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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 by1-2°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; Schückel &

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 km<sup>2</sup> 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. 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 (Hill-ebrand *et al.*, 2010, and references therein):

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

where  $\beta_{sim}$  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.  $\beta_{sim}$  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):

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

where  $I_{\rm Rd}$  is the index of relative dominance, AS<sub>2013</sub> is the abundance score of an individual species in the year 2013, and AS<sub>1981</sub> is the abundance score of the same species in 1981.  $I_{\rm Rd}$  ranges from -1 (species found in 1981 only) to +1 (species found in 2013 only).  $I_{\rm Rd}$  was flanked by the maximum abundance score of the species (AS<sub>max</sub>) 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/cgibin/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<sup>-2</sup> 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 longlines 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 (EL-NAIS, 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 (Kützing) M.Verlaque & Boudouresque, 1991 Scarce, on rocky reef at 6 m depth (site G).
PLANTAE, CHLOROPHYTA, ULVOPHYCEAE, CAULERPACEAE <i>Caulerpa racemosa</i> var. <i>cylindracea</i> (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 <i>Alepes djedaba</i> (Forsskål, 1775) A single fish of about 20 cm within a school of <i>Lithognathus mormyrus</i> , 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 <i>Posidonia oceanica</i> meadow at 10 m depth, often bearing ectoparasitic isopods ( <i>Anilocra</i> ?) 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 Forsskål & Niebuhr, 1775 Often in mixed schools with its congeneric S. luridus but less widespread. Always found in boulder fields (occasionally with some patches of <i>Posidonia oceanica</i> ) between 1 and 9 m depth (sites K, B and T).

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AprAstropycetes poissine (Echinodermata)11.0.lossAllArbacica Rival (Echinodermata)2-0.0little or no changeAllArbacica Rival (Echinodermata)21.0lossAorAglaphenia actionatic (Ciularia)11.0.1lossAorAglaphenia actionatic (Ciularia)11.0.0gainAnadyoenee stellaar (Chorophyta)11.0.0gainAstAnadyoenee stellaar (Chorophyta)11.0.0lossAstAnadyoenee stellaar (Chorophyta)11.0.0lossArdAgela turf30.5winnerArgAscidia virginea (Touicata)1-1.0lossBoBoops hoops (Pisces)20.1little or no changeBroBispira volutacornits (Ameida)1-1.0lossCall Codium abaceros (Chorophyta)20.4lossCall Codium abaceros (Chorophyta)20.4lossCall Codium abaceros (Chorophyta)20.0little or no changeCodium bursa (Chorophyta)20.0little or no changeCeCodium bursa (Chorophyta)20.0little or no changeCeCodium bursa (Chorophyta)20.0little or no changeCeCodium bursa (Chorophyta)3-1.0lossCeCodium bursa (Chorophyta)3-1.0lossCodium bursa (Chorophyta)3-1.0lossCeCodium bursa (Chorophyta) </td <td>Aim</td> <td>Apogon imberbis (Pisces)</td> <td>3</td> <td>0.1</td> <td>little or no change</td>	Aim	Apogon imberbis (Pisces)	3	0.1	little or no change
$a_{J}$ <	Aip	Astropecten irregularis peniacaninus (Echinodermata)	1	1.0	laga
An $Arobit (Linkinger (Linkinger)$ $2$ $-0.1$ lose in the lange $Aor$ $Agelias ordikes (Portfera)$ $2$ $1.0$ gain $Ari$ $Anghomen rigide (Modophyta)$ $2$ $1.0$ gain $Ait$ $Anghomen rigide (Modophyta)$ $1$ $1.0$ lose $Ast$ $Anadyomen stellara (Chlorophyta)$ $1$ $1.0$ loss $AgeAscidia visginee (Tunicata)1-1.0lossAgeAscidia visginee (Tunicata)2-1.0lossAbcAnadyomen stellara (Chlorophyta)20.1gainAgeAscidia visginee (Tunicata)1-1.0lossBboBoops hoops (Pisces)20.1gainBpoBoops hoops (Pisces)20.1little or no changeBpoBootys podae (Pisces)20.4loserCadCastane ating (Chlorophyta)20.4loserCadCastane ating (Chlorophyta)20.4loserCbcCastane cranbe (Postephyta)20.0little or no changeCcCastane cranbe (Postephyta)20.0little or no changeCcCastane cranbe (Postephyta)20.0little or no changeCcCastane cranbe (Postephyta)3-1.0loserCcCastane cranbe (Postephyta)3-1.0loserCcCastane cranbe (Postephyta)3-1.0<$	AJO 41;	Astropecter Jonstoni (Echinodermata)	1	-1.0	little or no change
ActAgging partner (Childran)1-1.0lossAriAmphiroa rigida (Rhodophyta)21.0gainAriAmphiroa rigida (Rhodophyta)11.0gainAualgal turf30.5winnerAgg. Ascilia vigine (Tunicata)1-1.0lossAviAnnovia virida (Chidaria)2-1.0lossAviAnemonia virida (Chidaria)2-1.0lossAviAnemonia virida (Chidaria)2-1.0lossBran Baltises captiscus (Fusces)11.0gainBran Baltises captiscus (Fusces)20.1little or ochangeBroBispira volutacornis (Annelida)1-1.0lossCadCodium adhaerns (Chilorophyta)2-0.4wimerCbrCystoscira barbad (Ochrophyta)2-0.4little or no changeCbrCostoscira barbad (Ochrophyta)20.0little or no changeCcCinas cellus (Porifera)20.0little or no changeCcCinas cellus (Porifera)3-1.0lossCcCinas cellus (Porifera)3-1.0lossCcCinas cellus (Porifera)3-1.0lossCcCinas cellus (Porifera)3 <td>All</td> <td>Arbacia itxula (Ecimodermata)</td> <td>2</td> <td>-0.1</td> <td></td>	All	Arbacia itxula (Ecimodermata)	2	-0.1	
nrr $anglinicourse (1000 LGa)$ $2$ $1.0$ $gain$ $ArtAnalyomen stellara (Chicrophya)11.0gainAstAnalyomen stellara (Chicrophya)11.00ssAstAnalyomen stellara (Chicrophya)1-1.00ssArgAscilia virgine (Tunicata)20.5winnerAgeAscilia virgine (Chicrophya)20.5winnerBabononia viridis (Chicrophya)20.5winnerBabononia viridis (Chicrophya)20.1title or no changeBroBahras podar (Pisces)20.1title or no changeBroBispira voltacorris (Annelida)20.4lossChaColtum adharens (Chicrophyta)20.4lossChaColtum barsa (Chicrophyta)20.4lossChaColtum barsa (Chicrophyta)20.6winnerCeCrane celata (Porifera)20.0little or no changeCeChane celata (Porifera)31.0lossCeClasserira corniculata (Ochrophyta)31.0lossCeClasserira corniculata (Ochrophyta)31.0lossCeClasserira formiculace (Ochrophyta)31.0lossCeClasserira formiculace (Ochrophyta)31.0lossCeClasserira formiculace (Ochrophyta)31.0lossCeCrasserira formiculace (Ochroph$	Aor	Aguas oroidas (Porifera)	1	-1.0	agin
$D_{11}$ Imprint Quark (Chickophyta)2110gainAualgal turf30.5winnerAualgal turf30.5winnerArgArsicial vriginea (Tunicata)111.0lossAviAnemonia viridis (Chidaria)2-1.0lossAviAnemonia viridis (Chidaria)2-1.0lossBoll Boby Shops (Pisces)20.1little or no changeBoard Body (Secs)20.1little or no changeBoard Body (Secs)20.4winnerCodCodum adheerns (Chiorophyta)2-1.0lossChrCystoseira barbata (Ochrophyta)20.0little or no changeChrCystoseira barbata (Ochrophyta)20.0little or no changeChrCystoseira conculation (Ochrophyta)20.0little or no changeCcCistoseira conculation (Ochrophyta)1-1.0lossCcCistoseira conculation (Ochrophyta)3-1.0lossCcCistoseira conculation (Ochrophyta)3-1.0lossCrCystoseira conculation (Ochrophyta)3-1.0lossCrCystoseira conculation (Ochrophyta)3-1.0lossCrCystoseira conculation (Ochrophyta)3-1.0lossCrCystoseira conculation (Ochrophyta)3-1.0lossCrCystoseira conculation (Ochrophyta)3-1.0lossCr	Ari	Amphirog rigida (Rhodonhyta)	2	1.0	gain
$T_{ab}$ $T_{ab$	Ast	Anadvomene stellata (Chloronhyta)	1	1.0	gain
NameJestJestJestAviAccidit virginea (Tunicata)1-1.0lossAviAnemonia viridis (Chidaria)2-1.0lossAviAnemonia viridis (Chidaria)2-1.0lossBobBoolys booge (Pisces)20.1little or no changeBroBothus podas (Pisces)2-1.0lossCadCodum adhaerens (Chlorophyta)2-1.0lossCadCodum burka (Chlorophyta)2-0.4winnerCbrCystoscira barbac (Oktrophyta)20.0little or no changeCbrCystoscira barbac (Oktrophyta)20.0little or no changeCccCinan celana (Ponifera)20.0little or no changeCccCinan celana (Ponifera)20.0little or no changeCccCystoscira corniculata (Oktrophyta)3-1.0lossCccCystoscira corniculata (Chorophyta)3-1.0lossCccCystoscira corniculata (Chorophyta)3-1.0lossCforCystoscira corniculata (Chorophyta)3-1.0lossCla Chein labrosus (Pisces)20.5winnerCla Chandrasus (Pisces)20.5winnerCla Chandrasus (Pisces)20.5winnerCla Chein labrosus (Pisces)3-0.1little or no changeCla Chein labrosus (Pisces)3-0.1little or no changeCrCladophora publifera (Chicorophyta)<	Atu	aloal turf	3	0.5	winner
NoteAmemonia viridis (Cnidaria)2-1.0lossBobBoogs boogs boogs (Pisces)11.0gainBroBisiger voluticorvis (Amelida)1-1.0lossBroBisiger voluticorvis (Amelida)2-1.0lossCadCodium adhaerens (Chlorophyta)2-0.4lossCbrCystoseira barbai (Ochrophyta)2-0.4lossCbrCystoseira barbai (Ochrophyta)20.0little or no changeCbrCystoseira barbai (Ochrophyta)20.0little or no changeCcCradium bursa (Chlorophyta)20.0little or no changeCcCradius callar (Porifera)20.0little or no changeCcCystoseira crinical (Ochrophyta)3-1.0lossCcCystoseira crinical (Ochrophyta)3-1.0lossCcCystoseira crinical (Ochrophyta)3-1.0lossCcCystoseira crinical (Ochrophyta)3-1.0lossCatappa granulata (Chustacca)11.0gainClaChelon labrosan (Pisces)20.5winnerClaChelon labrosan (Pisces)20.5winnerClaChelon labrosan (Pisces)11.0gainChelon labrosan (Pisces)20.5winnerClaChelon labrosan (Pisces)20.5winnerClaChelon labrosan (Pisces)3-0.1little or no changeCpfC	Avg	Ascidia virginea (Tunicata)	1	-1.0	loss
BboBogs boops (Pisces)20.5winnerBcaBalister capriscus (Pisces)11.0gainBroBolits podus (Pisces)20.1little or no changeBroBispira volutacornis (Amelida)1-1.0lossCadCodium adhaceres (Chlorophyta)2-0.4lossCbaCystoseira brachat (Ochrophyta)2-0.4loserCbrCystoseira brachycarpa (Ochrophyta)20.0little or no changeCccClona celtat (Portifera)20.0little or no changeCccChona celtat (Portifera)20.0little or no changeCccChoronis (Pisces)3-1.0lossCccCystoseira corriculuta (Ochrophyta)1-1.0lossCgrCystoseira corriculuta (Ochrophyta)3-1.0lossCgrCystoseira corriculuta (Ochrophyta)3-1.0lossCgrCystoseira corriculus (Ochrophyta)3-1.0lossCgrCystoseira corriculus (Ochrophyta)3-1.0lossCgrCalappa granulata (Crustaca)11.0gainCluCorris plus (Pisces)20.5winnerClaCholin labrosus (Pisces)20.5winnerClaChalin labrosus (Pisces)3-0.1little or no changeCprCladerpa prolifera (Chlorophyta)3-0.1little or no changeCrChoronis varigoing (Dichodermata)1 <td< td=""><td>Avi</td><td>Anemonia viridis (Cnidaria)</td><td>2</td><td>-1.0</td><td>loss</td></td<>	Avi	Anemonia viridis (Cnidaria)	2	-1.0	loss
BcaBalistes capriscus (Pisces)11.0gainBpoBothus podas (Pisces)20.1little or no changeBroBispira volutacornis (Annelida)1-1.0lossCadCadium adhaevens (Chicrophyta)2-0.4loserCheCystoseira brachycarpa (Ochrophyta)2-0.4loserCheCostoseira brachycarpa (Ochrophyta)2-0.4loserCheCostoseira brachycarpa (Ochrophyta)20.0little or no changeCccChonnis chronis (Pisces)30.5winnerCccChonnis chronis (Pisces)3-1.0lossCcrCystoseira corniculata (Ochrophyta)3-1.0lossCadipag granulata (Crustocea)11.0gainlossCgrCalappa granulata (Crustocea)20.5winnerClaChelon laborsus (Pisces)20.5winnerClaChelon laborsus (Pisces)20.5winnerClaChelon laborsus (Pisces)20.5winnerClaChelon laborsus (Pisces)3-0.1little or no changeCystoseira coniculacea (Chriophyta)3-0.1listleClaChelon laborsus (Pisces)20.5winnerClaChelon laborsus (Pisces)3-0.1listleClaChelon laborsus (Pisces)3-0.4loserCrCystoseira abradistra (Mollusca)11.0gainCr	Bho	Boons boons (Pisces)	2	0.5	winner
BpoBothus padas (Pisces)20.1little or no change $Bvo$ Bispira volutacornis (Annelida)111.0loss $Cad$ Codum adhacerns (Chlorophyta)21.0loss $Cba$ Cystoseira barbaia (Ochrophyta)20.4winner $Cbr$ Cystoseira barbaia (Ochrophyta)20.0little or no change $Cbr$ Costoseira barbaia (Ochrophyta)20.0little or no change $Ccc$ Clona celata (Porifera)20.0little or no change $Ccc$ Chona celata (Porifera)20.0little or no change $Ccc$ Chronis chronis (Pisces)3-1.0loss $Ccc$ Cystoseira corniculata (Ochrophyta)3-1.0loss $Cgr$ Cystoseira corniculata (Ochrophyta)3-1.0loss $Cgr$ Cystoseira corniculata (Ochrophyta)3-1.0loss $Cgr$ Cystoseira foniculacea (Ochrophyta)3-1.0loss $Cgr$ Calapa granulata (Crustoca)11.0gain $Cuc$ Chronis chrophyta)3-0.1little or no change $Cfa$ Chrophyta3-0.1little or no change $Cgr$ Chrophyta3-0.1loss $CreChrophyta3-0.1lossCreChrophyta3-0.1little or no changeCreChrophyta3-0.1little or no changeCgrChrophyta3-0.1littl$	Bca	Balistes capriscus (Pisces)	1	1.0	gain
$\dot{Bvo}$ Bispira' volutacornis (Annelida)1-1.0loss $Cad$ Colum adharens (Chicrophyta)20.4loss $Cbc$ Cystoseira brachycarpa (Ochrophyta)20.4loser $Cbr$ Colum bars (Chicrophyta)20.0little or no change $Cbc$ Cambe crambe (Porifera)20.0little or no change $Ccc$ Cinambe crambe (Porifera)20.0little or no change $Ccc$ Chronis chronis (Pisces)30.5winner $Ccc$ Cystoseira crinia (Ochrophyta)3-1.0loss $Ccc$ Cystoseira crinia (Ochrophyta)3-1.0loss $Ccc$ Cystoseira crinia (Ochrophyta)3-1.0loss $Cgr$ Calapa granulata (Chicrophyta)3-1.0loss $Cgr$ Calapa granulata (Chicrophyta)20.5winner $Cla$ Chelon labrosus (Pisces)20.5winner $Cla$ Chelon labrosus (Chicaria)11.0gain $CneCriardubus membranaceus (Chicaria)11.0gainCneChardosca nodosa (Tracheophyta)3-0.4loserCraChalerpa racensas (Chicophyta)3-0.4loserCraChalerpa racensas (Chicophyta)3-0.4loserCraCaladeph ar prolifera (Chicophyta)3-0.4loserCraCaladeph arenjoris (Porifera)30.2little or no changeCprChalerpa racensas ($	Bpo	Bothus podas (Pisces)	2	0.1	little or no change
CadCodum adhaerens (Chlorophyta)2-1.0lossCbaCystoseira barbaia (Oktrophyta)20.4winnerCbrCystoseira barbaia (Oktrophyta)20.0little or no changeCbrColum bursa (Chlorophyta)20.0little or no changeCcbCrambe crambe (Porticra)20.0little or no changeCccCliona celata (Porifera)20.0little or no changeCccCystoseira corniculata (Oktrophyta)3-1.0lossCrCystoseira corniculata (Oktrophyta)3-1.0lossCgrCalappa granulata (Crustacca)11.0gainClaChelon labrosus (Pisces)20.7winnerClaChelon labrosus (Pisces)20.5winnerClaChelon labrosus (Pisces)20.5winnerClaChelon labrosus (Crustacca)11.0gainCmeCerianthus membranaceus (Crustacca)11.0gainCmeCerianthus membranaceus (Crustacca)3-0.1little or no changeCfCymodocca nodosa (Tracheophyta)3-0.1little or no changeCfCymodocca nodosa (Tracheophyta)3-0.1little or no changeCfChandrosus realization (Chlorophyta)3-0.1little or no changeCfCladophora prolifera (Chlorophyta)3-0.1little or no changeCfCladophora prolifera (Chlorophyta)3-0.1little	Bvo	Bispira volutacornis (Annelida)	1	-1.0	loss
ChaCystoseira barbata (Ochrophyta)20.4winnerCbrCystoseira brachycarpa (Ochrophyta)20.0little or no changeCbrColim bursa (Chirophyta)20.0little or no changeCceCinan celtat (Porifera)20.0little or no changeCceChromis chromis (Pisces)30.5winnerCcoCystoseira cornicultata (Ochrophyta)1-1.0lossCrCystoseira cornicultata (Ochrophyta)3-1.0lossCfoCystoseira cornicultata (Ochrophyta)3-1.0lossCgrCalappa granulata (Custacea)11.0gainCfaCystoseira cornicultata (Ochrophyta)20.5winnerClaChelon labrosus (Pisces)20.5winnerClaCertonstephanus longispinus (Echinodermata)11.0gainCneCalappa granulata (Custacea)11.0gainCneCertainthus mebranaceus (Chidaria)11.0gainCneCalaphora prolifera (Chlorophyta)2-1.0lossCrCharobris (Prifera)30.6winnerCrCustopa tarcemosa (Chlorophyta)11.0gainCrCharonia variegata (Mollusca)11.0gainCrCharonia variegata (Mollusca)10.0little or no changeCprCaulerpa prolifera (Chlorophyta)3-0.4loserCraCharonia variegata (Mollusca) <t< td=""><td>Cad</td><td>Codium adhaerens (Chlorophyta)</td><td>2</td><td>-1.0</td><td>loss</td></t<>	Cad	Codium adhaerens (Chlorophyta)	2	-1.0	loss
$Cbr$ $\hat{C}$ staseira brachycarga (Ochrophyta)2-0.4loser $Cbu$ $Codium bursa (Chlorophyta)$ 20.0little or no change $Cbc$ $Cname crambe (Ponifera)$ 20.0little or no change $Cce$ $Choma clata (Ponifera)$ 20.0little or no change $Cce$ $Choms change (Fisces)$ 30.5winner $Cco$ $Cystoseira corniculata (Ochrophyta)3-1.0lossCcrCystoseira corniculata (Ochrophyta)3-1.0lossCgrCalappa granulata (Chstascea)11.0gainGuChelon labrosu (Pisces)20.5winnerClaChelon labrosu (Pisces)20.5winnerClaChelon labrosu (Pisces)3-0.1little or no changeCprCalappa granulata (Chstascea)11.0gainCnocornichus membranaceus (Chiodermata)11.0gainCnoCornichus membranaceus (Chiodian)3-0.1little or no changeCprCladophora gradifera (Chlorophyta)3-0.4loserCraCalalerpa arceamosa (Chlorophyta)3-0.1little or no changeCprCladophora gradifera (Chlorophyta)3-0.4loserCraChandosta remiformis (Porifera)3-0.4loserCraChandora archigera (Chlorophyta)10.0little or no changeCprCondorsta remiformis (Porifera)3$	Cba	Cystoseira barbata (Ochrophyta)	2	0.4	winner
Cbu $Codium bursa (Chlorophyta)$ 20.0little or no change $Ccb$ $Crambe crambe (Porifera)$ 20.6winner $Ccc$ $Chona celtat (Porifera)$ 20.0little or no change $Cch$ $Chromis chromis (Pisces)$ 30.5winner $Cco$ $Cystoseira corniculata (Ochrophyta)$ 1-1.0loss $Cco$ $Cystoseira corniculata (Ochrophyta)3-1.0lossCrcCystoseira corniculata (Costacea)11.0gainCgrCalappa granulata (Crustacea)20.7winnerClaChelon laborsus (Pisces)20.7winnerClaChelon laborsus (Pisces)20.10gainCmeCerinstephanus (Echinodermata)11.0gainCmeCerinstephanus (Echinodermata)11.0gainCmeCerinstephanus (Echinodermata)2-1.0lossCprCladophora prolifera (Chlorophyta)2-1.0lossCraCaulerpa racemosa (Chlorophyta)3-0.4loserCraCaulerpa racemosa (Chlorophyta)3-0.4loserCraCharonis variegata (Mollusca)11.0gainCreCharonis variegata (Mollusca)1-0.4loserCraCharonis variegata (Mollusca)21.0lossDroDiplodus annularis (Pisces)3-1.0lossDroDiplodus annulari$	Cbr	Cystoseira brachycarpa (Ochrophyta)	2	-0.4	loser
CcbCrambe crambe (Porifera)20.6winnerCceCliona celata (Porifera)20.0little or no changeCchChronsis (Pisces)30.5winnerCcoCystoseira coniculata (Ochrophyta)1-1.0lossCcrCystoseira crinita (Ochrophyta)3-1.0lossCgrCalappa granulata (Custacea)11.0gainCjuCoris julis (Pisces)20.7winnerClaChelon labrosus (Pisces)20.5winnerClaChelon labrosus (Pisces)3-0.1little or no changeClaChelon labrosus (Pisces)3-0.1little or no changeClaChelon labrosus (Pisces)3-0.1little or no changeClaControstephanus longispinus (Echinodermata)11.0gainCnoCymodocea nodosa (Trachcephyta)3-0.1little or no changeCprCladophora prolifera (Chlorophyta)3-0.4loserCraCaulerpa rotofiera (Chlorophyta)11.0gainCreChondrosia reniformis (Porifera)30.6winnerCvaCharonia variegata (Mollusca)1-0.4loserCraCaulerpa rotofiera (Mollusca)21.0gainDiplodus annularis (Pisces)20.2little or no changeDirDendostrae finos (Mollusca)3-1.0lossDanDiplodus annularis (Pisces)20.2li	Cbu	Codium bursa (Chlorophyta)	2	0.0	little or no change
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Cpr $Caulerpa prolifera (Chlorophyta)$ 3 $-0.4$ loser $Cra$ $Caulerpa racemosa (Chlorophyta)$ 11.0gain $Cre$ $Chondrosia reniformis (Porifera)$ 30.6winner $Cva$ $Charonia variegata (Mollusca)$ 1 $0.0$ little or no change $Cve$ $Conus ventricous (Mollusca)$ 1 $-1.0$ loser $Dan$ $Diplodus annularis (Pisces)$ 1 $-0.4$ loser $Dfr$ $Dendostrea frons (Mollusca)$ 2 $1.0$ gain $Dpo$ $Dictyopteris polypodioides (Ochrophyta)$ 3 $-1.0$ loses $Dpu$ $Diplodus puntazzo (Pisces)$ 1 $0.0$ little or no change $Dsa$ $Diplodus suntazzo (Pisces)$ 2 $0.2$ little or no change $Dvu$ $Diplodus sulgaris (Pisces)$ 3 $-1.0$ loss $Dvu$ $Diplodus vermicularis (Chlorophyta)$ 3 $-1.0$ loss $Dvu$ $Diplodus vulgaris (Pisces)$ 3 $0.2$ little or no change $Eae$ $Epinepheleus aeneus (Pisces)$ 1 $0.2$ little or no change $Eae$ $Epinepheleus aeneus (Pisces)$ 1 $0.2$ little or no change $Eue$ $Elisolandia elongata (Rhodophyta)$ 2 $0.1$ little or no change $Epu$ $Echinocyamus pusillus (Echinodermata)$ 1 $0.2$ little or no change $Epu$ $Echinocyamus pusillus (Mollusca)$ 1 $0.8$ loser $Far$ $Flabellina affinis (Mollusca)$ 1 $-1.0$ lo	Cpf	Cladophora prolifera (Chlorophyta)	2	-1.0	loss
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Her Haliclona cratera (Porifera) 2 -1 0 loss	Hcl	Hydroclathrus clathratus (Ochronhyta)	2	1.0	gain
	Hcr	Haliclona cratera (Porifera)	2	-1.0	loss

**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).

(continued)

(continued)

Code	Species (Higher taxon)	AS <sub>max</sub>	$I_{_{ m Rd}}$	
Htr	Hexaplex trunculus (Mollusca)	1	0.0	little or no change
Ior	Ircinia oros (Porifera)	2	-1.0	loss
Ire	Ircinia reticulata (Porifera)	2	0.8	winner
Jru	Jania rubens (Rhodophyta)	1	0.2	little or no change
Lmo	Lithognathus mormyrus (Pisces)	2	1.0	gain
Lob	Laurencia obtusa (Rhodophyta)	2	1.0	gain
Lom	Laevicardium oblongum (Mollusca)	1	1.0	gain
Lpr	Leptopsammia pruvoti (Cnidaria)	3	-1.0	loss
Lst	Lithophyllum stictaeforme (Rhodophyta)	2	-1.0	loss
Lvi	Liagora viscida (Rhodophyta)	2	-0.1	little or no change
Mcr	Maja crispata (Crustacea)	1	-1.0	loss
Mgl	Marthasterias glacialis (Echinodermata)	1	-1.0	loss
Mhe	Muraena helena (Pisces)	2	0.0	little or no change
Msu	Mullus surmuletus (Pisces)	3	-1.0	loss
Ome	Oblada melanura (Pisces)	2	0.5	winner
Оор	Ophidiaster ophidianus (Echinodermata)	1	0.0	little or no change
Ovu	Octopus vulgaris (Mollusca)	1	0.2	little or no change
Pat	Peltodoris atromaculata (Mollusca)	1	-1.0	loss
Pca	Patella caerulea (Mollusca)	2	1.0	gain
Pdi	Pennaria disticha (Cnidaria)	1	1.0	gain
Pfi	Petrosia ficiformis (Porifera)	2	0.4	winner
Pha	Portunus hastatus (Crustacea)	1	-1.0	loss
Pli	Paracentrotus lividus (Echinodermata)	1	0.0	little or no change
Pno	Pinna nobilis (Mollusca)	2	0.0	little or no change
Poc	Posidonia oceanica (Tracheophyta)	3	-0.1	little or no change
Ppa	Padina pavonica (Ochrophyta)	3	-1.0	loss
Psq	Peyssonnelia squamaria (Rhodophyta)	3	-0.5	loser
Ptu	Protula tubularia (Annelida)	3	0.2	little or no change
Rne	Rhyncozoon neapolitanum (Bryozoa)	2	1.0	gain
Rvi	Reptadeonella violacea (Bryozoa)	2	1.0	gain
Sca	Serranus cabrilla (Pisces)	1	0.5	winner
Sct	Sparisoma cretense (Pisces)	3	0.6	winner
Scu	Spirastrella cunctatrix (Porifera)	2	-0.1	little or no change
Sdu	Schizoporella dunkeri (Bryozoa)	2	1.0	gain
Sfo	Sarcotragus foetidus (Porifera)	3	0.4	winner
Sga	Spondylus gaederopus (Mollusca)	2	-0.1	little or no change
Sgr	Spharechinus granularis (Echinodermata)	1	1.0	gain
Slu	Siganus luridus (Pisces)	3	1.0	gain
Sma	Spicara maena (Pisces)	2	1.0	gain
Smd	Scorpaena maderensis (Pisces)	2	-1.0	loss
Sof	Spongia officinalis (Portfera)	2	-1.0	loss
Sre	Synaptula reciprocans (Echinodermata)	2	1.0	gain
Sri	Siganus rivulatus (Pisces)	3	1.0	gain
Sro	Symphodus roissali (Pisces)	2	-0.2	little or no change
Ssa	Sarpa salpa (Pisces)	3	-0.2	little or no change
SSD	Serranus scriba (Pisces)	1	0.5	winner
Ssc	Stypopodium schimperi (Ochrophyta)	1	1.0	gain
Ssn	Stenopus spinosus (Crustacea)	1	-1.0	loss
Ssp	Stypocaulon scoparium (Ochrophyta)	2	-0.4	loser
SSZ Swi	Sabella spallanzanii (Annelida)	1	1.0	gain
SVI	Sphyraena viriaensis (Pisces)	2	1.0	gain
SVU Tar	<i>Thylacodes grangeius</i> (Mollycco)	∠ 1	-1.0	1055
1ar T.J.,	Thylacodes arenarius (Mollusca)	1	1.0	gain
1 ar Tar	Truchinus araco (Misces)	1	-1.0	1055
1 ga Tou	Tonna galea (Mollusca)	2 1	1.0	gain
Tna	Thalassoma pays (Pisces)	1	1.0	gain
1pa Tno	Theorem and the second se	5	0.4	winner
тре Пла	<i>Libra lastuag</i> (Chlorophyte)	1	1.0	gain
Ula Vtr	Varmatus triguatrus (Mollycoc)	2	1.0	gain
v tr Va	<i>Vermetus triquetrus</i> (Monusca)	3	1.0	
ANO	Ayrichtys novacula (Pisces)	1	0.1	intrie 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 - *Sphyraena viridensis* at site T (UW photograph by G. Chrisopoulous). D – The sponge *Chondrosia reniformis* and the bryozoan *Schizoporella dunkeri* in a rocky reef at site G (UW photograph by G. Chrisopoulous).

species richness (Table 1): 82 species were found in 1981, 89 in 2013; 51 species were common to both surveys, leading to a turnover  $\beta_{sim}$  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<sub>max</sub> and  $I_{\rm Rd}$  values for all species, while Fig. 7 shows details for some selected examples. The 38 gains evidently exhibited  $I_{\rm Rd} = 1$ , the 30 losses  $I_{\rm Rd} = -1$ ; fixing arbitrarily limits for the values of  $I_{\rm Rd}$  comprised between 1 and -1, 16 species ('winners') increased their abundance ( $I_{\rm Rd} > 0.3$ ), 28 underwent little or no change ( $0.2 \le I_{\rm Rd} \le -0.2$ ), and 8 ('losers') got scarcer ( $I_{\rm Rd} < -0.3$ ).

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



*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).

disticha, Sphyraena 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 *Cysto*seira 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. 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 Stypopodium 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



*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.

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. 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 infrastructures 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. Raitsos 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 Stypopodium 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 semiquantitative 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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- http://www.deyakos.gr, Municipal service for water provisiondistribution and waste treatment
- https://services.ath.hcmr.gr, Hellenic Network for Aquatic Invasive Species: ELNAIS