12–18 | 10–20 | 4–17 | 12–25 | 10–25 | 6–17 | 7–18 |
| Transects AR | 49 | 34 | 48 | 33 | 35 | 31 | 45 |
| Transects NR | 22 | 26 | 21 | 13 | - | - | 31 |

AR = artificial reef; NR = adjacent natural reef.

characterized according to their structural features (i.e. orientation and structural complexity) as well as according to their facing and zone (e.g. ship's bow, hull, stern). However, these features were not statistically tested in this study and all transects of each site were pooled together. Each transect was 2 m long, shorter than the standard 10 m transects previously used in coral community studies in the Red Sea (e.g. Loya, 1972; Perkol-Finkel & Benayahu, 2004; 2005). The length of a transect was dictated by SCUBA diving safety limitations, as most of the studied shipwrecks were located in deep open water (20–30 m). Since the length of a transect on a coral reef is correlated to the species count and diversity (Loya, 1972), a downscaling of the recorded features was expected when applying a 2 m transect. Consequently, conducting several transects on surfaces with similar structural features would compensate for the length of the transects (2 m *vs* 10 m long), in terms of coral species count and diversity was examined. This allowed the accumulating pooled stony and soft coral species count and coverage diversity for a series of 2 m x 5 transects (see Figure 2) to be checked. Since a plateau in species count and diversity was achieved, similarly to the analysis presented by Loya (1972) for Eilat's (Red Sea) reefs, it was concluded that as long as at least five transects with similar environmental features were recorded at each site, an accurate representation of the community features would be obtained. Therefore, an attempt was made to make sets of at least five transects in close proximity to each other and with similar features, as dictated by the structure of the ARs.

Fouling invertebrates, including stony and soft corals, sponges, tunicates, sea anemones and hydrozoans that intercepted the transects were recorded, and their projected length on the transects was measured. Due to the frequent appearance of monospecific patches, mainly of soft corals, the size of individual colonies within a patch were not measured, its total projected length was recorded

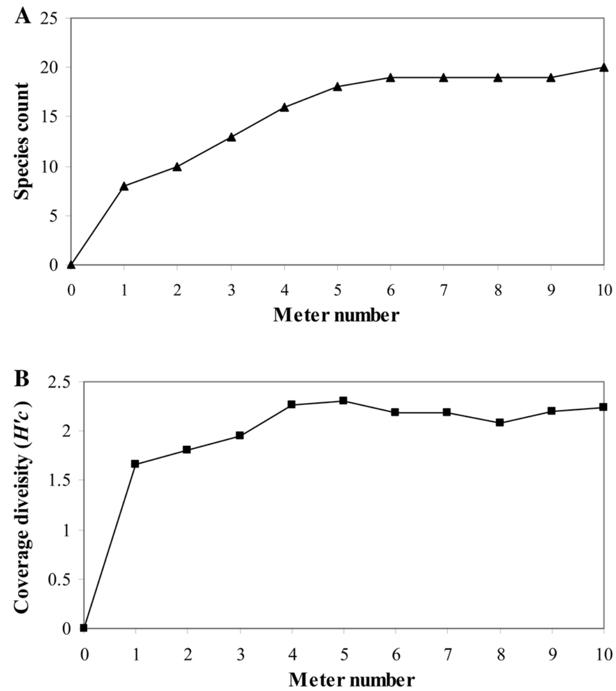



Figure 2. Cumulative stony and soft corals species count (A) and coverage diversity (B) as a function of meter number along a 10 m transect comprised of pooled 2 m x 5 transects conducted on sites with similar environmental features.

on the transect. Quantitative data presented here include stony and soft corals as well as for the hermatypic hydrozoan *Millepora dichotoma*, since these comprised the vast majority of the living cover on the studied Red Sea reefs (Benayahu & Loya, 1981) while other fouling organisms produced a far smaller contribution to the fouling community (personal observations). Taxa were identified underwater mostly to species level, and when this was not possible they were assigned to genera. All species of the family Gorgoniidae were grouped together into *Gorgonia* sp. (see Results). The fieldwork totaled 130 dives, made by the ten authors, working simultaneously at each dive. All participants were jointly trained in advance to ensure uniform data collection and to minimize bias in species identification.

*Data analysis and statistics*

The relative abundance (RA) of each coral species was calculated according to its contribution to the living cover at each site (see Perkol-Finkel & Benayahu, 2004): $RA = P_i/P_{total} \times 100$, where $P_i =$ pooled living cover of the *i*th species from all transects at a given site and $P_{total}$ = pooled total living cover of all species in all transects at a given site. RA was calculated separately for stony and soft corals (see Tables II and III). RA was also calculated for stony and soft corals pooled together, separately for ARs and NRs.

For each site the following community parameters were calculated, separately for stony and soft corals: living cover, species count and cover diversity ($H'_c$). The latter was calculated using the Shannon-Weaver function (Shannon & Weaver, 1964), from values of species contribution to living cover (Loya, 1972). All the above were calculated as averaged values per 1 meter transect and presented with standard deviations (SD). Differences between the two reef types (AR and NR) were tested using one-way ANOVA tests, for each of the community parameters examined.

To meet ANOVA assumptions the stony and soft coral cover data were arcsin $\sqrt{X}$ transformed and the stony and soft coral species counts were $\sqrt{X}$ transformed. The non-parametric Mann-Whitney *U* test (Sokal & Rohlf, 1985) was performed on original cover diversity data, since they did not distribute normally even after transformation. Differences between the community parameters of the young and old ARs, and differences between the ships, were tested using a nested ANOVA (ships nested within the age groups).

Scheffe tests were used for analysing differences between all pairs of ships. The non-parametric Mann-Whitney *U* test and the Kruskal-Wallis ANOVA tests (Sokal & Rohlf, 1985) were performed on coral diversity data.

In order to visualize differences among the sites multi-dimensional scaling (MDS) of the Bray-Curtis similarity matrix was used between all sites. The similarity index was calculated using $\log(x+1)$ transformed species percentage cover at each site (Clarke & Warwick, 2001). Statistical analysis was carried out using Statistica (Version 6, Statsoft, Inc.); the multivariate analysis was carried out using PRIMER-E (Version 5.2.9).

## Results

*Species composition*

A total of 74 stony coral species from 14 families was recorded from the studied locations (see Table II). Since some of the taxa that appear in this Table as "genus sp.", were in fact several indistinguishable species pooled together (see Materials and methods), the actual number of species is probably higher than that given here. This is particularly applicable to the soft coral species count, as many of these could not be identified to a species level underwater. The families Faviidae, Acroporidae and Pocilloporidae had the largest number of species, and were found at all sites. *Porites* sp. and *Millepora dichotoma* were the most abundant species and appeared at both the ARs and NRs (e.g. Table II, *Millepora dichotoma*, Carnatic AR 26.23% and NR 34.31% cover). Species of the family Acroporidae were more abundant at the NRs than at the ARs. However, species of the family Pocilloporidae, predominantly *Pocillopora danae* and *P. damicornis*, contributed as much as 23% to the cover of the ARs, but a maximum of 10% only of the NRs. While most Faviidae species usually contributed $< 1\%$ to the cover at both reef types, ARs still had more species of Faviidae compared to the NRs. The ahermatypic species *Cladopsamia gracilis* and *Tubastrea micrantha* (family Dendrophylliidae) contributed much to the cover at the ARs, but were absent or found in low abundance at the NRs (e.g. Table II, *Tubastrea micrantha*, Ulysses AR 40.04% and absent from the adjacent NR).

A total of 24 soft coral species from seven families was recorded from the studied locations (see Table III). The ARs had more soft coral species compared to the NRs. However, both reef types had the same assemblage of the most dominant species, which comprised the genera *Sinularia* (Alcyoniidae), *Nephthea* (Nephtheidae) and *Xenia* (Xeniidae). Species of the azooxanthelate genus *Dendronephthya* were highly abundant at the ARs, yet were mostly absent from the NRs (e.g. Carnatic AR 30.43% and absent from the surrounding NR). An exception to this was the Ulysses, which had 18.65% cover compared to 10.84% at its adjacent NR, which had a steep slope. The old ARs ($> 100$ years old) had a high dominance of soft corals, mainly of the Xeniidae, while the young ones (*ca* 20 years old) had a greater contribution of stony corals in the total live cover, mainly comprised of the families Pocilloporidae and Poritidae.

The composition of the ten most abundant species at each reef type differed considerably between the ARs and NRs. Almost total similarity existed in species composition within the ARs (see Figure 3A) and within the NRs (Figure 3B). The genus *Xenia* ranked first at both reef types, *Sinularia* was second at the ARs and seventh at the NRs, while *Nephthea* ranked ninth at the ARs and sixth at the NRs. However, among the ten most abundant species of the ARs more soft coral species were found than at the NRs. The top ten species of the ARs comprised

Table II. Relative abundance of stony corals per meter of transect at each study site, according to their contribution to live cover.

| | | Carnatic | | Dunraven | | The Kingston | | Ulysses | | Kimon M | Crisoula K | Giannis D | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Family | Species | AR | NR | AR | NR | AR | NR | AR | NR | AR | AR | AR | NR |
| Acroporidae | *Acropora eurystoma* | 0.31 | | | 4.57 | 2.73 | 12.92 | 2.77 | 4.52 | | | 0.62 | 7.61 |
| | *Acropora hemprichi* | | 6.92 | 0.19 | 0.70 | 5.79 | 10.14 | 2.60 | 2.53 | | | 0.40 | 9.87 |
| | *Acropora humilis* | 7.27 | 10.27 | | | 2.83 | 2.38 | 0.88 | | | 1.38 | 1.41 | 2.34 |
| | *Acropora hyacinthus* | | | | | | 1.63 | | 0.40 | | | | 0.07 |
| | *Acropora nasuta* | | | | | 0.55 | | | | | | | 16.97 |
| | *Acropora scandens* | 2.95 | | | | 10.98 | 7.10 | 8.65 | 8.65 | 1.62 | 1.10 | 0.69 | 10.38 |
| | *Acropora* sp. | 1.53 | | 0.38 | | 8.17 | 5.38 | 6.05 | 6.05 | | 0.74 | | 7.25 |
| | *Acropora variabilis* | | 3.64 | 0.26 | | 8.89 | 9.88 | 9.71 | 9.71 | 0.26 | | 0.57 | 3.47 |
| | *Astreopora myriophthalma* | | | | 0.94 | | | | | | 0.14 | | |
| | *Montipora* sp. | 1.02 | | 6.07 | 17.65 | 0.47 | 1.94 | 3.83 | 5.59 | | 0.23 | 0.07 | 0.46 |
| Pocilloporidae | *Pocillopora damicornis* | 9.12 | | 2.62 | 2.93 | 0.53 | 3.31 | 3.30 | | 16.68 | | 23.13 | |
| | *Pocillopora danae* | 4.68 | 4.42 | 4.60 | 2.35 | 7.41 | | 1.37 | 9.18 | 10.42 | 20.63 | 2.35 | 9.65 |
| | *Pocillopora verrucosa* | 2.91 | 2.35 | | | 2.55 | 0.66 | 0.88 | 6.25 | 1.93 | 6.16 | 4.85 | 0.29 |
| | *Seriatopora angulata* | 0.12 | | | 2.58 | 0.16 | 0.13 | | | | | | |
| | *Seriatopora caliendrum* | 0.16 | | 4.73 | 2.64 | 0.70 | | 1.19 | | | | | |
| | *Stylophora pistillata* | | | 0.29 | 0.29 | 1.72 | 1.90 | 0.74 | 0.27 | 0.57 | | | 0.36 |
| | *Stylophora wellsi* | 0.31 | 2.43 | | 0.65 | 4.47 | 7.85 | | 5.06 | | 0.18 | | 3.39 |
| Oculinidae | *Galaxea fascicularis* | 1.18 | | | | | 3.97 | 0.21 | 1.60 | | 0.51 | | |
| Siderastreidae | *Coscinaraea monile* | | | 0.83 | | | | 0.21 | 0.60 | 0.16 | 0.78 | | 0.22 |
| | *Psammocora nierstraszi* | 3.58 | 0.71 | 1.34 | 4.63 | 0.08 | 0.22 | 1.40 | 2.73 | 0.52 | 2.71 | 0.22 | 0.10 |
| | *Siderastrea lilacea* | | 0.50 | 0.58 | | | | | | | | | |
| Agariciidae | *Gardineroseris palmate* | 0.28 | | | | 0.16 | | | | | | 0.27 | |
| | *Leptoseris* sp. | | | | | 0.31 | | | | | | | |
| | *Pachyseris* sp. | | | | | | | | | 0.21 | | | |
| | *Pavona decussata* | | | 0.19 | | | 0.40 | 0.21 | | | | | |
| | *Pavona varians* | 0.35 | | 0.32 | 1.41 | 2.20 | 2.20 | 1.58 | 1.33 | | | | 0.53 |
| Fungiidae | *Fungia* sp. | 0.43 | 2.28 | 0.19 | 1.35 | | 1.37 | 0.18 | 0.13 | | 0.23 | 0.17 | 0.34 |
| | *Herpolitha limax* | | | | | | 1.37 | | | | | | |
| Pectiniidae | *Echinophyllia aspera* | | | | | 0.74 | | | | | | | |
| | *Mycedium tubifex* | | 1.14 | | | | | 2.00 | 0.40 | | 0.74 | 0.17 | |
| Merulinidae | *Hydnophora contignatio* | | | | | | 0.22 | | | | | | 0.43 |
| | *Hydnophora microconos* | | | | | 0.88 | 0.79 | 1.62 | | 0.94 | 1.56 | 0.57 | 0.29 |
| Dendrophylliidae | *Balanophyllia gemmifera* | 0.12 | | 0.83 | 0.70 | | | | | | 0.14 | | |
| | *Cladopsammia gracilis* | 6.76 | | | 0.12 | 14.41 | 0.13 | 0.67 | 4.06 | 2.81 | 0.14 | 0.05 | |
| | *Tubastrea micrantha* | 4.36 | | | | 9.69 | 0.13 | 40.04 | | 0.26 | 0.51 | 0.12 | |
| | *Turbinaria* sp. | | | 1.34 | | | | | | | | | |
| Caryophylliidae | *Gyrosmilia interrupta* | | | | | | | | | | | 0.35 | |
| Mussidae | *Acanthastrea echinata* | 1.18 | | 1.02 | 0.82 | 1.50 | 1.06 | 0.67 | 0.40 | 4.85 | 3.31 | 5.40 | 0.55 |
| | *Balastomussa* sp. | | | | | | | | 0.47 | | | | |
| | *Cynarina* sp. | | | 0.26 | 0.18 | | | 0.39 | 0.60 | 0.78 | | 0.07 | |

(*continued*)

Table II. (*continued*)

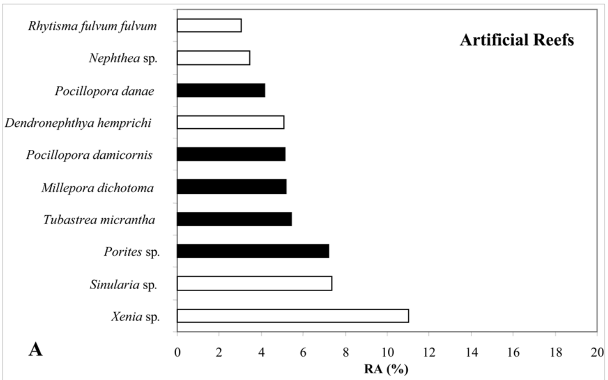
| Family | Species | Carnatic | | Dunraven | | The Kingston | | Ulysses | | Kimon M | Crisoula K | Giannis D | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | AR | NR | AR | NR | AR | NR | AR | NR | AR | AR | AR | NR |
| | *Lobophyllia corymbosa* | 0.2 | | | | | | 0.25 | | | 0.41 | | |
| | *Lobophyllia hemprichii* | 0.2 | | | | | 0.71 | 0.35 | | | | | |
| Faviidae | *Cyphastrea chalcidicum* | 1.57 | 0.21 | | 0.18 | 1.03 | | 1.58 | | 2.61 | 0.74 | 0.97 | |
| | *Cyphastrea microphthalma* | 0.39 | 0.78 | 0.38 | | 1.11 | 0.49 | 0.91 | 0.73 | 0.36 | 4.00 | 0.89 | |
| | *Cyphastrea serailia* | 0.59 | 0.57 | | | 0.23 | | 0.11 | | | 1.06 | 0.74 | 0.10 |
| | *Cyphastrea* sp. | 0.43 | 0.29 | 1.85 | | | | | 0.20 | 0.16 | 1.15 | 0.37 | |
| | *Echinopora gemmacea* | 0.98 | 5.71 | 0.26 | 0.70 | | 1.90 | 0.84 | 2.40 | 0.78 | 2.34 | 2.40 | 3.15 |
| | *Echinopora lamellosa* | | | | | | 6.00 | | | 0.21 | 0.60 | 0.50 | |
| | *Favia doreyensis* | | | 0.19 | 0.41 | | 0.35 | 0.28 | | 0.21 | | 0.32 | |
| | *Favia favus* | 0.94 | 0.57 | 1.09 | 1.11 | | 0.40 | 2.88 | 0.20 | 9.74 | 5.56 | 3.62 | |
| | *Favia* sp. | 0.28 | 1.21 | 3.07 | 0.53 | 1.72 | | 3.41 | 2.59 | 2.92 | 0.78 | 0.64 | 0.26 |
| | *Favia speciosa* | 0.16 | | | | | 0.75 | 0.21 | | 1.41 | 1.19 | 3.10 | 0.19 |
| | *Favia stelligera* | 0.75 | | 0.96 | | | | | | 0.63 | 0.55 | 0.94 | 1.88 |
| | *Favites abdita* | 0.63 | 0.64 | 0.51 | 1.00 | 0.37 | 0.97 | 0.53 | | 2.19 | 1.38 | 1.02 | |
| | *Favites halicora* | 2.67 | 1.14 | 1.34 | 0.41 | 0.62 | 1.72 | 1.90 | 1.40 | 1.35 | 1.98 | 3.49 | 0.24 |
| | *Favites pentagona* | 0.24 | | 1.60 | 1.11 | | | 0.28 | 0.40 | 0.31 | 0.14 | | |
| | *Favites* sp. | 0.43 | 1.64 | 1.21 | | | | 0.14 | | 0.47 | 0.41 | 0.07 | 0.22 |
| | *Favites virens* | | | 10.35 | | | | 0.60 | | 0.99 | 2.85 | 0.84 | |
| | *Goniastrea pectinata* | 0.55 | 1.93 | | 2.46 | | | 0.14 | 0.20 | 3.86 | 1.33 | 1.96 | 2.53 |
| | *Goniastrea retiformis* | | | 0.51 | 0.35 | 0.45 | 0.40 | 0.14 | 0.93 | 0.36 | 0.14 | 2.23 | 1.85 |
| | *Leptastrea bottae* | 0.63 | | 0.77 | 0.65 | | 0.44 | 0.14 | 2.26 | 2.50 | 1.75 | 1.51 | 0.31 |
| | *Leptastrea purpurea* | 0.24 | 0.21 | 0.96 | | | 0.53 | 1.58 | 0.20 | | 1.29 | 0.72 | 0.36 |
| | *Leptastrea transversa* | 0.55 | 0.93 | 1.98 | | 0.39 | | | 0.27 | 2.81 | 2.76 | 2.03 | 0.46 |
| | *Leptoria phrygia* | 0.16 | | | | 0.33 | | | | | | 0.17 | 0.51 |
| | *Platygyra* sp. | 1.06 | | 1.02 | 0.23 | | | | | 1.20 | 3.03 | 3.79 | 1.40 |
| | *Plesiastrea laxa* | | | 0.32 | | | | | | | 0.18 | 0.25 | |
| | *Plesiastrea mammilosa* | | 0.29 | | | | 0.22 | 0.07 | | 0.57 | 0.87 | | |
| Poritidae | *Alveopora* sp. | 0.24 | | | | | | 1.30 | | | | | |
| | *Goniopora* sp. | | | 1.34 | 0.47 | | 0.18 | 0.49 | | | | | |
| | *Porites lutea* | 0.43 | | 1.09 | 5.92 | 0.72 | | | 1.66 | 0.16 | 0.69 | 0.40 | 0.10 |
| | *Porites mayeri* | 0.63 | 0.78 | 1.92 | 5.28 | | | | | | 0.28 | 1.02 | |
| | *Porites* sp. | 9.32 | 14.12 | 20.77 | 18.30 | 2.32 | 3.92 | 5.83 | 12.91 | 16.57 | 19.79 | 18.99 | 5.25 |
| Milleporidae | *Millepora dichotoma* | 26.23 | 34.31 | 19.30 | 15.66 | 4.80 | 2.47 | 2.63 | 2.46 | 5.37 | 3.40 | 5.25 | 5.13 |
| | *Millepora platyphylla* | | | 1.09 | | | | | | | | | 1.28 |

Species are listed according to families. AR = artificial reef; NR = natural reef.

Table III. Relative abundance of soft corals per meter transect at each study site, according to their contribution to live cover.

| | | Carnatic | | Dunraven | | The Kingston | | Ulysses | | Kimon M | Crisoula K | Giannis D | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Family | Species | AR | NR | AR | NR | AR | NR | AR | NR | AR | AR | AR | NR |
| Alcyoniidae | *Cladiella* sp. | | | | | 1.05 | | | | | | | |
| | *Klyxum* sp. | | | | 0.74 | | 1.03 | 0.36 | 5.59 | 1.09 | 0.41 | | |
| | *Lobophytum* sp. | | | | | | | | 0.25 | | | | |
| | *Rhytisma fulvum fulvum* | 10.33 | 7.94 | 9.01 | 5.88 | | 0.63 | 14.25 | 15.35 | | 1.49 | 2.61 | |
| | *Sarcophyton* sp. | 2.62 | | 4.83 | 1.03 | | 5.14 | 7.81 | 0.42 | | | 3.23 | |
| | *Sinularia macrodactyla* | | | | | | | | 3.92 | | | | |
| | *Sinularia* sp. | 28.42 | 39.33 | 17.92 | 2.97 | 11.10 | 15.48 | 29.22 | 28.52 | 5.43 | 0.95 | 3.23 | 10.86 |
| Gorgoniidae | *Gorgonia* sp. | | | 0.09 | 0.21 | 3.33 | | 1.80 | 5.00 | | | | |
| Melithaeidae | *Acabaria* sp. | | | 0.12 | | | | 0.40 | 0.50 | | | | |
| | *Clathraria* sp. | | | | | | 0.70 | | | | | | |
| Nephtheidae | *Dendronephthya hemprichi* | 30.43 | | 4.65 | | 5.39 | 1.52 | 18.65 | 10.84 | | 1.49 | 6.83 | |
| | *Dendronephthya sinaiensis* | 0.65 | | 0.29 | | | | | | | | 0.62 | |
| | *Litophyton* sp. | | | 9.39 | 6.66 | 2.83 | 12.31 | 0.80 | 0.50 | | | | |
| | *Nephthea* sp. | 1.44 | 3.70 | 11.98 | 10.48 | 33.04 | 24.43 | 0.68 | 6.67 | | 7.72 | 0.50 | 7.89 |
| | *Paralemnalia thyrsoides* | | | 0.85 | | | | | 0.50 | | | | |
| | *Scleronephthya corymbosa* | 8.83 | 8.99 | 0.68 | 1.40 | 4.11 | 1.59 | 1.04 | 12.09 | 1.09 | 57.72 | 12.30 | 2.96 |
| | *Stereonephthya cundabiluensis* | 0.36 | | 4.33 | 1.60 | | 0.30 | 0.44 | | | | 1.24 | |
| Nidaliidae | *Siphonogorgia* sp. | | | | | | | | 5.00 | | | | |
| Tubiporidae | *Tubipora musica* | 0.22 | | 0.15 | | | | 0.40 | | | | | 31.25 |
| Xeniidae | *Anthelia* sp. | 0.68 | | 5.15 | 3.70 | 0.33 | | 1.48 | | | 0.54 | 0.75 | |
| | *Cespitularia* sp. | | | | 0.08 | | | | | | 0.27 | | |
| | *Heteroxenia fuscescens* | | | 1.62 | 1.48 | | 1.03 | 2.64 | | | | | |
| | *Sympodium* sp. | | | 0.18 | | | 0.11 | | 1.42 | | 0.95 | 5.47 | 1.64 |
| | *Xenia* sp. | 15.39 | 40.04 | 26.02 | 63.83 | 38.81 | 35.74 | 16.90 | 2.92 | 92.38 | 28.46 | 63.23 | 46.38 |

Legend as in Table II.



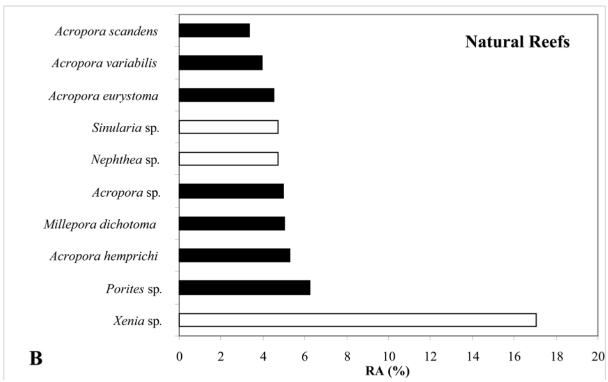




Figure 3. Relative abundance (RA) of the ten most abundant coral species on the shipwrecks (artificial reefs) (A) and natural reefs (B) according to their contribution to live cover at each reef type. Stony corals = black bars; soft corals = white bars.

two species that did not appear among the top species of the NRs, namely, *Dendronephthya hemprichi* and *Rhytisma fulvum fulvum*. An opposite trend was recorded among the most abundant stony coral species appearing in the ARs and NRs, as the latter had a higher number of stony corals than the former. Only *Porites* sp. and *Millepora dichotoma* appeared on both reef types. The NRs had five *Acropora* species, while the ARs had two *Pocillopora* species as well as the ahermatypic coral *Tubastrea micrantha*.

*Community analyses*

Differences between the AR and NR of each location were examined for each of the five community parameters (see Figure 4A-F).

Differences between the reef types varied among the locations. At most locations reef types differed in one or two of the five community parameters. Stony coral cover was significantly lower at the young ARs (*ca* 20 years old) than at their reference NR (the Giannis D NR), while at most of the old ARs ( $>$ 100 years old) no difference was found compared to their adjacent NRs (Figure 4A). Soft coral cover however did not differ between the young ARs and their reference NR, but did differentiate two of the four old ARs from their adjacent NRs (Figure 4B). Stony coral species count did not differentiate young ARs from their reference NR, but was higher at two of the older ARs (The Kingston and Ulysses) than at their respective NRs (Figure 4C). Soft coral species count differentiated between most pairs of ARs and NRs; apart from two of the young ARs, all locations revealed differences in soft coral species count between the AR and NR (Figure 4D). However, no clear trend was found, as at some locations the ARs had a greater soft coral count than their adjacent NRs (Carnatic, Dunraven and Giannis D), while other locations (Kingston and Ulysses) showed an opposite trend. Stony coral cover diversity ($H'_c$) did not differentiate between young ARs and their reference NR, while it did differentiate two of the old ARs (Kingston and Ulysses) from their adjacent NRs, which had greater diversity (Figure 4E). Similarly, soft coral cover diversity did not differentiate young ARs from their reference NR but did differentiate all old ones from their adjacent NRs (Figure 4F). However, while two of the old ARs (Kingston and Ulysses) had lower diversity than the NRs, the other two had a higher diversity compared to their adjacent NRs.

Differences between old and young ARs were highly significant for five out of the six fouling community parameters (see Table IV). Soft coral cover, count and diversity were lower at the young ARs compared to the old ARs, while stony coral count and diversity showed an opposite trend. In addition, there were significant differences in all the community parameters examined among the different ships (see Table V). Sheffee and Kruskal-Wallis tests revealed that old ARs differed more among each other compared to the young ones; however, no obvious trend was found. For example, the Kingston and Ulysses had higher stony coral cover than the Carnatic and Dunraven, while the latter had higher soft coral cover. In contrast, the young ARs differed among themselves only in soft coral count and diversity.

Differences between the fouling communities of young and old shipwrecks were also demonstrated by the MDS plot (see Figure 5). The three young ARs were clustered together at the lower right side of the plot, while all the old ARs, as well as the NRs, were to its left. For example, this analysis revealed that the Dunraven AR and NR showed great similarity to each other and clustered tightly together, while the Giannis D AR was quite dissimilar to its NR, as indicated by the large distance between them (Figure 5). Old ARs were more similar to their adjacent NRs than the young ones to their reference NR (the Giannis D NR). The location of the reef also influenced its community structure, as, for example, all reefs located at Sha'ab Abu Nuhas (Giannis D,

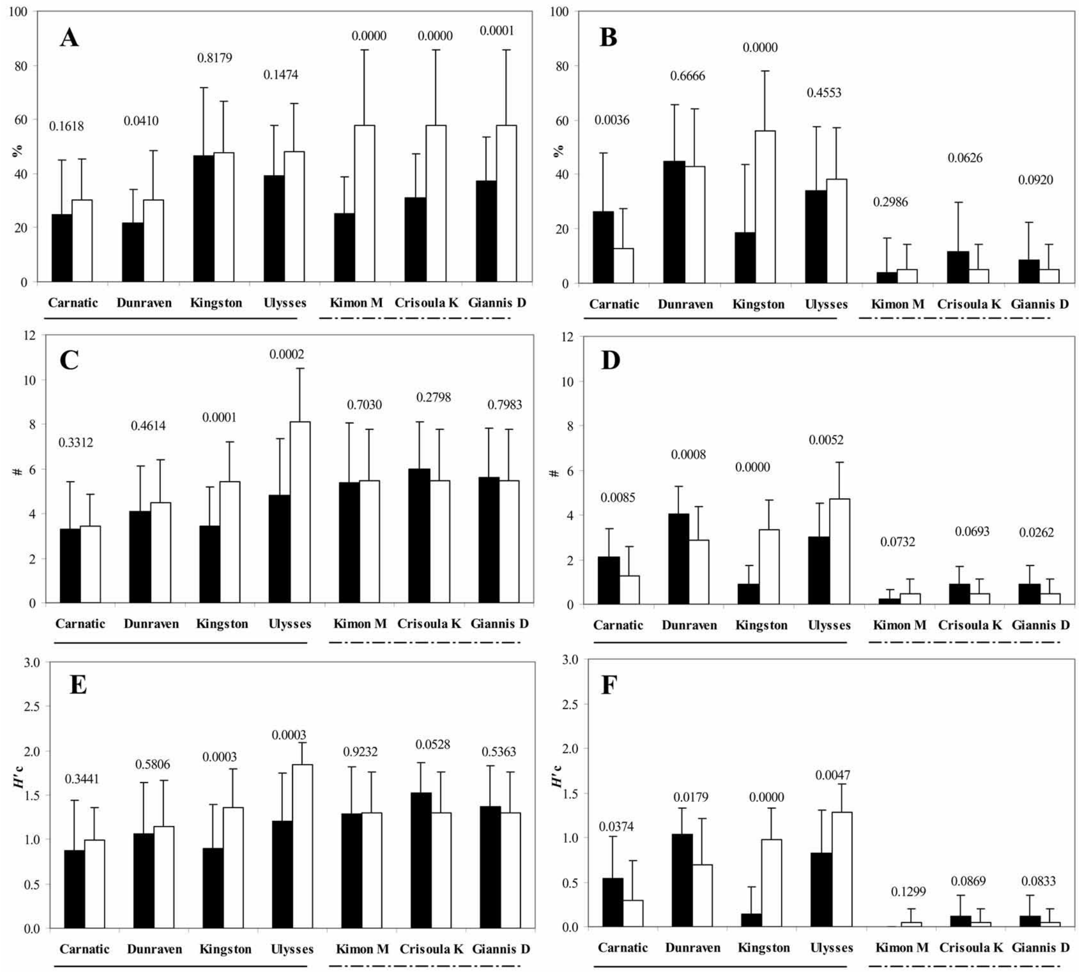



Figure 4. Community features (average per meter transect) on shipwrecks (ARs = black columns) and natural reefs (white columns) of each site. A = percentage stony coral cover; B = percentage soft coral cover; C = stony coral species coun; D = soft coral species count; E = stony coral cover diversity – $H'_c$; F = soft coral cover diversity – $H'_c$. Error bars = 1 standard deviation. Levels of significance between pairs of artificial and natural reefs were tested using one-way ANOVA and Mann-Whitney *U* tests. *p* values for each site appear above its respective columns. Number of transects at each site (AR, NR) in order of appearance from left to right: 49,22; 34,26; 48,21; 33,13; 35,31; 31,31; 45,31. Old ARs ( > 100 yrs) = black line, Young ARs (*ca*. 20 yrs) = dashed line. Note that all young ARs were compared to a single reference NR (The Giannis D NR).

Crisoula K, Kimon M and Carnatic) were situated closer to each other than to reefs of other locations, while the five NRs of different locations were scattered on the plot, indicating differences in community structure between them.

## Discussion

The stony and soft coral species composition at the surveyed shipwrecks (ARs) and NRs corresponded to the typical Red Sea coral reef fauna (e.g. Loya, 1972; Benayahu, 1985), with prevalent dominance of these two groups (Benayahu & Loya, 1981). The slow-growing massive stony coral *Porites* sp. and the rapid-growing, branching or encrusting hydrozoan *Millepora dichotoma* were most prominent at both reef types (Figure 3, Heiss, 1996; Edmunds, 1999). The pronounced appearance of these two frame builders, at both the young (*ca* 20 years old) and old ( > 100 years old) ARs, indicates that even the young ARs were already at an advanced stage of their fouling community development. Moreover, the colony size of the dominant frame builders was similar at both young and old ARs, as well as in comparison to colony size at the NRs (data not shown). Nonetheless, some differences in the species composition of branching stony corals were found between the ARs and NRs, particularly the proliferation of *Acropora* species at the NRs, and the dominance of *Pocillopora* species at the ARs. The appearance of *P. damicornis* and *P. danae* was most pronounced at the young ARs (see Table II). This may be due to the highly opportunistic nature of this genus, particularly on artificial substrata (Schuhmacher, 1977; Clark & Edwards, 1999), due to its long reproductive season and the long competence period of its planulae (e.g.

Baird & Hughes, 2000; Harii et al. 2002), as well as to its rather massive skeleton compared to other, more fragile, branching species such as *Acropora* or *Seriatopora*, which enables it to better endure the currents associated with elevated artificial substrata. The high abundance of *Acropora* species on the NRs corresponds to the findings of other studies of Red Sea reefs, describing *Acropora*-dominated reefs (Riegl, 2001). In the present study, their dominance on the NRs as well as on some of the old ARs (Table II) may result from the high competitive ability of this genus achieved by its fast overgrowth and resulting prevention of nearby coral recruitment (e.g. Baird & Hughes, 2000). Thus it possible to predict that young ARs, *ca* 20 years old, will be dominated by opportunistic robust species such as *Pocillopora* species, while old ARs, > 100 years old, and NRs will both be dominated by species with good competitive capabilities such as *Acropora*, and slow-growing, long-lived species like *Porites*, which in the long run overcome other opportunistic species.

A dominance of the ahermatypic corals *Tubastrea micrantha* and *Cladopsammia gracilis* on the shipwrecks was discovered, which were absent or uncommon at the NRs (Table II). This was most prominent on ARs with vertical surfaces (Carnatic, Kingston and Ulysses). Notably, the Ulysses NR had a vertical reef formation, and similarly had a common appearance of *C. gracilis*. The distributional pattern of these species corresponded to the preference of ahermatypic species to utilize vertical surfaces or overhangs, derived from the negative phototaxis of their planulae (Oakley, 1988; Fenner & Banks, 2004). Vertical inclination on the surveyed ARs similarly explains the high abundance of the azooxanthellate soft coral *Dendronephthya hemprichi*. While zooxanthellate genera such as *Xenia, Sinularia* and *Nephthea* were abundant at both the ARs and NRs (Figure 3), *D. hemprichi* dominated most of the ARs, yet was absent or rare at the NRs (Table III). The proliferation of this fouling species on vertical ARs has been recently documented in Eilat (Perkol-Finkel & Benayahu, 2004; 2005). This soft coral is also known to flourish on steep NRs and on inclined ARs that are exposed to current regimes that provide an ample supply of the phytoplankton required for its nutritional demands (Fabricius et al. 1995). It is likely that the differences in species composition between ARs and NRs, regardless of age, were not related to successional processes, but derived from the structural and environmental features offered by the two reef types. Thus it is expected that vertical surfaces, both artificial and natural, will most likely be colonized by ahermatypic stony coral species as well as azooxanthellate corals, while horizontal ones will better support frame builders and zooxanthellate soft coral species. These results further strengthen the notion that ARs may increase local heterogeneity and space availability through adding novel habitats suitable for settlement of a unique species assemblage (Perkol-Finkel & Benayahu, 2004).

According to the MDS analysis (Figure 5) NRs at different locations demonstrated a low similarity to each other, hence, it is important to compare fouling communities between pairs of artificial and natural reefs at the same location in order to decrease between-site variability. When comparing between adjacent ARs and NRs it was found that the age of the AR had influenced its degree of similarity to its adjacent NR. For example, young ARs, < 20 years of age, had a lower stony coral cover compared to that of nearby NRs (Figure 4A). This finding resembles those of other studies comparing coral communities of ARs to those of NRs (Baynes & Szmant, 1989; Wilhelmsson et al. 1998). It is thus possible that while the live cover on the present studied shipwrecks was lower than on the surveyed pristine NRs, such cover can still be greater than that of NR areas damaged by the impact of a ship sunk at the site, as described by Riegl (2001) for other Red Sea shipwreck sites. However, the present study demonstrated that after more than 100 years most of the ARs had a stony coral cover similar to their adjacent NRs (Figure 4A); this extensive period of time is similar to that predicted by Riegl (2001) for the full recovery of a damaged NR. Nonetheless, the number of stony coral species did not differ between the young and most of the old ARs, compared to their adjacent NRs (Figure 4C). This may imply that a submersion period of *ca* two decades may suffice for ARs to recruit assemblages of local stony corals, but not be enough to achieve a live cover similar to that of adjacent NRs. The longer time span required to attain a higher cover of stony corals is an outcome of their relatively slow growth (Heiss, 1996; Harriott, 1998). The present study indicates for the first time that stony coral species count and cover on ARs may resemble that of NRs after several decades. However, this is not to say that, even then, ARs will necessarily have a similar species assemblage to that of their adjacent NRs.

Soft coral cover hardly differentiated any of the ARs studied from their adjacent NRs (Figure 4B). The young ARs had lower soft coral cover than the old ones. However, their reference NR (Figure 1: Giannis D NR, Sha'ab Abu Nuhas) also had a relatively low soft coral cover, suggesting that this difference correlated to the location of the reefs rather than to their age or environmental features. The soft coral species count appears to indicate an age effect, as most young ARs did not differ from their reference NR while all old ARs did differ from this (Figure 4D). Differences in the number of soft coral species between the reef types were not consistent, possibly due to slight differences in the structural features of the reefs. The high soft coral species count appears to correlate to high levels of structural complexity (Figure 4D). Structural complexity is critical for achieving a diverse coral community (Spieler et al. 2001). Young ARs are usually characterized by bare surfaces, whose structural complexity tends to increase over time through recruitment of frame builders, such as corals or other benthic organisms, making the surroundings attractive and more suitable for later arrivals (Connell & Slatyer, 1977; Schuhmacher, 1977). Indeed, the present results support the notion that the structural complexity of ARs increases over time. Consequently, deployment of ARs with an *a priori* high structural complexity will most likely facilitate rapid fouling community development.

The age of the ARs was reflected in differentiation of all the biological parameters examined, apart from stony coral cover (Table IV). However, despite both young (*ca* 20 years old) and old ( > 100 years old) ARs having a similar stony coral cover, the young ARs had not yet reached the same extent of coral cover as their reference NR, while the old ones had done so (Figure 4A). Moreover, the young ARs were characterized by a high stony coral count, but had a significantly lower soft coral cover and count compared to the old ARs (Table IV).

Cover diversity showed opposite trends for stony and soft corals, as the old ARs had higher soft coral diversity while the young ones had higher stony coral diversity. These differences illustrate the prolonged developmental processes occurring on the reefs, and indicate that even two decades post deployment the ARs were still undergoing a process of shifting from the stony coral dominated community in young ARs, composed of both frame builders and opportunistic species, to a community rich in soft corals in old ARs. Differences in the examined fouling community parameters among the young ARs were, however, less pronounced than those of the old ones (Table V). The coral communities of the ARs thus appear to have become unique over time, with each having developed the individual species assemblage derived from its particular structural features. Nonetheless, such difference in fouling assemblages may also have resulted from episodic settlement processes influencing the distribution and abundance of benthic organisms (Ben-David-Zaslow & Benayahu, 1998).

The findings of the current study enable several conclusions to be drawn concerning the development of fouling communities on ARs. Regarding age, when structure is alike, similarity in coral species composition between ARs and NRs may already be achieved after *ca* 20 years, although obtaining a similar extent of coral coverage may require a full century. Regarding structure, irrespective of age, differences in structural features between ARs and NRs will lead to major differences in their respective species composition, which persist even after 100

Table IV. Comparison of average values of biological parameters ( ± SD) per metre, between old and young shipwrecks (ARs).

| Parameter | Old ARs ( > 100 yrs) | Young ARs (*ca* 20 yrs) | *p value* |
|---|---|---|---|
| Stony coral cover | 33.44 ± 22.50 | 31.62 ± 16.30 | 0.9553 |
| Soft coral cover | 29.42 ± 24.65 | 7.98 ± 14.88 | 0.0000 |
| Stony coral count | 3.79 ± 2.15 | 5.63 ± 2.34 | 0.0000 |
| Soft coral count | 2.34 ± 1.66 | 0.68 ± 0.79 | 0.0000 |
| Stony cover diversity | 0.98 ± 0.55 | 1.38 ± 0.46 | 0.0000 |
| Soft cover diversity | 0.58 ± 0.51 | 0.07 ± 0.20 | 0.0000 |

Number of transects: old ARs = 164, young ARs = 111.

Table V. Comparison of average values of biological parameters ( ± SD) per metre, between the shipwrecks (ARs).

| | Old ARs ( > 100 yrs) | | | | Young ARs (*ca* 20 yrs) | | | |
|---|---|---|---|---|---|---|---|---|
| Parameter | Carnatic | Dunraven | The Kingston | Ulysses | Kimon M | Crisouls K | Giannia D | *p value* |
| Stony coral cover | 24.77 ± 20.01 | 21.88 ± 12.12 | 46.59 ± 25.18 | 39.12 ± 18.60 | 35.17 ± 13.64 | 30.90 ± 16.38 | 37.13 ± 16.53 | 0.0000 |
| Soft coral cover | 26.43 ± 21.47 | 44.78 ± 20.76 | 18.42 ± 25.24 | 34.09 ± 23.57 | 3.94 ± 12.67 | 11.63 ± 17.99 | 8.62 ± 13.65 | 0.0000 |
| Stony coral count | 3.29 ± 2.12 | 4.12 ± 1.98 | 3.42 ± 1.77 | 4.79 ± 2.53 | 5.34 ± 2.69 | 6.00 ± 2.11 | 5.60 ± 2.23 | 0.0097 |
| Soft coral count | 2.10 ± 1.29 | 4.06 ± 1.20 | 0.90 ± 0.83 | 3.03 ± 1.51 | 0.23 ± 0.43 | 0.87 ± 0.85 | 0.91 ± 0.85 | 0.0000 |
| Stony cover diversity | 0.87 ± 0.56 | 1.05 ± 0.57 | 0.90 ± 0.49 | 1.19 ± 0.55 | 1.28 ± 0.52 | 1.51 ± 0.35 | 1.36 ± 0.45 | 0.0239 |
| Soft cover diversity | 0.54 ± 0.47 | 1.02 ± 0.29 | 0.14 ± 0.29 | 0.82 ± 0.48 | 0.00 ± 0.00 | 0.11 ± 0.23 | 0.11 ± 0.23 | 0.0000 |

Number of transects at each wreck from left to right: 49, 34, 48, 33, 35, 31 and 35 respectively.

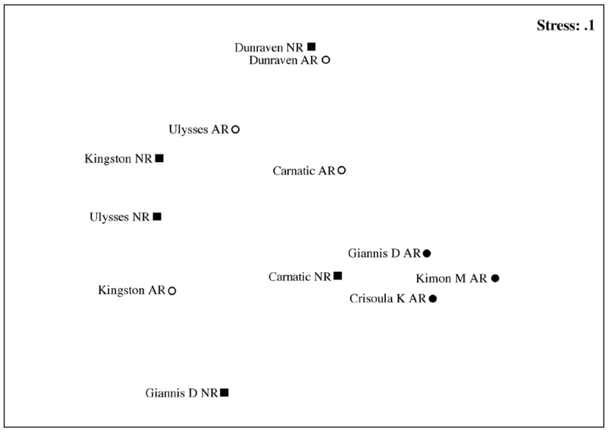



Figure 5. Two-dimensional MDS of stony and soft coral cover after log(x + 1) transformation, averaged per site. ○ = old shipwrecks (ARs, > 100 years); ● = young ARs (*ca* 20 years); ■ = NRs.

years. Hence, ARs will not necessarily mimic their surrounding NR communities, even long after their deployment. These differences in species composition between ARs and NRs as well as between young and old ARs are most likely to be correlated to a synergistic effect of reproduction strategies, growth rates and competitive abilities of the dominant taxa. Differences between fouling community parameters of young and old ARs indicate that changes in species assemblage continue to take place more than two decades post deployment, shifting from a stony coral dominated community in young ARs to one rich in soft corals in old ARs. The level of similarity between the two reef types appears to be correlated to structural features such as substratum orientation and complexity level. Additionally, ARs may present niches for the recruitment of fouling organisms that are scarce or even absent from the nearby NRs, and consequently elevate the structural heterogeneity and species diversity in the surroundings.

In summary, the use of shipwrecks as a natural experiment on unplanned ARs provided valuable information on the long-term development of AR reefal communities in tropical systems, and enabled some predictions to be made regarding the expected fouling species assemblage on young and old ARs in respect to their adjacent NR communities. It is hoped that the current study will generate future surveys along similar lines of ARs of an intermediate age (40 – 60 years) and of older ones ( > 120 years). Such surveys will provide further knowledge on the successional processes that occur during the development of fouling reefal communities on ARs over time. It is anticipated that a comprehensive study of this nature will also provide tools for modeling the development of these communities on ARs in relation to their age and structural features, as well as to their natural surroundings.

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