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Thirty years after: dramatic change in the coastal marine ecosystems of Kos Island (Greece), 1981-2013

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Abstract

Results of recent fieldwork were compared with data collected in 1981, taken as a reference condition. Surveys were conducted with the same method (time-based visual census along random paths), in the same sites, by the same people. Semi-quantitative inventories of conspicuous species were analysed by univariate and multivariate techniques. Available information on the main potential stressors indicated that a regime shift has occurred in these 30+ years: sea surface temperature rose by 1-2°C, human pressure grew impressively, and invasion by several alien species took place. Consistently, a phase shift occurred in the biological communities. Of the 120 conspicuous species found in total, only 51 were common to both surveys; 30 species ('losses') were found in 1981 but not again in 2013, 38 ('gains') were found exclusively in 2013, 16 ('winners') increased their abundance, 8 ('losers') got scarcer, and 28 underwent little or no change. Gains included 7 alien, 2 nitrophilic, and 7 thermophilic species. Multivariate analysis evidenced biotic homogenisation in 2013 and huge change in rocky reef habitats. The once flourishing algal forests have disappeared to leave space to sponges and wide areas of bare substratum. This has most probably been the result of overgrazing by alien herbivorous fishes (*Siganus luridus* and *S. rivulatus*), whose establishment and spread has been favoured by seawater warming; the synergic action of local human impacts was also evidenced.

Keywords: Regime shift, phase shift, reference conditions, global change, seawater warming, human pressure, alien species, Mediterranean Sea.

Introduction

Coastal marine ecosystems are changing world-wide under the action of global and local stressors, ranging from climate change, such as sea water warming, to direct human pressures, including pollution, overexploitation, and habitat modification (Barange *et al.*, 2010). Spread of invasive species adds as a further major component, which may alter biodiversity and trophic webs of the receiving ecosystems (Occhipinti Ambrogi & Savini, 2003). These drivers of change act in connection (Brown *et al.*, 2013), and it is therefore difficult to individuate a unique responsible for a specific observed change (Morri & Bianchi, 2001). Por (2009) adopted the term 'equifinality', borrowed from geomorphology, to express the principle that different ecological factors may lead to similar results.

In addition, climate change, human pressures and invasive species are intertwined in their ultimate causality: ocean warming is mostly an effect of the anthropogenic introduction of greenhouse gases in the atmosphere and biological invasions are favoured both by ocean warming and human activities (Stachowicz *et al.*, 2002). Humans, a

driver of change that was not present in the geological past, are modifying marine ecosystems at an unprecedented fast rate (Bianchi *et al.*, 2012a). These abrupt changes may imply phase shifts, leading to alternative stable states of the ecosystems (Montefalcone *et al.*, 2011).

While change is evident, evaluating its magnitude is difficult because proper reference conditions against which to contrast the on-going situation are seldom available (Al-Abdulrazzak *et al.*, 2012). Lack of reference conditions may lead to what has been called 'sliding baseline syndrome' (Hobday, 2011): without any benchmark criteria, an already degraded environmental status might be accepted as reference (Knowlton & Jackson, 2008).

Reference conditions may be set thanks to historical data (Borja *et al.*, 2012). Long-time series are precious to measure magnitude and rate of change (Sukhotin & Berger, 2013). Without historical information, the sliding baseline syndrome leaves scientists and managers with no reliable reference to be used once a phase shift has occurred. In absence of data series, revisiting sites that had been described in the past has proved a successful alternative to assess stability or change (Barry *et al.*, 1995; Hiscock, 2005; Schükel &

Kröncke, 2013), especially when coupled with information on the potential drivers of change (Bruggemann *et al.*, 2012).

The difficulty of evaluating change in marine ecosystems is even greater for the Mediterranean, a semi-enclosed basin experiencing heavy demographic, urban and industrial pressures (Bianchi & Morri, 2000), and where climate change is showing large impacts (Bianchi & Morri, 2004). Yet, most research on Mediterranean marine ecosystems has traditionally been directed toward identification and classification purposes, as if they were stable units (Bianchi, 1997). On the contrary, recent research has shown that these alleged stable units have been undergoing rapid alteration in the last decades (Roghi *et al.*, 2010; Parravicini *et al.*, 2013).

Bianchi & Morri (1983a, b) provided a first description of the coastal marine habitats of the Island of Kos (Greece, SE Aegean) on the basis of field work done in 1981, when tourism and coastal development were still in an early phase and sea water warming was not perceived yet. In 2013, we visited Kos again; studying the same habitats, with the same method, by the same people, offers a unique opportunity to assess long-term change of a coastal marine area.

The aim of this paper is to quantify the change (if any) that has occurred in the coastal marine habitats of Kos in these 30+ years, using species as ecological descriptors and taking into account existing information on sea water temperature, local human pressures and marine biological invasion.

Materials and Methods

Study area and stressors' regime

Kos is one of the major islands of the Dodecanese Archipelago, located in the south-eastern corner of the Aegean

Sea near the coasts of Turkey. Kos, elongated in a SW-NE direction, measures 40 km by 8 km, and is only 4.6 km from the coast of Bodrum, Turkey (Fig. 1). The island has a total area of about 290 km² and a coastline of 112 km; its shores are prevalently sandy to the north and prevalently gravelly and rocky to the south, with plunging cliff behind; however, beaches are common all around the island. Basic information on the geography of the island dates back to Martelli (1912) and Desio (1924), while recent research concentrates on volcanology (e.g., Bachmann *et al.*, 2012).

A time-series of surface water temperature for the last three decades has been derived from NOAA satellite data, freely available at <http://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl>. The monthly trends from 1981 and 2013 have been taken from Bianchi & Morri (1983b) and from http://rhodes.marmarisinfo.com/kos_island.php, respectively. In situ measurements of sea water temperature at 2 m depth in the near Island of Rhodes (Afandou area) by the local Hydrobiological Station were also consulted.

Socio-economic information was provided primarily by the National Statistic Service of Greece. Additional data on population increase and tourism were made available by the Research Institute for Tourism, the Hotel Union of Kos, the Hellenic Tourism Organization, and the Kos Ippokratis Airport, further information being contained in the papers of Finas (1991), Fokas (2001), Prokopiou (2005) and Zacharatos (2013). Data on shipping activity were obtained from the Port Authority of Kos and the Municipal Port Fund Office of Kos (2013), whereas data on fishing fleet structure were found in the IMAS-fish database (Kavadas *et al.*, 2013).

Information on alien marine species that have reached Kos waters in the last decades was obtained from the local

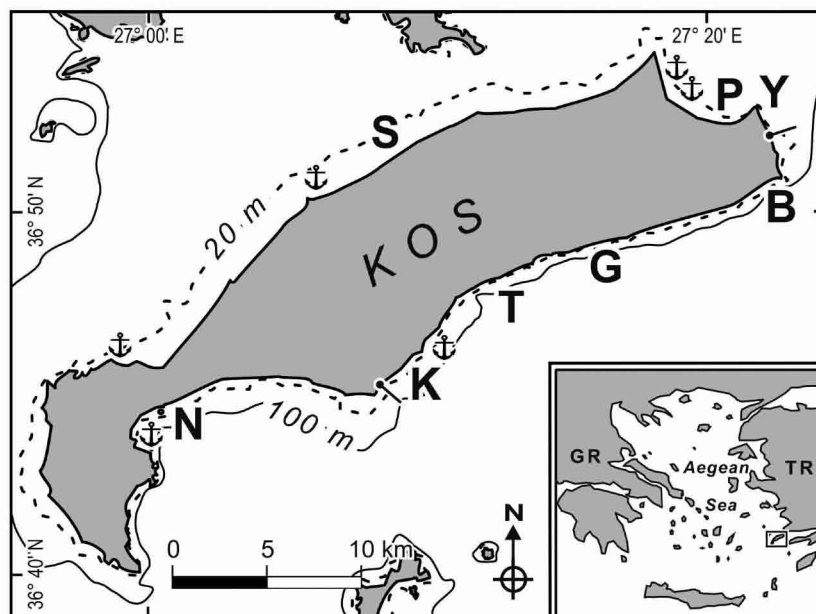


Fig. 1: The Island of Kos with study sites: B, Agios Fokas; G, Kako Skali; K, Kardamena; N, Agios Nikolaos; P, Psalidi; S, Marmari; T, Piso Thermi; Y, Cape Louros. The anchor symbol indicates harbour and marinas (clockwise from NW: Limnionas, Mastichari, Kos port, Kos marina, Kardamena, Kamari-Kefalos), the drumstick coastal wastewater treatment plants (Kos to the NE, Kardamena to S). Inset: the Aegean Sea between Greece (GR) and Turkey (TR), with the Island of Kos framed.

fishery authority, the Hellenic Network on Aquatic Invasive Species (ELNAIS: Zenetos *et al.*, 2009) and from the specialist literature (Peristeraki *et al.*, 2006; Lefkaditou *et al.*, 2010; Pancucci-Papadopoulou & Corsini-Foka, 2010; Zenetos *et al.*, 2011; Pancucci-Papadopoulou *et al.*, 2012; Katsanevakis *et al.*, 2013).

Field activity

In both 1981 and 2013, shallow marine habitats were surveyed by free and scuba diving, to about 10 m depth. Both surveys were conducted in early summer, applying the same sampling effort (eight dives of about 40 minutes each). The same eight sites were studied in both years: B, G, K, N, P, S, T, and Y (Fig. 1). Sites B and T were essentially boulders fields, G and N rocky reefs, K and S sandy seafloor with submerged beachrocks and few seagrass, P and Y seagrass meadows, with coarse sand to gravel and rocks.

Conspicuous species, big enough to be easily recognised and identified underwater, non-cryptic and physiognomically remarkable (Hiscock, 1987), were visually inventoried on a time basis along random paths (Kingsford & Battershill, 1998), using a simple semi-quantitative score to estimate their abundance (Bianchi *et al.*, 2004): 1 = scarce (< 5 specimens); 2 = abundant (5-20 specimens); 3 = very abundant (> 20 specimens). Species were named according to the World Register of Marine Species (WoRMS Editorial Board, 2013).

Ecological data analysis

The number of species found in either 1981 or 2013 was counted, as was the grand total of the species found in all. Species turnover between the two years was measured according to the following formula, which has the advantage to be independent of species richness (Hillebrand *et al.*, 2010, and references therein):

$$\beta_{\text{sim}} = \min(N_{1981}, N_{2013}) \times [N_{1981} + N_{2013} + N_c]^{-1},$$

where β_{sim} is an index of turnover, N_{1981} is the number of species recorded only in 1981, N_{2013} is the number of species recorded only in 2013, and N_c is the number of species recorded in both surveys. β_{sim} can range from 0 (complete overlap, no change in the species list) to 1 (no overlap, completely different species composition).

For each species the mean abundance score was computed for both 1981 and 2013. To appreciate change with time, the following index of relative dominance was applied (Parravicini *et al.*, 2008):

$$I_{\text{rd}} = (AS_{2013} - AS_{1981}) \times (AS_{2013} + AS_{1981})^{-1},$$

where I_{rd} is the index of relative dominance, AS_{2013} is the abundance score of an individual species in the year 2013, and AS_{1981} is the abundance score of the same species in 1981. I_{rd} ranges from -1 (species found in 1981 only) to +1 (species found in 2013 only). I_{rd} was flanked by the maximum abundance score of the species (AS_{max}) to give an indication of the importance of the observed change, as, e.g., the loss of a scarce species should not have the same value than the loss of a formerly abundant species.

The percent proportion in the number of three kinds of indicator species (Bianchi *et al.*, 2012b, and references therein), namely, native thermophilic species, nitrophilic species, and alien species, was considered in order to explore the possibility of a link with sea warming, human pressure, and biological invasion, respectively.

The overall, multivariate change in the eight study sites was explored through CA (Correspondence Analysis), using the open-access software PaSt. An interesting property of CA is the possibility of plotting both site-points and species-points on the same factorial plane, which allows for an immediate reading of their affinities; time trajectories were drawn for site-points, while species-points were clustered by space density analysis on the factorial plane of CA (Morri *et al.*, 2010, and references therein).

Results

Change in stressor regime

Sea water temperature

Based on satellite data, average sea surface temperature has apparently raised in the last decades: despite the large fluctuations from year to year, the increase appears significant (linear regression, $R^2 = 0.496$, $n = 38$, $p < 0.01$) and would imply a rise of 1-2° C between 1981 and 2013 (Fig. 2A). Sea water warming has been especially obvious in winter months (Fig. 2B). In the near island of Rhodes (Afandou area), sea water temperature was as high as 18.44° C in January 2012 and 17.47° C in February 2013.

Human pressures

Resident population of Kos Island grew from 20,350 in 1981 to 33,388 in 2011 (Fig. 3A) while the growth of tourism in the same period was exponential: with re-

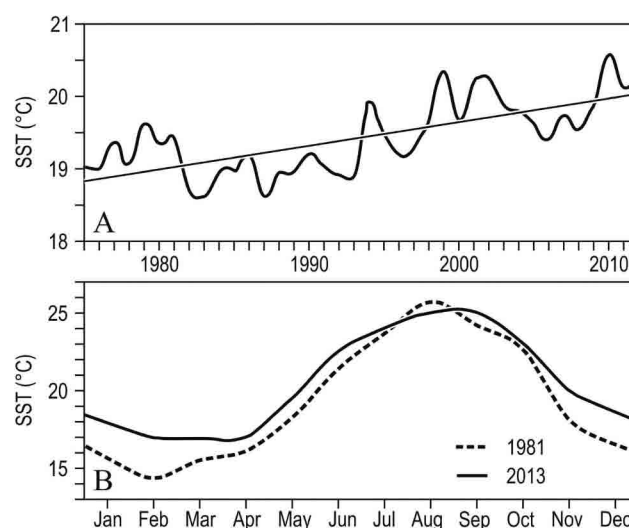


Fig. 2: Change in sea surface temperature (SST) in the coastal waters of Kos. A - Trend of yearly means from 1975 to 2012, based on satellite-derived data from <http://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl>. B - Monthly means for 1981 and 2013; data for 1981 from Bianchi & Morri (1983b), data for 2013 from http://rhodes.marmarisinfo.com/kos_island.php.

spect to 1981, the island has today an enormous receptive capacity for tourists (Vlachos *et al.*, 2011), with many resorts and hotels capable of hosting many tens of thousands of guests during the summer (Fig. 3B).

Tourism pressure indicators for Kos are higher than for Rhodes, one of the most favoured tourist destinations worldwide: the total number of beds km^{-2} in Kos increased from 14.7 in 1981 to 120.18 in 1997 and 163.2 in 2012 (Spilanis & Vayanni, 2004). The 4,262 bedrooms (52 hotels) registered in 1980 became 13,314 (151 hotels) in 1990 and climbed to approximately 50,000 in 2010 (300 hotels). The number of overnights (in hotels) increased more than four times in the same period (Fig. 3C); the actual number of beds, however, could be the double, due to the high number of rooms not officially declared (Lagos & Diakomihalis, 2011).

The majority of tourists are foreign, and arrive with direct international chartered flights at Kos Ippokratis Airport. The number of arrivals today is about 9 times higher as compared to that of the 1980s (Fig. 3D). The number of arriving maritime passengers is not comparable to the number of arrivals by flight; however, it is growing fast, particularly during the tourism season: passenger movement on national lines has growth from 156,000 in 2003 to 201,000 in 2012. After the recent facilitation of visa release for Turkish citizens, passenger movement from Turkey doubled from 132,000 in 2009 to 266,000 in 2012. Passenger movement between Kos and the nearby islands is intense, mainly to Mastihari (connection with Kalymnos Island), but also to Kardamena and Kefalos (connection with Nisiros Island): 263,000 passengers in 2011 and 243,600 in 2012, considering the three harbours together.

According to UNEP (2011), 70% of Kos total annual waste is produced during the tourism season; the average waste production per day by tourists is 10% to 15% higher than those by the inhabitants. A Biological Wastewater Treatment Plant (BWT) has been operational since the early 1990s for the town of Kos, the capital of the island, and serves about 40,000 people; after treatment, water is discharged 250 m offshore through an underwater pipe (P. Liodakis, personal communication). A second BWT was established in 2011 at Kardamena, to serve 30-35,000 people; since the sewage system is still under construction, waste is collected with tankers from cesspools and processed. A third BWT is under economic evaluation for the Dikaio area, and its sewage canalization is under construction, while a fourth BWT for Kefalos is under planning (P. Liodakis, personal communication). In the rest of the island, domestic waste is collected and discharged in a special place inland. Hotels are provided with their own treatment systems: because of the huge seasonal fluctuation of the presences, these are rarely efficient, and the risk of coastal water eutrophication cannot be excluded (G. Chrisopoulous, personal communication).

Arrivals of both Greek and foreign dry cargo ships and tankers to Kos port, regardless of their origin, increased steadily from 2,200,000 NRT (Net Registered Tons) in 1980 to approximately 7,200,000 in 2000, then peaking to 12,100,000 in 2006 (Fig. 3E). A well organized marina next to Kos port operates since 2001, with a capability to host 250 boats, while, after recent improvement works, yachts may also anchor in the harbour of Kardamena; other marinas exist in the island. Arrivals of yachts to the port of Kos doubled from about 500 in the early 1980s to 1100

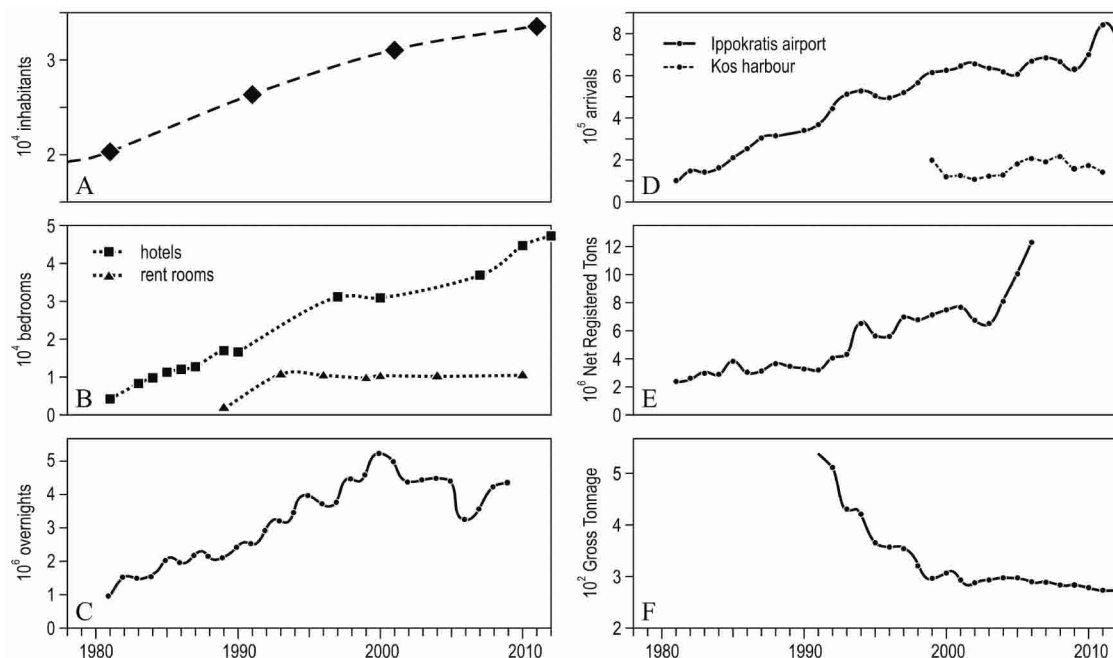


Fig. 3: Change in human pressure intensity at Kos. A - Resident population. B - Receptive capacity for tourists (the number of rooms rent by privates is probably underestimated). C - Number of overnights (in hotels). D - Passenger arrivals by flight and by ship. E - Arrivals of dry cargo ships and tankers to Kos port. F - Total gross tonnage of fishing vessels. Data from various sources (see text).

in the early 1990s; arrivals of yachts in 2012 were 2940 to Kos port, 2969 to Kos marina, and 249 to Kardamena. Today, Kos is also a cruise destination: indicatively, cruise ship arrivals were 20 in 2005, 33 in 2010, 48 in 2011, and 64 in 2012; cruise ship passengers have been 16,600 in 2010, 23,400 in 2011 and 42,000 in 2012.

As the main economy source for the island shifted to tourism, fishery diminished. Since the early 1990s, fishing at Kos was mainly performed by nets and long-lines vessels (90-95% of the total), the remaining by boat seines with a length of 10-11 m (IMAS-Fish Program, in Kavadas *et al.*, 2013). In two decades, a decrease of approximately 20% was registered for nets and long-lines and by 55% of boat seines, while the total number of fishing vessels decreased from 106 to 81. Their total engine power and gross tonnage decreased similarly (Fig. 3F).

Biological invasions

A chronicle of alien species occurrence exists for the whole Dodecanese area, to which Kos belongs (Pancucci-Papadopoulou & Corsini-Foka, 2010; Pancucci-Papadopoulou *et al.*, 2012). Out of the 109 alien species recorded (ELNAIS, updated to September 2013), 83% have Indo-Pacific origin, entering the Mediterranean through the Suez Canal (Lessepsian immigration): after almost a century of 'smooth' colonization, the introduction rate of the Lessepsian immigrants increased during the 1980s and assumed the character of invasion during the 1990s and the 2000s (Fig. 4), producing evident changes in coastal ecosystem composition and function (Pancucci-Papadopoulou *et al.*, 2012).

Information concerning specifically Kos is scarce. In 1981, Morri & Bianchi (1999) collected the alien hydro-

zoan *Clytia linearis* on algae, but did not observe any conspicuous alien species during their visual surveys. In 2013, seven conspicuous alien species were observed: *Alepes djedaba*, *Caulerpa racemosa* var. *cylindracea*, *Dendostrea frons*, *Siganus luridus*, *Siganus rivulatus*, *Stypopodium schimperi* and *Synaptula reciprocans* (Box 1). The occurrence of *A. djedaba* in Greek waters was hitherto reported as questionable in ELNAIS dataset. According to the local fishery authority, *Fistularia commersoni*, *Lagocephalus sceleratus* and *Siganus* spp are abundant in fish catches. Other alien fish species reported from Kos island include *Etrumeus teres*, *Lagocephalus spadiceus*, *Pteragogus pelycus*, *Stephanolepis diaspros*, and *Upeneus moluccensis*, all well established in the south Aegean Sea (Peristeraki *et al.*, 2006; Zenetos *et al.*, 2009; Lefkaditou *et al.*, 2010).

Change in biological communities

A total of 120 conspicuous species was found, belonging to invertebrates, algae, fishes, and seagrasses, in order of

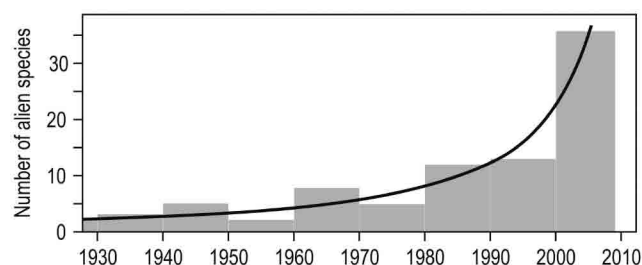


Fig. 4: Number of alien marine species per decade (bars) and overall trend for the last century (line) in the Dodecanese area (to which Kos belongs). Redrawn and modified from Pancucci-Papadopoulou *et al.*, 2012).

Box 1: Conspicuous alien species observed at Kos in 2013.

CHROMISTA, OCHROPHYTA, PHAEOPHYCEAE, DICTYOTACEAE

Stypopodium schimperi (Kützinger) M. Verlaque & Boudouresque, 1991
Scarce, on rocky reef at 6 m depth (site G).

PLANTAE, CHLOROPHYTA, ULVOPHYCEAE, CAULERPACEAE

Caulerpa racemosa var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque, 2003
Scarce, on rock at 0.5 m depth (site Y).

ANIMALIA, MOLLUSCA, BIVALVIA, OSTREIDAE

Dendostrea frons (Linnaeus, 1758)

Several individuals on a reef overhang at 4 m depth, encrusted by the native sponge *Crambe crambe* (site G).

ANIMALIA, ECHINODERMATA, HOLOTHUROIDEA, SYNAPTIDAE

Synaptula reciprocans (Forskål, 1775)

Amidst *Caulerpa prolifera* on muddy sand and dead *Posidonia* matte at 7 m depth (site P). Abundant on reef at 10 m depth (site G).

ANIMALIA, CHORDATA, ACTINOPTERYGII, CARANGIDAE

Alepes djedaba (Forsskal, 1775)

A single fish of about 20 cm within a school of *Lithognathus mormyrus*, on fine sand with ripple marks and shallow beach-rocks, at 2 m depth (site K).

ANIMALIA, CHORDATA, ACTINOPTERYGII, SIGANIDAE

Siganus luridus (Rüppell, 1829)

Common in all sites and virtually all habitats. On rock at 1 m depth (juveniles) and within seagrass patches at 3-4 m depth (site Y). Abundant among artificial structures and in *Posidonia oceanica* meadow at 10 m depth, often bearing ectoparasitic isopods (*Anilocra*?) on the caudal peduncle (site P). Extremely abundant on boulders at 6-9 m depth (sites B and T). Scarce on reef at 7-10 m depth (sites G and N) and on sand with stones at 6-7 m depth (sites K and S).

ANIMALIA, CHORDATA, ACTINOPTERYGII, SIGANIDAE

Siganus rivulatus Forsskal & Niebuhr, 1775

Often in mixed schools with its congeneric *S. luridus* but less widespread. Always found in boulder fields (occasionally with some patches of *Posidonia oceanica*) between 1 and 9 m depth (sites K, B and T).

Table 1. List of the conspicuous species observed in the coastal marine habitats of Kos, ordered alphabetically according to their code (as used in Figs. 9, 11, 12 and 13). The higher taxon to which individual species belong is also indicated. AS_{max} = maximum abundance score, I_{Rd} = index of relative dominance (see Materials and Methods).

| Code | Species (Higher taxon) | AS_{max} | I_{Rd} | |
|------|---|------------|----------|---------------------|
| Aac | <i>Acetabularia acetabulum</i> (Chlorophyta) | 3 | -0.6 | loser |
| Aae | <i>Aplysina aerophoba</i> (Porifera) | 2 | 1.0 | gain |
| Adj | <i>Alepes djedaba</i> (Pisces) | 1 | 1.0 | gain |
| Aim | <i>Apogon imberbis</i> (Pisces) | 3 | 0.1 | little or no change |
| Aip | <i>Astropecten irregularis pentacanthus</i> (Echinodermata) | 1 | 1.0 | gain |
| Ajo | <i>Astropecten jonstoni</i> (Echinodermata) | 1 | -1.0 | loss |
| Ali | <i>Arbacia lixula</i> (Echinodermata) | 2 | -0.1 | little or no change |
| Aoc | <i>Aglaophenia octodonta</i> (Cnidaria) | 1 | -1.0 | loss |
| Aor | <i>Agelas oroides</i> (Porifera) | 2 | 1.0 | gain |
| Ari | <i>Amphiroa rigida</i> (Rhodophyta) | 2 | 1.0 | gain |
| Ast | <i>Anadyomene stellata</i> (Chlorophyta) | 1 | 1.0 | gain |
| Atu | algal turf | 3 | 0.5 | winner |
| Avg | <i>Ascidia virginea</i> (Tunicata) | 1 | -1.0 | loss |
| Avi | <i>Anemonia viridis</i> (Cnidaria) | 2 | -1.0 | loss |
| Bbo | <i>Boops boops</i> (Pisces) | 2 | 0.5 | winner |
| Bca | <i>Balistes capriscus</i> (Pisces) | 1 | 1.0 | gain |
| Bpo | <i>Bothus podas</i> (Pisces) | 2 | 0.1 | little or no change |
| Bvo | <i>Bispira volutacornis</i> (Annelida) | 1 | -1.0 | loss |
| Cad | <i>Codium adhaerens</i> (Chlorophyta) | 2 | -1.0 | loss |
| Cba | <i>Cystoseira barbata</i> (Ochrophyta) | 2 | 0.4 | winner |
| Cbr | <i>Cystoseira brachycarpa</i> (Ochrophyta) | 2 | -0.4 | loser |
| Cbu | <i>Codium bursa</i> (Chlorophyta) | 2 | 0.0 | little or no change |
| Ccb | <i>Crambe crambe</i> (Porifera) | 2 | 0.6 | winner |
| Cce | <i>Cliona celata</i> (Porifera) | 2 | 0.0 | little or no change |
| Cch | <i>Chromis chromis</i> (Pisces) | 3 | 0.5 | winner |
| Cco | <i>Cystoseira corniculata</i> (Ochrophyta) | 1 | -1.0 | loss |
| Ccr | <i>Cystoseira crinita</i> (Ochrophyta) | 3 | -1.0 | loss |
| Cfo | <i>Cystoseira foeniculacea</i> (Ochrophyta) | 3 | -1.0 | loss |
| Cgr | <i>Calappa granulata</i> (Crustacea) | 1 | 1.0 | gain |
| Cju | <i>Coris julis</i> (Pisces) | 2 | 0.7 | winner |
| Cla | <i>Chelon labrosus</i> (Pisces) | 2 | 0.5 | winner |
| Clo | <i>Centrostephanus longispinus</i> (Echinodermata) | 1 | 1.0 | gain |
| Cme | <i>Cerianthus membranaceus</i> (Cnidaria) | 1 | 1.0 | gain |
| Cno | <i>Cymodocea nodosa</i> (Tracheophyta) | 3 | -0.1 | little or no change |
| Cpf | <i>Cladophora prolifera</i> (Chlorophyta) | 2 | -1.0 | loss |
| Cpr | <i>Caulerpa prolifera</i> (Chlorophyta) | 3 | -0.4 | loser |
| Cra | <i>Caulerpa racemosa</i> (Chlorophyta) | 1 | 1.0 | gain |
| Cre | <i>Chondrosia reniformis</i> (Porifera) | 3 | 0.6 | winner |
| Cva | <i>Charonia variegata</i> (Mollusca) | 1 | 0.0 | little or no change |
| Cve | <i>Conus ventricus</i> (Mollusca) | 1 | -1.0 | loss |
| Dan | <i>Diplodus annularis</i> (Pisces) | 1 | -0.4 | loser |
| Dfr | <i>Dendostrea frons</i> (Mollusca) | 2 | 1.0 | gain |
| Dpo | <i>Dictyopteris polypodioides</i> (Ochrophyta) | 3 | -1.0 | loss |
| Dpu | <i>Diplodus puntazzo</i> (Pisces) | 1 | 0.0 | little or no change |
| Dsa | <i>Diplodus sargus</i> (Pisces) | 2 | 0.2 | little or no change |
| Dve | <i>Dasycladus vermicularis</i> (Chlorophyta) | 3 | -1.0 | loss |
| Dvu | <i>Diplodus vulgaris</i> (Pisces) | 3 | 0.2 | little or no change |
| Eae | <i>Epinepheleus aeneus</i> (Pisces) | 1 | 1.0 | gain |
| ecr | encrusting corallines (Rhodophyta) | 2 | 0.1 | little or no change |
| Eel | <i>Ellisolandia elongata</i> (Rhodophyta) | 1 | 0.2 | little or no change |
| Epu | <i>Echinocyamus pusillus</i> (Echinodermata) | 1 | 1.0 | gain |
| Era | <i>Eudendrium racemosum</i> (Cnidaria) | 3 | -0.4 | loser |
| Faf | <i>Flabellina affinis</i> (Mollusca) | 1 | -1.0 | loss |
| Fpe | <i>Flabellia petiolata</i> (Chlorophyta) | 3 | -0.8 | loser |
| Gre | <i>Gloiocladia repens</i> (Rhodophyta) | 2 | -1.0 | loss |
| Gum | <i>Gibbula umbilicalis</i> (Mollusca) | 2 | 1.0 | gain |
| Hca | <i>Hermodice carunculata</i> (Annelida) | 3 | 0.1 | little or no change |
| Hcl | <i>Hydroclathrus clathratus</i> (Ochrophyta) | 2 | 1.0 | gain |
| Hcr | <i>Haliclona cratera</i> (Porifera) | 2 | -1.0 | loss |

(continued)

(continued)

| Code | Species (Higher taxon) | AS _{max} | I _{Rd} | |
|------|--|-------------------|-----------------|---------------------|
| Htr | <i>Hexaplex trunculus</i> (Mollusca) | 1 | 0.0 | little or no change |
| Ior | <i>Ircinia oros</i> (Porifera) | 2 | -1.0 | loss |
| Ire | <i>Ircinia reticulata</i> (Porifera) | 2 | 0.8 | winner |
| Jru | <i>Jania rubens</i> (Rhodophyta) | 1 | 0.2 | little or no change |
| Lmo | <i>Lithognathus mormyrus</i> (Pisces) | 2 | 1.0 | gain |
| Lob | <i>Laurencia obtusa</i> (Rhodophyta) | 2 | 1.0 | gain |
| Lom | <i>Laevicardium oblongum</i> (Mollusca) | 1 | 1.0 | gain |
| Lpr | <i>Leptopsammia pruvoti</i> (Cnidaria) | 3 | -1.0 | loss |
| Lst | <i>Lithophyllum stictaeforme</i> (Rhodophyta) | 2 | -1.0 | loss |
| Lvi | <i>Liagora viscida</i> (Rhodophyta) | 2 | -0.1 | little or no change |
| Mcr | <i>Maja crispata</i> (Crustacea) | 1 | -1.0 | loss |
| Mgl | <i>Marthasterias glacialis</i> (Echinodermata) | 1 | -1.0 | loss |
| Mhe | <i>Muraena helena</i> (Pisces) | 2 | 0.0 | little or no change |
| Msu | <i>Mullus surmuletus</i> (Pisces) | 3 | -1.0 | loss |
| Ome | <i>Oblada melanura</i> (Pisces) | 2 | 0.5 | winner |
| Oop | <i>Ophidiaster ophidianus</i> (Echinodermata) | 1 | 0.0 | little or no change |
| Ovu | <i>Octopus vulgaris</i> (Mollusca) | 1 | 0.2 | little or no change |
| Pat | <i>Peltodoris atromaculata</i> (Mollusca) | 1 | -1.0 | loss |
| Pca | <i>Patella caerulea</i> (Mollusca) | 2 | 1.0 | gain |
| Pdi | <i>Pennaria disticha</i> (Cnidaria) | 1 | 1.0 | gain |
| Pfi | <i>Petrosia ficiformis</i> (Porifera) | 2 | 0.4 | winner |
| Pha | <i>Portunus hastatus</i> (Crustacea) | 1 | -1.0 | loss |
| Pli | <i>Paracentrotus lividus</i> (Echinodermata) | 1 | 0.0 | little or no change |
| Pno | <i>Pinna nobilis</i> (Mollusca) | 2 | 0.0 | little or no change |
| Poc | <i>Posidonia oceanica</i> (Tracheophyta) | 3 | -0.1 | little or no change |
| Ppa | <i>Padina pavonica</i> (Ochrophyta) | 3 | -1.0 | loss |
| Psq | <i>Peyssonnelia squamaria</i> (Rhodophyta) | 3 | -0.5 | loser |
| Ptu | <i>Protula tubularia</i> (Annelida) | 3 | 0.2 | little or no change |
| Rne | <i>Rhyncozoon neapolitanum</i> (Bryozoa) | 2 | 1.0 | gain |
| Rvi | <i>Reptadeonella violacea</i> (Bryozoa) | 2 | 1.0 | gain |
| Sca | <i>Serranus cabrilla</i> (Pisces) | 1 | 0.5 | winner |
| Sct | <i>Sparisoma cretense</i> (Pisces) | 3 | 0.6 | winner |
| Scu | <i>Spirastrella cunctatrix</i> (Porifera) | 2 | -0.1 | little or no change |
| Sdu | <i>Schizoporella dunkeri</i> (Bryozoa) | 2 | 1.0 | gain |
| Sfo | <i>Sarcotragus foetidus</i> (Porifera) | 3 | 0.4 | winner |
| Sga | <i>Spondylus gaederopus</i> (Mollusca) | 2 | -0.1 | little or no change |
| Sgr | <i>Spharechinus granularis</i> (Echinodermata) | 1 | 1.0 | gain |
| Slu | <i>Siganus luridus</i> (Pisces) | 3 | 1.0 | gain |
| Sma | <i>Spicara maena</i> (Pisces) | 2 | 1.0 | gain |
| Smd | <i>Scorpaena maderensis</i> (Pisces) | 2 | -1.0 | loss |
| Sof | <i>Spongia officinalis</i> (Porifera) | 2 | -1.0 | loss |
| Sre | <i>Synaptula reciprocans</i> (Echinodermata) | 2 | 1.0 | gain |
| Sri | <i>Siganus rivulatus</i> (Pisces) | 3 | 1.0 | gain |
| Sro | <i>Symphodus roissali</i> (Pisces) | 2 | -0.2 | little or no change |
| Ssa | <i>Sarpa salpa</i> (Pisces) | 3 | -0.2 | little or no change |
| Ssb | <i>Serranus scriba</i> (Pisces) | 1 | 0.5 | winner |
| Ssc | <i>Stypopodium schimperi</i> (Ochrophyta) | 1 | 1.0 | gain |
| Ssn | <i>Stenopus spinosus</i> (Crustacea) | 1 | -1.0 | loss |
| Ssp | <i>Stypocaulon scoparium</i> (Ochrophyta) | 2 | -0.4 | loser |
| Ssz | <i>Sabella spallanzanii</i> (Annelida) | 1 | 1.0 | gain |
| Svi | <i>Sphyræna viridensis</i> (Pisces) | 2 | 1.0 | gain |
| Svu | <i>Sargassum vulgare</i> (Ochrophyta) | 2 | -1.0 | loss |
| Tar | <i>Thylacodes arenarius</i> (Mollusca) | 1 | 1.0 | gain |
| Tdr | <i>Trachinus draco</i> (Pisces) | 1 | -1.0 | loss |
| Tga | <i>Tonna galea</i> (Mollusca) | 2 | 1.0 | gain |
| Tov | <i>Trachinotus ovatus</i> (Pisces) | 1 | 1.0 | gain |
| Tpa | <i>Thalassoma pavo</i> (Pisces) | 3 | 0.4 | winner |
| Tpe | <i>Tylodina perversa</i> (Mollusca) | 1 | 1.0 | gain |
| Ula | <i>Ulva lactuca</i> (Chlorophyta) | 2 | 1.0 | gain |
| Vir | <i>Vermetus triquetrus</i> (Mollusca) | 3 | 1.0 | gain |
| Xno | <i>Xyrichtys novacula</i> (Pisces) | 1 | 0.1 | little or no change |

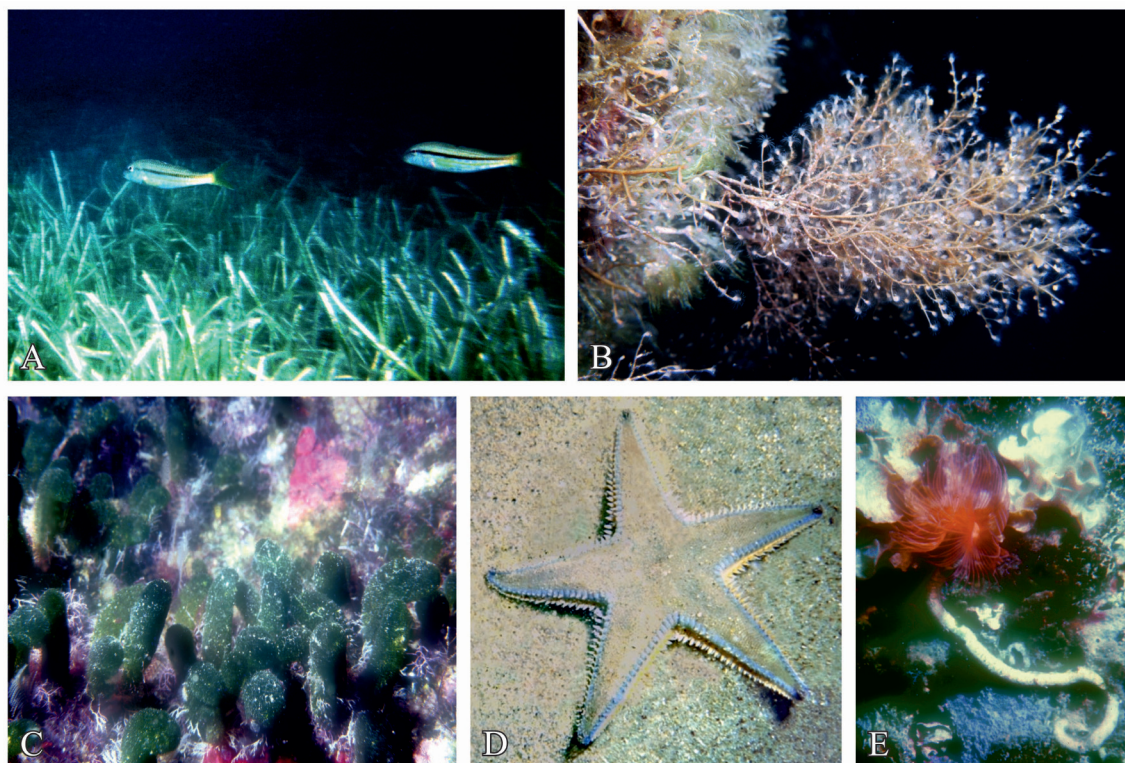


Fig. 5: Species characterising the shallow benthic habitats of Kos in 1981. A - *Mullus surmuletus* in a *Posidonia oceanica* bed at site P (UW photograph by C.N. Bianchi). B - *Eudendrium racemosum* on a reef wall at site N (UW photograph by C. Morri). C - *Dasycladus vermicularis* at site N (UW photograph by C. Morri). D - *Astropecten jonstoni* on sand at site S (UW photograph by C. Morri). E - The tube worm *Protula tubularia* amidst *Padina pavonica* at site Y (UW photograph by C. Morri).

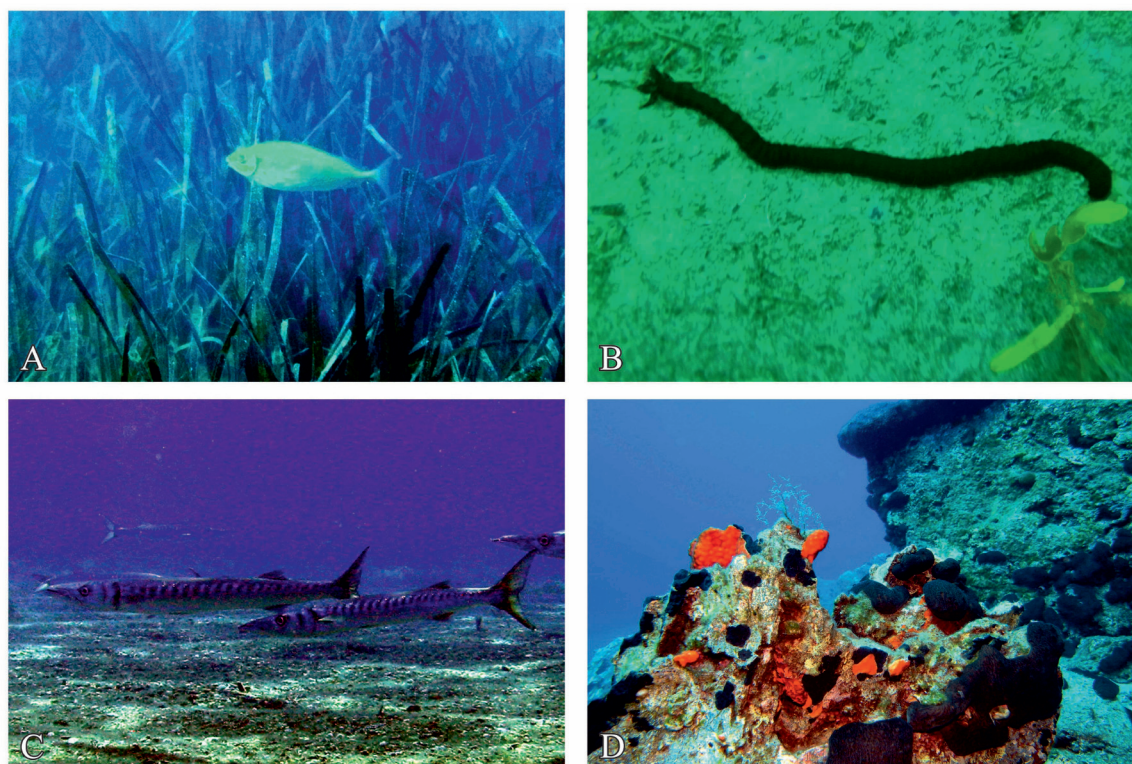


Fig. 6: Species characterising the shallow benthic habitats of Kos in 2013. A - *Siganus luridus* in a *Posidonia oceanica* bed at site P (UW photograph by M. Gómez Sel). B - *Synaptula reciprocans* on dead matte with some *Caulerpa racemosa* at site P (UW photograph by M. Gómez Sel). C - *Sphyræna viridensis* at site T (UW photograph by G. Chrisopoulos). D - The sponge *Chondrosia reniformis* and the bryozoan *Schizoporella dunkeri* in a rocky reef at site G (UW photograph by G. Chrisopoulos).

species richness (Table 1): 82 species were found in 1981, 89 in 2013; 51 species were common to both surveys, leading to a turnover β_{sim} of 0.61. The number of species found in 1981 but not again in 2013 ('losses') was 30, the number of species found exclusively in 2013 ('gains') was 38. Figure 5 and Figure 6 illustrate some species characterising the shallow benthic habitats of Kos in 1981 and 2013, respectively.

From a (semi-)quantitative point of view, Table 1 reports AS_{max} and I_{Rd} values for all species, while Fig. 7 shows details for some selected examples. The 38 gains evidently exhibited $I_{Rd} = 1$, the 30 losses $I_{Rd} = -1$; fixing arbitrarily limits for the values of I_{Rd} comprised between 1 and -1, 16 species ('winners') increased their abundance ($I_{Rd} > 0.3$), 28 underwent little or no change ($0.2 \leq I_{Rd} \leq -0.2$), and 8 ('losers') got scarcer ($I_{Rd} < -0.3$).

Apart from the 7 alien species (Box 1), gains included 2 nitrophilic species (*Hydroclathrus clathratus* and *Ulva lactuca*), and 7 thermophilic species (*Balistes capricus*, *Centrostephanus longispinus*, *Epinepheleus aeneus*, *Pennaria*

disticha, *Sphyræna viridensis*, *Tonna galea*, *Trachinotus ovatus*). Thermophilic species were also included among winners (*Sparisoma cretense* and *Thalassoma pavo*), among species that underwent little or no change (*Charonia variegata*, *Hermodice carunculata*, *Liagora viscida*, *Ophidiaster ophidianus*, and *Xyrichtys novacula*), among losers (*Caulerpa prolifera*), and among losses (*Dasycladus vermicularis* and *Gloiocladia repens*). No alien species or nitrophilic species were present among the groups of winners, little or no change, losers and losses.

Losses and losers included many algae: *Acetabularia acetabulum*, *Caulerpa prolifera*, *Cladophora prolifera*, *Codium adhaerens*, *Cystoseira brachycarpa*, *C. corniculata*, *C. crinita*, *C. foeniculacea*, *Dasycladus vermicularis*, *Dictyopteris polypodioides*, *Flabellia petiolata*, *Gloiocladia repens*, *Lithophyllum stictaeforme*, *Padina pavonica*, *Peyssonnelia squamaria*, and *Sargassum vulgare*. The large hydroid *Eudendrium racemosum* was replaced by the similarly tall but more thermophilic species *Pennaria disticha*. Well represented among both gains and winners were sponges: *Agelas oroides*, *Aplysina aerophoba*, *Chondrosia reniformis*, *Crambe crambe*, *Ircinia retidermata*, *Petrosia ficiformis*, and *Sarcotragus foetidus*. Among the few algae, the algal turf and *Cystoseira barbata* increased their abundance. The appearance of *Vermetus triquetrus* is worth noting.

Between 1981 and 2013, the percent proportion in the number of native thermophilic species nearly doubled (10 to 19), whereas that of nitrophilic and alien species, not found in 1981, reached 2 and 6, respectively (Fig. 8).

CA provided two significant axes (Lebart test, $p < 0.05$), together explaining 26.3 % of the total inertia (Fig. 9). The ordination model plotted on the plane formed by these two axes showed a dense cloud of spe-

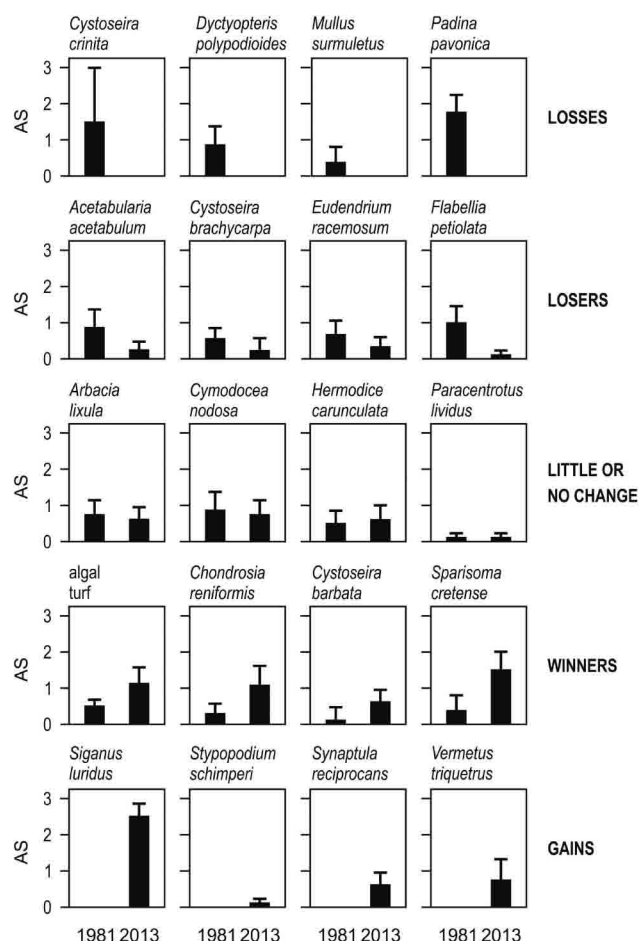


Fig. 7: Mean (\pm se) abundance score (AS) for selected examples of species found in 1981 but not found again in 2013 (losses); of species whose abundance decreased between 1981 and 2013 (losers); of species that showed little or no change between the two years; of species that showed more abundant in 2013 than in 1981 (winners); and of species that were found in 2013 but not in 1981 (gains).

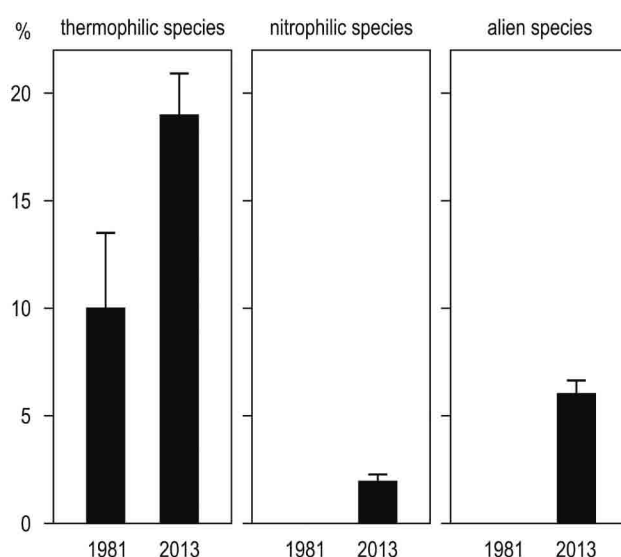


Fig. 8: Change in mean (\pm se) percent proportion in the number of native thermophilic species, nitrophilic species, and alien species, in the shallow benthic habitats of Kos between 1981 and 2013.

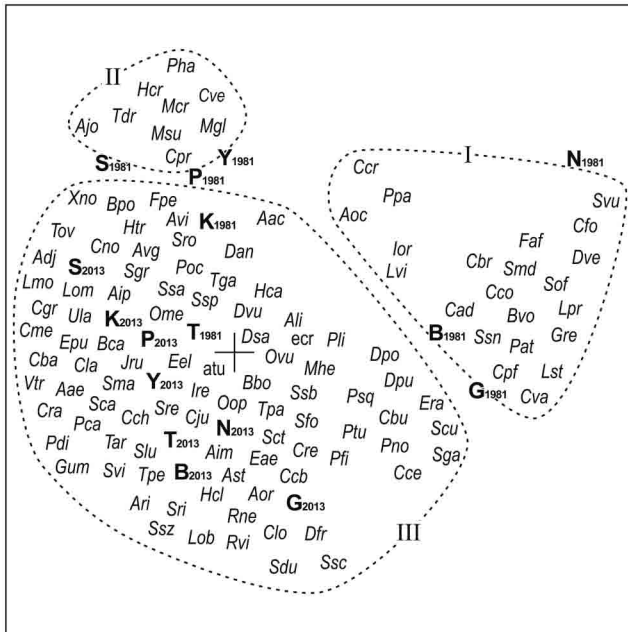


Fig. 9: Correspondence Analysis ordination model on the plane formed by the first two axes extracted. 1st axis (horizontal) explains 14.2 % of the total variance, 2nd axis (vertical) 12.1 %. Site-points are represented by capital letters, followed by the relevant year of survey; species-points are represented by codes as in Table 1. Species-points are grouped into three clusters (I, II and III) according to space density analysis.

cies-points and site-points on the left side, and a more open cloud on the right side around the site-points N, B, and G for 1981. The species characterising these sites,

predominantly rocky, were mostly algae: *Cladophora prolifera*, *Codium adhaerens*, *Cystoseira corniculata*, *C. foeniculacea*, *Dasycladus vermicularis*, *Gloiocladia repens*, *Lithophyllum stictaeforme*, and *Sargassum vulgare*. On the left side of the diagram, the site-points S, Y, P, K and T, for both 1981 and 2013, are close to each other: although they exhibit different proportion of sandy seafloor, seagrass meadows and boulders, all correspond to mixed bottoms, with many species in common. The points of the species found exclusively or mostly in 1981 lay on the upper left corner, including *Portunus hastatus*, *Trachinus draco*, *Mullus surmuletus*, *Caulerpa prolifera*, and *Astropecten jonstoni*; in 2013 the latter has been replaced on sand by *Astropecten irregularis pentacanthus*. The lower corner of the point cloud was occupied by the site-points N, B, and G (reefs and rocks) for 2013, together with the corresponding species-points: these species included some encrusting bryozoans, namely *Reptadeonella violacea*, *Rhyncozoon neapolitanum* and *Schizoporella dunkeri*, and some aliens, such as *Dendostrea frons* and *Styopodium schimperi*.

Consistently, three species clusters were individuated (Fig. 9): cluster I included the species that characterised reefs in 1981, while cluster II was formed by the species that characterised sandy seafloors and seagrass meadows in 1981; finally, the far larger cluster III contained all the remaining species.

Position of site-points in the CA diagram was used for axes interpretation (Fig. 10A). The 1st axis showed mainly an expression of the habitat differences among

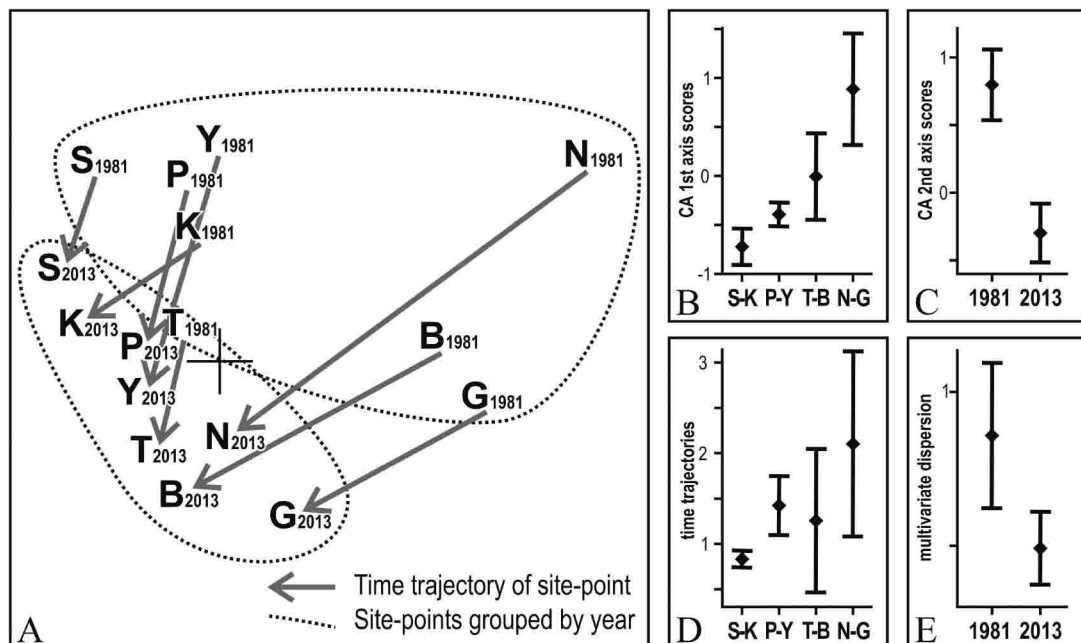


Fig. 10: CA axes interpretation. A - Same diagram of Fig. 9, but only site-points are plotted; sites are grouped by year of survey and time trajectories of individual sites are also indicated. B - Mean (\pm se) 1st axis scores of the site-points, coupled according to the prevalent seafloor type (S and K were sandy with submerged beachrocks and few seagrass; P and Y were seagrass meadows, with coarse sand to gravel and rocks; T and B were essentially boulders fields; N and G were rocky reefs). C - Mean (\pm se) 2nd axis scores of the site-points grouped by year of survey. D - Mean (\pm se) length of the time trajectories of the site-points coupled as in B. E - Mean (\pm se) multivariate dispersion of the site-points in the two years of survey.

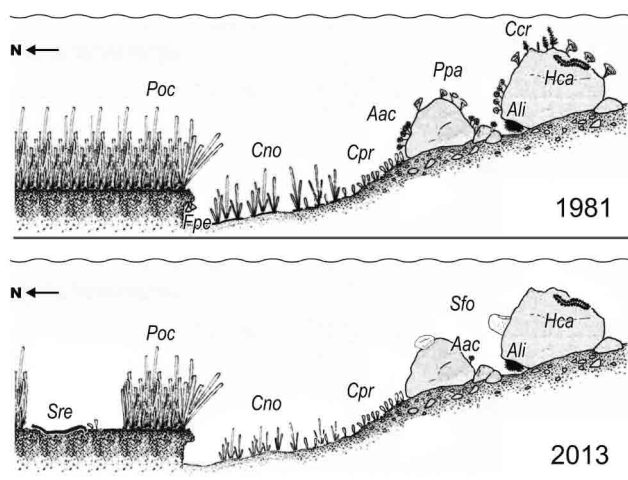


Fig. 11: Schematic profile of the seafloor down to about 6 m depth and to 100 m from the shore at site P, to illustrate change between 1981 and 2013. Species codes as in Table 1.

sites (Fig. 10B), with sands (sites S and K) on the left of the diagram (low 1st axis scores), followed by seagrass meadows (P and Y), boulders fields (sites T and B) and finally reefs (sites N and G); the two boulder fields showed different from each other, as the greater proportion of gravelly sand and seagrass at site T made it more similar to sandy and seagrass sites, while the larger boulders of site B brought it nearer to reef sites. The 2nd axis essentially illustrated change with time (Fig. 10C), scores for

1981 being higher on average than scores for 2013. Time trajectories (computed from CA scores of the first two axes) for sandy and seagrass sites were comparatively shorter than those for boulder and reef sites (Fig. 10D), suggesting greater change with time in the latter. Multivariate dispersion of the site-points (again computed from CA scores of the first two axes) was greater for 1981 than for 2013 (Fig. 10E), indicating increased biotic homogenisation in these 30+ years.

On the whole, minor change was observed in sandy habitats, notwithstanding the disappearance of some characteristic species. Change was more obvious for seagrass and boulders (Fig. 11). No sharp diminution of seagrass was detected with the semi-quantitative metrics adopted: mapping and cover assessment would have been necessary. However, field observations suggested that *Cymodocea nodosa* shoots were less vigorous in 2013 than in 1981, with shorter plants and stolons buried in rather than creeping on the sand, and that dead *Posidonia oceanica* matte extent increased. On boulders, algae nearly disappeared: even the formerly abundant and nearly ubiquitous *Padina pavonica* had disappeared. On the contrary, massive sponges got more abundant. On reefs, change was even more impressive (Figs. 12 and 13). The once flourishing algal forests, mainly by *Cystoseira* and other canopy species (Fig. 14A), disappeared almost completely, leaving space for sponges (Fig. 14B) and wide areas of bare substratum colonised by encrusting organisms, aliens included.

Discussion

During the last three decades, increased intensity of three main categories of stressors (climate change expressed as sea water temperature, local human pressure, and occurrence of alien species) drove the shallow marine

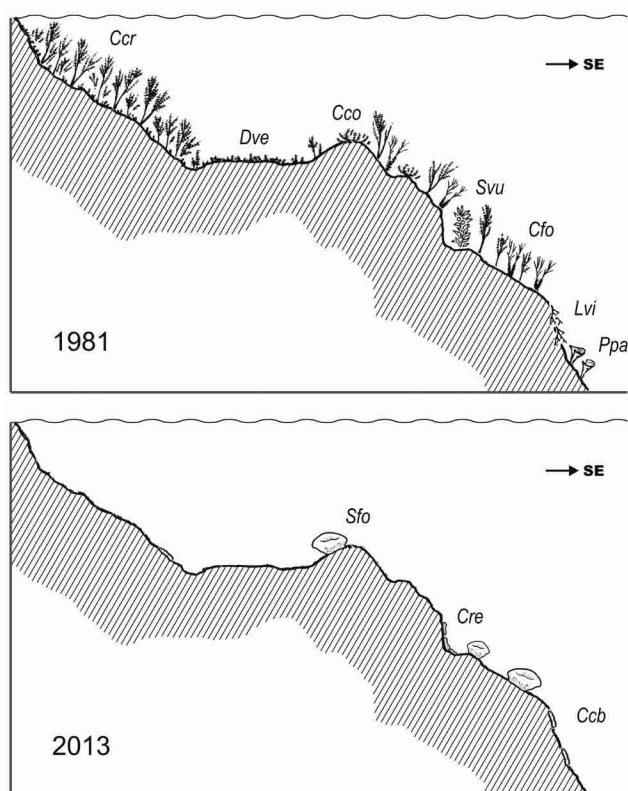


Fig. 12: Schematic profile of a reef slope down to about 7 m depth at site N, to illustrate change between 1981 and 2013. Species codes as in Table 1.

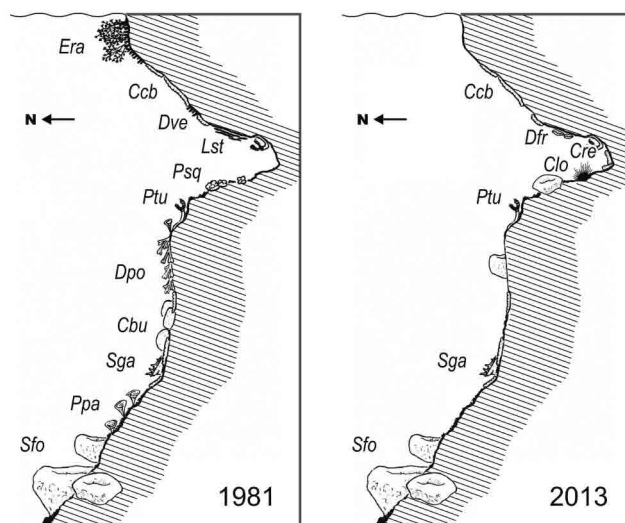


Fig. 13: Schematic profile of a reef wall down to about 10 m depth at site N, to illustrate change between 1981 and 2013. Species codes as in Table 1.

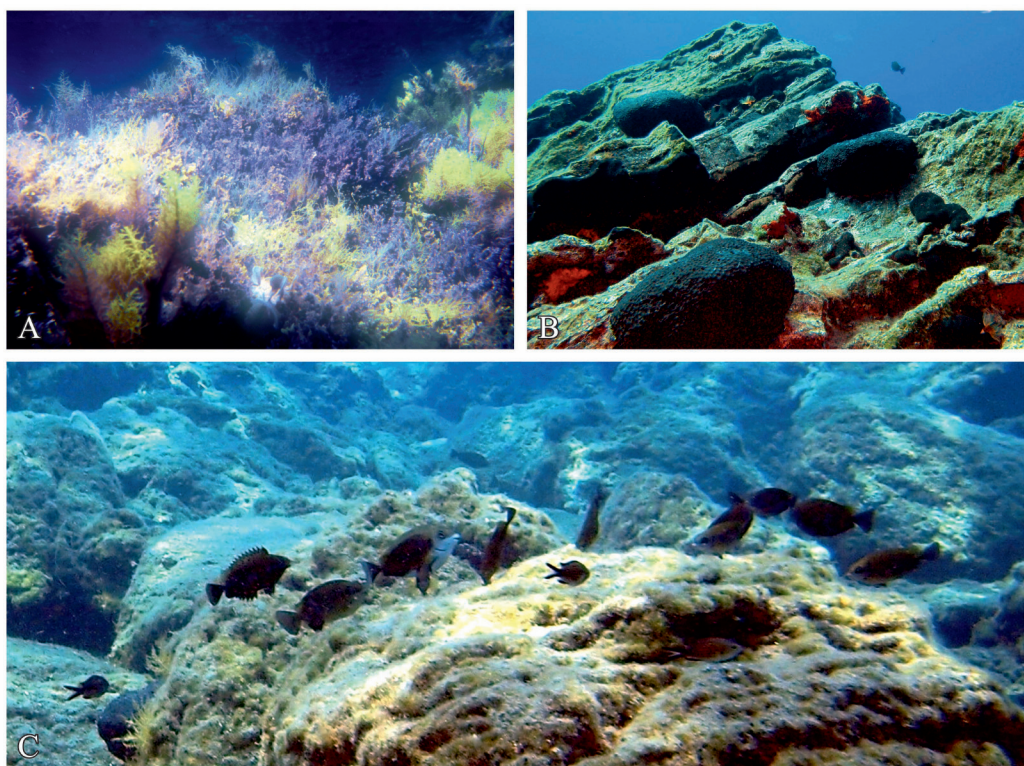


Fig. 14: Structural change on rocky reefs. A - Forest of *Cystoseira* spp in 1981 at site N (UW photograph by C.N. Bianchi). B - *Sarcotragus foetidus* and other sponges on a substratum deprived of algal cover in 2013 at site N (UW photograph by G. Chrisopoulous). C - School of *Siganus luridus* overgrazing algal turf on otherwise barren rock in 2013 (UW photograph by G. Chrisopoulous).

ecosystems of Kos toward a regime shift (as defined by Montefalcone *et al.*, 2011). In the last 30 years, resident population of Kos has increased by 160%, tourism by more than 1000%, and shipping by 550%, all of which supposedly induced higher pollution levels. The only human activity that has declined is fishing (perhaps as an indirect effect of the greater possibility of employment offered by tourism), probably reducing pressure from direct extraction of marine resources. In addition, growing tourism has induced the development of coastal infrastructures (marinas, roads, etc.) not existing in 1981 and of armoured and replenished beaches to contrast coastal erosion.

Based on the observed stressors trend and the scanty recent ecological literature on the area (Pancucci-Papadopoulou *et al.*, 2012), the regime shift has probably occurred somewhere in the 1990s, similarly to what happened in other Mediterranean regions (Parravicini *et al.*, 2013). Comparing only two points in time (1981 vs. 2013), might not be enough to assess whether a parallel change has occurred in biotic community. However, the same kind of ecological information was gathered using the same method, in the same sites, by the same people, and showed parallelism with the corresponding documented regime shift: similarly to what has been already done by Barry *et al.* (1995), this provides suggestive evidence that a phase shift (as defined by Montefalcone *et al.*, 2011) in biotic communities has also occurred.

The situation observed in 1981 may well serve as a reference condition to estimate the magnitude of this phase shift. Bianchi & Morri (1983b) discussed their results also in the light of early descriptive information collected during the Italian zoological expedition of 1926 (Issel, 1928); although differences in methods prevented any formal comparison, they estimated that no major environmental alterations had occurred in more than fifty years. On the contrary, in the subsequent thirty years the amplitude of change was impressive.

From a compositional point of view, native thermophilic species were already conferring a nearly subtropical character to the marine biota of Kos in 1981 (Bianchi & Morri, 1983a), in harmony with its biogeographic context (Bianchi & Morri, 2000). The proportion of these species, however, nearly doubled in 2013 consistently with sea water warming, especially in winter—i.e., the critical period for the establishment of such species (Astraldi *et al.*, 1995). On the other hand, the occurrence, although still rare, of nitrophilic species might be an early warning of eutrophication risk in Kos waters - a possible consequence of mass tourism (Davenport & Davenport, 2006). In 1981, Bianchi & Morri (1983b) found one of these species (*Ulva lactuca*) only in the harbour of Kos (not resurveyed in 2013): now, it occurs outside harbours. Field observations in 2013 detected potential clues of the impact by coastal infrastruc-

tures and managed beaches not observed in 1981: such were, for instance, the reduced prosperity of seagrasses (Montefalcone *et al.*, 2010); the increased occurrence of *Cystoseira barbata*, a species linked to infralittoral sands (Tsekos & Haritonidis, 1974); the large number of *Vermetus triquetrus* shells bearing signs of sand abrasion on beachrocks; the substitution of *Astropecten irregularis pentacanthus*, which thrives in poorly sorted sand, for *A. jonstoni*, preferring well-sorted fine sand. The latter, however, is known to have suffered by temperature induced disease in the late 1990s (Staehli *et al.*, 2009). Finally, in 1981 Bianchi & Morri (1983b) were surprised not to find conspicuous alien species, whereas in 2013 these comprised a momentous proportion of the conspicuous species observed in the coastal marine habitats of Kos.

From a structural point of view, the greatest change was detected in rock and reef habitats, which have lost the once flourishing algal communities, dominated by *Cystoseira* species as in other Aegean localities (Montesanto & Panayotidis, 2001; Giakoumi *et al.*, 2012). In temperate reefs, extirpation of macroalgae has been shown to be caused either by sea water warming (Duarte *et al.*, 2013; Wernberg *et al.*, 2013) or human impact (Claudet & Fraschetti, 2010; Parravicini *et al.*, 2013). In the rocky infralittoral ecosystems of Turkey, Sala *et al.* (2011) demonstrated experimentally that the main cause of algal depletion was the overgrazing by two Lessepsian herbivorous fishes: *Siganus luridus* and *S. rivulatus*. One of the sites studied by Sala *et al.* (2011), namely Bodrum, is very close to Kos, where abundance and grazing activity of *Siganus* schools have been common sights during our survey of 2013 (Fig. 14C). The expected future increase of these invasive species and their interaction with native herbivores will result in unprecedented community-wide change in shallow Mediterranean Sea habitats (Giakoumi, 2014).

The possibility that the change observed at Kos is due to a synergic action of climate, humans, and alien species cannot be excluded. Raitzos *et al.* (2010) demonstrated that recent sea water warming favoured the spread of marine alien species in Greek waters. Coastal development and other human pressures may facilitate the establishment of new invaders (Bianchi *et al.*, 2012a): the alien newcomer *Synaptula reciprocans* has been seen colonising dead matte areas, probably a result of coastal development impact on *Posidonia oceanica* meadows (Lasagna *et al.*, 2011). Establishment of invasive species is argued to be favoured by already stressed ecosystems (Kiparissis *et al.*, 2011). Aliens may in turn facilitate the establishment of further alien species: the rocky barrens originated by *Siganus* overgrazing represented a free space for the settlement of *Styopodium schimperi*, an alien alga resistant to grazing that has already become dominant in other Aegean localities (Cocito *et al.*, 2000; Tsiamis *et al.*, 2010).

Arrival of aliens and loss of natives implied a species turnover of more than 60 % ($\beta_{sim} = 0.61$): high turnover values may be linked to warming (Hillebrand *et al.*, 2010). This result is consistent with the prediction by Cheung *et al.* (2009) that in semi-enclosed seas (such as the Mediterranean Sea) species extinction plus species invasion will result in dramatic species turnovers of over 60%, implying ecological disturbances that potentially disrupt ecosystem services. Nevertheless, diversity at Kos has not decreased, as alien newcomers have overcompensated in number the natives that were not found again in 2013. The number of conspicuous species recorded in our surveys, therefore, slightly augmented from the 83 of 1981 to the 91 in 2013 (9.6%), apparently supporting the view of those who maintain that establishment of alien species is leading to a higher richness of the Mediterranean (Por, 2009; but see Bianchi *et al.*, 2012a). However, this very rough result should be taken with caution: conspicuous species richness is not necessarily a proxy for overall species richness, as most biodiversity is hidden in inconspicuous species (Bianchi & Morri, 2002). Loss of algal canopies is likely to have negatively affected numerous associated epiphytic and motile organisms, whose diversity and abundance is known to be facilitated by habitat cascades via habitat provision and ecosystem engineering (Thomsen *et al.*, 2010). Habitat modification and species invasion are known to interact to cause native species decline (Didham *et al.*, 2007). At Kos, 30 conspicuous species in 1981 were not found again in 2013 ('losses').

Some of the sponge species that gained supremacy in Kos reefs are massive (*Ircinia reticulata*, *Sarcotragus foetidus*) or submassive (*Chondrosia reniformis*, *Petrosia ficiformis*) but others are encrusting (*Crambe crambe*), and in any case large portions of the rocky substrate remained virtually bare. Lack of erect organisms able to form canopies, contrarily to what the pre-existing tall macroalgae used to do, implied loss of three-dimensional structure and hence of architectural complexity in rocky reef habitats (Parravicini *et al.*, 2013). Similarly, the nursery value and functional importance of *Cystoseira* forests suggest that their loss may strongly affect the recruitment of littoral fishes (Cheminée *et al.*, 2013). Reduced habitat complexity is a sign of degradation that has been highlighted as one of the major threats to marine biodiversity worldwide (Airoldi & Beck, 2007). Habitat simplification combined with across-habitat spread of alien species to cause biotic homogenisation at Kos, as illustrated by multivariate analysis.

The methodological approach here adopted has several inherent limits: revisiting instead of time series analysis cannot help individuating when exactly a phase shift has occurred (Spencer *et al.*, 2012); using only semi-quantitative data may blur the understanding of ecosystem shifts (Giakoumi, 2014); adopting time-based random paths rather than rigorous fixed quadrats or transects

augments the possibility of haphazard effects (Bianchi *et al.*, 2004). This notwithstanding, our results proved successful in illustrating ecological change and evaluating its magnitude. Unfortunately, in an era of global change not many examples of this kind are available (e.g., Roghi *et al.*, 2010; Parravicini *et al.*, 2013). Nevertheless, there are numerous old descriptions of Mediterranean shallow water habitats buried in forgotten ‘regional’ publications or technical reports, often written in languages others than English and therefore little available to the international reader. We recommend that research effort be directed to verify the possibility of using them as reference conditions in order to assess ongoing change on coastal marine ecosystems.

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