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Coccolithophore export production in NE Mediterranean: comparison from sediment trap fluxes.

Ελισάβετ Σκαμπά
Α.Μ. 21501

Μεταπτυχιακή Διατριβή

Τριμελής Επιτροπή:
Καθηγήτρια Μ. Β. Τριανταφύλλου (επιβλέπουσα)
Επίκουρη Καθηγήτρια Μ. Δ. Δήμιζα (μέλος)
Research Director HCMR Δρ. Α. Γώγου (μέλος)

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Summary/ Περίληψη

Στην παρούσα μεταπτυχιακή διατριβή μελετήθηκε η εξαγόμενη παραγωγικότητα των κοκκολιθοφόρων της ΒΑ Μεσογείου και έγινε σύγκριση των ροών από δείγματα ιζηματοπαγίδων. Η εξαγόμενη παραγωγικότητα των κοκκολιθοφόρων μελετήθηκε σε δείγματα ιζηματοπαγίδων που συλλέχθηκαν κατά τη διάρκεια διαφόρων χρονικών διαστημάτων από τρεις περιοχές της Ανατολικής Μεσογείου: το μεσοτροφικό Βόρειο Αιγαίο (λεκάνη Άθου) σε βάθος 500m από την επιφάνεια της θάλασσας κατά το διάστημα Ιούνιος 2011-Νοέμβριος 2015, το υπερ-ολιγοτροφικό Νότιο Αιγαίο / Κρητικό Πέλαγος σε βάθος 1500m στο διάστημα Φεβρουάριος 2001-Ιανουάριος 2002, Ιανουάριος 2015 -Δεκέμβριος 2015) και το ολιγοτροφικό ΝΑ Ιόνιο Πέλαγος σε βάθος 2000m στο διάστημα Ιανουάριος 2010-Σεπτέμβριος 2015. Τα δεδομένα συγκρίθηκαν προκειμένου να καθοριστεί η χωρική και εποχική μεταβλητότητα στη σύνθεση των συναθροίσεων των κοκκολιθοφόρων και στις ροές των κοκκοσφαιρών σε διαφορετικά βάθη. Με την παρούσα μελέτη αντικατοπτρίζεται στην εξαγόμενη παραγωγικότητα των κοκκολιθοφόρων το πλαίσιο της βιογενούς ιζηματογένεσης στην υδάτινη στήλη.

Κατά τη διάρκεια του Δεκεμβρίου 2014-Δεκεμβρίου 2015, οι ροές των κοκκολιθοφόρων αποκαλύπτουν έντονη εποχικότητα, με μέγιστες τιμές να καταγράφονται από τον Φεβρουάριο έως τον Μάρτιο (Ν. Αιγαίο Πέλαγος: μέγιστο 8,56 x 10^6 coccospheres m^{-2} day^{-1}, Ιόνιο Πέλαγος: μέγιστο 0,81 x 10^6 coccospheres m^{-2} day^{-1} και Κρητικό Πέλαγος: μέγιστο 3.37 x 10^6 coccospheres m^{-2} day^{-1}). Τα μέγιστα ροής συνέβησαν κατά τη φάση της ανάμιξης της υδάτινης στήλης και συμπίπτουν με το διάστημα παρουσίας μειωμένων θερμοκρασιών της επιφάνειας της θάλασσας. Η ροή των κοκκοσφαιρών κυριαρχείται από το είδος *Emiliania huxleyi* (75% κατά μέσο όρο στο Βόρειο Αιγαίο, με μέσο όρο ελαφρώς πάνω από 50% στο Κρητικό και στο Ιόνιο πέλαγος), ακολουθούμενα από τα είδη *Syracosphaera* spp. (14% κατά μέσο όρο στο Βόρειο Αιγαίο, ~ 10% κατά μέσο όρο στο Κρητικό και στο Ιόνιο Πέλαγος) και το είδος *Algirosphaera robusta* (έως 14% κατά μέσο όρο στο Ιόνιο Πέλαγος, πάνω από 45% τον Φεβρουάριο του 2015). Το είδος *Umbilicosphaera sibogae* είναι το σημαντικότερο από τα είδη με μικρότερες εμφανίσεις, ιδιαίτερα στο Κρητικό Πέλαγος (13% κατά μέσο όρο, μέγιστη ροή 1,01 x 10^6 coccospheres m^{-2} day^{-1} το Μάρτιο του 2015).

Όπως παρατηρείται, η συνολική ροή των κοκκοσφαιρών στο Β. Αιγαίο είναι σημαντικά υψηλότερη, λόγω της ιδιαίτερα υψηλής εποχικής αύξησης του είδους *E. huxleyi* (> 95% της συνάθροισης των κοκκολιθοφόρων τον Ιανουάριο του 2015, μέγιστη ροή *E. huxleyi*: 7,92 x 10^6 coccospheres m^{-2} day^{-1}). Ένα παρόμοιο εποχιακό σήμα στις ροές των κοκκοσφαιρών παρατηρήθηκε επίσης σε προηγούμενες δειγματοληπτικές χρονοσειρές στις ίδιες θέσεις. Ωστόσο, παρατηρείται τάση αύξησης των ροών των κοκκοσφαιρών κατά τη διάρκεια των τελευταίων ετών στο Κρητικό Πέλαγος (μέγιστο 0,4 x 10^6 coccospheres m^{-2} day^{-1} το 2001) και το Β. Αιγαίο (μέγιστο 0,29 x 10^6 coccospheres m^{-2} day^{-1} το 2011). Συνολικά, οι ροές εξαρτώνται σε μεγάλο βαθμό από τον εμπλουτισμό της υδάτινης στήλης σε θρεπτικές ουσίες λόγω της κάθετης ανάμειξης των υδάτων το χειμώνα στο Βόρειο Αιγαίο και / ή τη επίδραση των επεισοδίων εισόδου Αφρικανικής σκόνης στο Νότιο Αιγαίο και στο Ιόνιο Πέλαγος, γεγονός που αυξάνει τα θρεπτικά συστατικά σε αυτές τις ολιγοτροφικές περιοχές, όπως αποδεικνύεται από τις ροές λιθογενετικού υλικού και θρεπτικών ουσιών.

Μια συγκριτική μελέτη σχετικά με τη μορφολογία και το βαθμό ασβεστοποίησης των κοκκόλιθων του είδους *E. huxleyi* πραγματοποιήθηκε μέσω εικόνων που φωτογραφήθηκαν σε ηλεκτρονικό μικροσκόπιο σάρωσης (SEM) από δείγματα ιζηματοπαγίδων του ΝΑ Ιονίου και Κρητικού πελάγους, αποκαλύπτοντας υψηλότερες τιμές σχετικού πλάτους των κρυσταλλικών στοιχείων της κεντρικής περιοχής (~ 0,3 στο Κρητικό Πέλαγος, > 0,35 στο Ιόνιο) κατά τη διάρκεια των περιόδων αυξημένης

παραγωγικότητας των κοκκολιθοφόρων. Πολλές δειγματοληψίες από τη στήλη νερού του Αιγαίου έχουν ήδη δείξει ότι το είδος *E. huxleyi* έχει ελαφρώς μεγαλύτερα και σημαντικά πιο ασβεστοποιημένους κοκκόλιθους το χειμώνα και νωρίς την άνοιξη, διάστημα κατά το οποίο καταγράφονται χαμηλότερες θερμοκρασίες και υψηλότερη παραγωγικότητα σε σχέση με την περίοδο του καλοκαιριού. Τα δεδομένα που προέκυψαν από τις παρούσες δειγματοληψίες ιζηματοπαγίδων αποκαλύπτουν τις υψηλότερες τιμές σχετικού πλάτους κρυσταλλικών στοιχείων κεντρικής περιοχής στην ιζηματοπαγίδα του Ιονίου που παρατηρήθηκε τον Φεβρουάριο του 2015, σύμφωνα με τις ελάχιστες θερμοκρασίες θαλάσσιας επιφάνειας. Ομοίως, οι μέγιστες τιμές σχετικού πλάτους κρυσταλλικών στοιχείων κεντρικής περιοχής εμφανίστηκαν μέσα στον Απρίλιο του 2015 στην χρονοσειρά του Κρητικού πελάγους, παρουσιάζοντας μια καθυστέρηση ενός μηνός σε σχέση με την μικρότερη θερμοκρασία της επιφάνειας της θάλασσας, αλλά συνολικά διατηρώντας το πρότυπο εποχιακής ασβεστοποίησης του είδους *E. huxleyi* στην ΒΑ Μεσόγειο.

Συνδυάζοντας τις πληροφορίες από τα αποτελέσματα της παρούσας έρευνας μπορούμε να αποκτήσουμε μια σαφή εικόνα για την χωρική και χρονική μεταβλητότητα των ροών των κοκκολιθοφόρων στο Αιγαίο και Ιόνιο πέλαγος καθώς και την απόκριση αυτών των οργανισμών στο αυξανόμενο CO_2 της ατμόσφαιρας.

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1. Introduction

1.1. Site description

The Mediterranean Sea is a marginal sea that is proposed to have a significant role in the absorbing of anthropogenic carbon (Aıt-Ameur and Goyet, 2006; Alvarez et al., 2005). Temperature, combined with other less important parameters, cause annual variation in pCO_2 in the surface of the sea (Copin-Montégut et al., 2004). The winter water column becomes inconstant at low temperatures (below 13 ^{o}C) and the upper water masses mix with the subjacent intermediate waters, whose content in dissolved inorganic carbon is high (Meier et al., 2014). As a result, this fact causes a seasonal pattern, in which surface waters in autumn and early winter, when biological production is low, are characterised by an increment in pCO_2. Nevertheless, the mentioned mixing contributes to the enrichment of the photic zone in nutrients that cause phytoplankton blooms in late winter and early spring. Consequently, that bloom leads to a pCO_2 decrease (Copin-Montégut and Bégovic, 2002; Copin- Montégut et al., 2004).

Evaluations in anthropogenic CO_2 (Cant) indicated that the C_{ant} inventory for the Mediterranean is _ 1.7PgC. That fact shows that Mediterranean Sea' s C_{ant} concentrations display higher values than the global average, something mainly caused by the astonishingly high anthropogenic carbon content of the Eastern Mediterranean Sea (Stavrakakis et al, 2013).

High alkalinity combined with the winter time dense water formation events cause strong absorbing of anthropogenic CO_2 by the Mediterranean Sea. Many sediment trap researches have been done over past decades in the Mediterranean, in open sea and continental shelf environments, regarding budgets of particulate organic carbon, major and minor elements, mass fluxes (Boldrin et al., 2002; Gogou et al., 2012; Lee et al., 2009; Miquel et al., 2011; Sanchez-Vidal et al., 2005; Zuniga et al., 2007) and variability of particle fluxes the mechanisms that control the transference of particulate matter to the open sea (Canals et al., 2006; Heussner et al., 2006; Martin et al., 2010; Monaco et al., 1999; Pasqual et al., 2010; Stavrakakis et al., 15 2000; Stavrakakis and Lykousis, 2011).

The high supersaturation of carbonate throughout the entire Mediterranean's basin from the surface to depth is a known fact (Álvarez et al., 2014; Schneider et al., 2010, 2007). As it already mentioned, Mediterranean Sea also has an important role in the sinking of anthropogenic CO2, which is drawdown into upper water column layers of the basin and then, because of the water's mixing, is tranfered to the deeper layers mixing (Ait-Ameur and Goyet, 2006; Bethoux et al., 2005). The combination of the decrease in pH between 0.061 and 0.148 since the preindustrial age (Schneider et al., 2010; Touratier and Goyet, 2011; Touratier et al., 2012) and the considerably high absolute values of anthropogenic carbon makes Mediterranean Sea an appropriate location to study the effect of anthropogenic acidification on calcifying organisms.
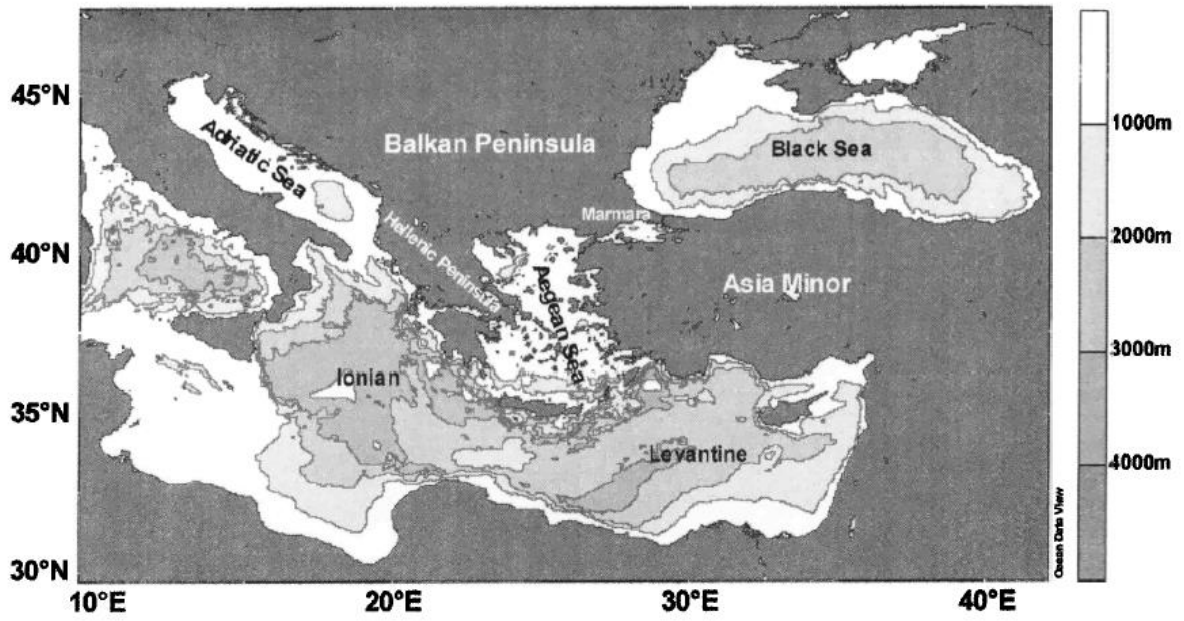
Fig. 1: The locations of the various subbasins of the Eastern Mediterranean (Levantine, Ionian, Aegean, and Adriatic) (source Zervakis et al., 2000).

Fig. 2: Main geotechnical and morphological features of the Aegean Sea (source Unesco / IOC).

1.2. Interaction between atmosphere and ocean

The atmosphere and the ocean interact as one independent system. Changes in one causes influence the other and both are linked by complex feedback loops (Trujillo and Thurman, 2008). The ocean displays some climate patterns, which are closely related to the distributions of the wind belts of the world (Trujillo and Thurman, 2008). The major circular-moving loops of the world are named gyres and are driven by the main wind belts (Palumbo, 2012).

Oceans absorb large quantities of CO_2, almost half of the produced atmospheric CO_2, by forming carbonates. In this absorbing ability of the oceans, the transfer of organic material inside them is also involved. The biological carbonate pump by the precipitation of the organic matter from the surface mixed layer in the deep ocean and sediments is a result of particles' formation and sinking (Honjo et al., 2008). It should be mentioned that all these processes that transform, enrich and transfer organic carbon to the water column is particularly important for the biogeochemical cycles of the ocean and are crucial to the global carbon cycle (Fig. 3).
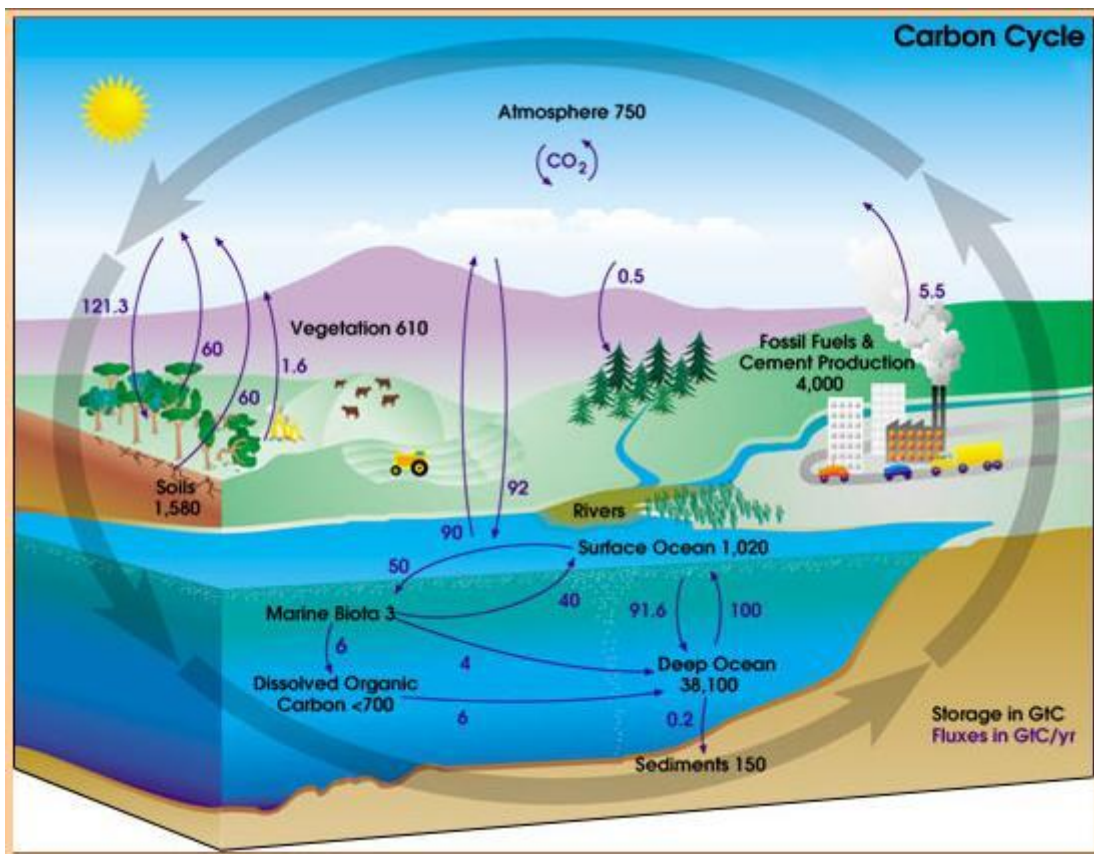
Fig. 3: Carbon cycle: interactions between lithosphere, atmosphere and oceans.

It is awaited to believe that the uptake of anthropogenic CO_2 from the atmosphere into the ocean will have direct influences in the ocean ecosystem in the near future (Bindoff et al., 2007; Kleypas et al., 2006; Kroeker et al., 2013). By the end of the century, significant modifications will be obsered in the global carbonate system, as model projections have shown (Orr et al., 2005; Zeebe, 2012). The strong decline in pH cause ocean acidification (OA), which influence negatively calcifying organisms. A series of studies have shown that different organism groups respond to OA with a sensitivity in

calcification (Kleypas, 1999; Lischka et al., 2011; Moy et al., 2009; Riebesell et al., 2000; van de Waal, 2013; Meier et al., 2014). As coccolithophores are one of the major calcifying phytoplankton group, a decline in their calcium carbonate production could cause changes in the global carbonate cycle and reduces organic carbon export (Gehlen et al., 2007; Wilson et al., 2012).

It has been observed that environmental parameters cause variations in *Emiliania huxleyi* coccolith morphological parameters, mostly weight and length, that could be as seasonal as long-term, too. A fist explanation is that *E. huxleyi* morphotype may display selectivity to some environmental factors causing these changes. Otherwise this could be an expected response to the changes of the environment and E*. huxleyi* show differentiations in coccolith calcification caused by seasonal variations or ever global changes as ocean acidification and global warming (Meier et al, 2014).

1.3. Coccolithophores and Sediment traps

Coccolithophores, considered to be one of the main groups of marine primary producers, are the main planktonic group producing carbonate in the eastern Mediterranean Sea (Knappertsbusch, 1993; Ziveri et al., 2000a, b; Malinverno et al., 2003a,b; Triantaphyllou et al., 2004) and one of the most important contributor to biogenic particle export production, based on seasonal variations. Coccolithophore communities display strong sensitivity to seasonal variations on oceanographic and environmental conditions of the upper water column. Particularly, the response of some opportunistic species with considerably higher values than expected in their abundance and as a consequence export production to the fertilization occurring during the time periods of deep water mixing and external nutrient input (Ziveri and Thunell, 2000). Furthermore, coccolithophore's deep community, flourish in waters below the seasonal thermocline with high nutrient content but low illumination (Malinverno et al., 2009). The preservation of the deep chlorophyll maximum is a characteristic feature of the oligotrophic eastern Mediterranean, and those species of the deep community are, to some extent, responsible (Georgopoulos et al., 2000).

Coccolithophores, as photosynthetic unicellular organisms, are an important factor in the CO_2 - O_2 exchange between oceans and atmosphere. Sedimentation of coccoliths and coccospheres in fecal pellets (material shed by zooplankton organisms) leads to their abundance in seabed. Coccolithophores display a seasonal pattern of high concentrations (blooms), through which they contribute to a great part of the direct sedimentation flux.

To presume, it is quite important to study the sedimentation of particles of the water column as well as the mechanisms that change it.

The term flux is defined as the quantity of a component that sinks in a given horizontal area at a given time. To estimate fluxes of sinking particles, special devices called sediment traps are used. The sinking material of the water column enters the trap by openings at time rotating containers and is being collected inside it for a specified interval. In this way, it can be given a measure of the mass of particles (mg) that sink across the sediment trap surface (m^2) during a specific time period, usually days (Patara et al., 2009). Outcomes from sediment traps, which may be moored at various depths and in different geographical settings (Honjo et al., 2008) yield an important variability in particle flux magnitudes and sinking velocities as a result of physical and biological processes (Berelson, 2002; Francois et al., 2002; De La Rocha and Passow, 2007; Lutz et al., 2007; Trull et al., 2008). Furthermore, deep particle fluxes, in some cases, are decoupled from surface ocean primary production (Buesseler, 1998; Conte et al., 2001; Lutz et al., 2002).

1.4. Aim of study

The aim of this study was to investigate coccolithophores export production in the NE Mediterranean Sea, to compare fluxes from different sediment traps and time intervals and to record the seasonal variability in coccolith fluxes as well as the composition of the assemblages. Coccolithophore export has been investigated in sediment trap samples collected during various time intervals from three Eastern Mediterranean sites (Fig. 4; Table 1): the mesotrophic North Aegean Sea (Athos Basin, M2 site) at 500 m depth (June 2011-November 2015), the ultra-oligotrophic South Aegean/Cretan Sea (M3 site) at 1500 m depth (February 2001-January 2002, January 2015-December 2015) and the oligotrophic SE Ionian Sea (NESTOR site) at 2000 m depth (January 2010-September 2015). The data are compared in order to define the spatial and seasonal variability in assemblage composition and in coccosphere fluxes at different depths. Samples originating from the North Aegean and Ionian traps were analyzed only for coccosphere fluxes in order to investigate how the export production signal is transferred at different depths. This study, is an attempt to compare three different areas with coccolithophores abundance. In particular, it is analyzed their participation in different marine environments with a variety of hydro-thermodynamic conditions such as sea surface temperature, ocean currents, weather conditions, concentrations and nutrient flows, the oligotrophic region of Cretan Sea (north-eastern sea area of Crete) and south-west Ionian compared to eutrophic North Aegean region (Athos basin). Moreover, through this study an attempt was made to compare the morphology of *E. huxleyi* coccolith, the size and the degree of calcification in SE Ionian and Cretan Sea. Environmental and oceanographic conditions are constantly changing over time, thus make sediment traps time-series results of particle flux a really valuable tool to understand world oceans.

Fig. 4: The three investigated areas of our study; Ionian Sea (Nestor site), North Aegean Sea (M2 site), Cretan Sea (M3 site).

Investigated Areas	Investigated time	Depth from sea	Coordinates

	interval	surface (m)	
Ionian Sea	Oct 2014- Sept 2015	2000	36o 2.96 N 21o28.93' E
Cretan Sea	Jan 2015- Dec 2015	1550	35o 44.76'N 25o09.29'E
North Aegean Sea	Oct 2014- Nov 2015	500	39o 58.16'N 24o43.48'E

Table 1: Investigated time interval, depth from sea surface and coordinates of the investigated areas in our study.

2. Study areas

2.1. Ionian Sea (NESTOR site)

NESTOR site is located in SE Ionian Sea (Fig. 5). The submarine morphology of this region is complicated with steep slopes close to the Messinia/Pylos, valleys and deep basins. Steep slope formations, which are almost free of sediments (acoustic basement), extend in short distances from the shore from 600 to 3000m depth, while the area further offshore is dominated by valleys and morphological plateaus, from 3000 to 4000m depth, which incorporate the deepest basins of the Mediterranean Sea (4600 and 5264m depth; Fig.6) and they are covered by undisturbed sediments (lack of slumps or massive sediment failures) (Stavrakakis et al, 2013). Very thin bottom sediment sequences were revealed by continuous sub-bottom seismic profiling, due to the insignificant sediment inputs from the nearby continent. The continuous weak and parallel reflectors of the sub-bottom strata of the deep basins, indicate purely pelagic sedimentation with the absence of turbidity flows (KM3NeT Collaboration, 2007) (Stavrakakis et al 2013).

Ionian's Sea hydrological settings are complex and the area is thought as a transition in where water masses formed in the Levantine, the Aegean Sea and the Adriatic Sea meet and interact with the water masses of the Western Mediterranean Sea that enter through the Sicily Straits. The structure of the local water mass is consisted by : (1) the Modified Atlantic Waters (MAW), which is characterized by a salinity minimum and occupying the approximately upper 25–100 m; (2) the Levantine Intermediate Waters (LIW) occupy typically the 100–500m layer and showing a salinity maximum; (3) the Transitional Waters (TW) in the layer between 500 and 1200 m; and (4) the Eastern Mediterranean Deep Waters (EMDW) occupying the layers below 1200m (Malanotte-Rizzoli et al., 1997; Nittis et al., 1993). The Eastern Mediterranean Transient (EMT) of the early 1990s' cause this structure more complex (Theocharis et al., 1999). In the deep layers of water column in Ionian Sea the newly formed warm and saline Cretan Deep Water (CDW) replaced the older EMDW of Adriatic origin (Klein et al., 1999). Cretan Intermediate Waters (CIW) are located to the intermediate waters and show characteristics similar to LIW (Malanotte-Rizzoli et al., 1999).

Ionian Sea display a seasonal pattern with high variability in the productivity values. Higher values are occurred during the late winter/spring convective mixing period. Climatological factors that generate mesoscale instabilities, cause limited events in space and time leading to the new production of the area. (Boldrin et al., 2002; Casotti et al., 2003; Civitarese et al., 2010; Mazzocchi et al., 2003). E.Mediterranean Sea's nutricline is located normally well below the euphotic layer. In 1987, a 300–400m deep nutricline was measured in the southeastern Ionian Sea (Klein et al., 1999), and a 600m deep nutricline, in correspondence of anticyclonic structures, was measured in Levantine Basin (Ediger and Yilmaz 1996). In the open areas of the Ionian Sea surface chlorophyll concentrations are

generally lower than 0.5 mgm^{-3} with the DCM (deep chlorophyll maximum) located at 80-100m depth. That makes Ionian Sea, the deepest basin of the Eastern Mediterranean Sea, a highly oligotrophic region (Boldrin et al., 2002; Malinverno et al., 2003; Ignatiades, 2005). There is a north-south and west-east gradient along which oligotrophic feature increase as a result of possibly circulation patterns and different water mass characteristics (Bosc et al., 2004; Casotti et al., 2003; D'Ortenzio et al., 2003). In the E. Ionian, surface Chl *a* concentration displays a seasonal pattern with the highest values occurring during late winter and early spring and the lowest during summer. Chl *a* concentration does not exceed 0.2mgm^{-3}(D'Ortenzio et al., 2003). E. Ionian's stable oligotrophic conditions cause low seasonality (Casotti et al., 2003). this fact is revealed by a deep chlorophyll maximum found at around 80–100m depth (Boldrin et al., 2002; Casotti et al., 2003; Crombet et al., 2011; Karageorgis et al., 2012; Rabitti et al., 1994). According to previous studies, Ionian Sea is oligotrophic, display a complex microbial food web (review by Siokou et al., 2010; Yokokawa et al., 2010), and dissolved organic matter (DOM) is partially bioavailable in surface layers as well as in mesopelagic and bathypelagic layers (Meador et al., 2010, Stavrakakis et al, 2013). Coccolithophores occupy a major role in the phytoplankton assemblage, larger than 3μm, of the area (Boldrin et al., 2002; Malinverno et al., 2003). Their contribution to the calcium carbonate export to the deep layers is important and is due to their sinking calcitic remains (Ziveri et al., 2000).

Zooplankton fecal pellets, marine aggregates and marine snow particles are mainly responsible for the fraction of organic matter export in the ocean interior, that sinks out from the upper mixed layer (Knappertsbusch and Brummer, 1995; Stemmann et al., 2002; Turner, 2002). This process is one of the most important of these that maintain the CO2 partial pressure gradient between surface and deep layers (Sarmiento and Gruber, 2006). Through this procedure, ocean's absorbing ability about atmospheric CO2 is being understood. As a consequence of the above, quantifying the particle sedimentation through the water column is quite important and the mechanisms affecting its variability as well (Patara et al., 2009). Although oligotrophic regions are characterized by quite low particle fluxes, their strong reaction is noted with localized and episodic phenomena like the passage of mesoscale eddies (Sweeney et al., 2003), the existence of lithogenic dust events (Zuniga et al., 2008) and high values of zooplankton biomass (Conte et al., 2003; Goldthwait and Steinberg, 2008). Still, the relevant physical and biological mechanisms controlling particle sedimentation in oligotrophic regions need to be more understood (Patara et al. 2009).
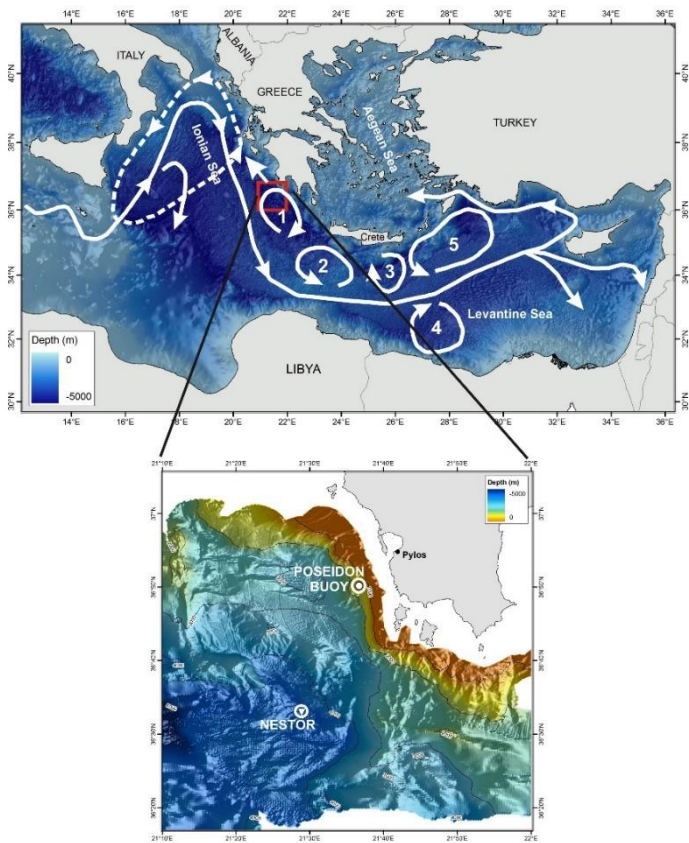
Fig. 5: NESTOR site sediment trap location in the Ionian Sea (source Stavrakakis et al., 2013).
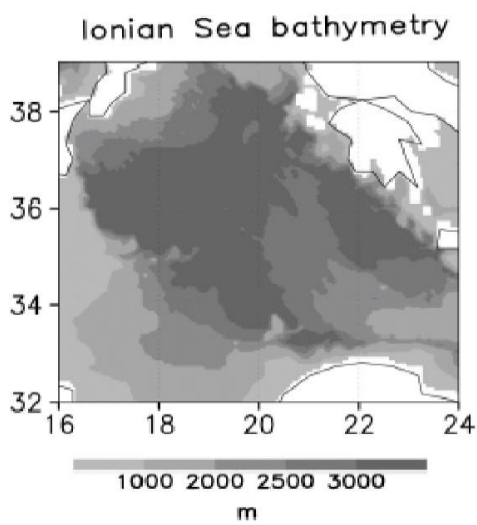

Fig. 6: Ionian Sea bathymetry (source Patara et al., 2009)

2.2. Cretan Sea

South Aegean and specifically the Cretan Sea is the largest and deepest basin of the Aegean Sea. More specifically, the depth of the Cretan Sea reaches 2,500 meters. The basin of the Cretan Sea communicates with the Levantine Basin and the Ionian Sea through straits to the east and west, through trenches that vary in depth from 150 to 1100 m. To the north of the Cretan Basin there is a shallow margin of the plateau of Cyclades (less than 200 m depth) (Georgopoulos, 1989).

The Cretan Sea, the major part of the Southern Aegean Sea, is between the Kiklades islands and the islands of the Cretan arc (Fig. 7). The communication of Cretan Sea with the Levantine basin is achieved through the eastern straits of Kassos, Karpathos and Rhodos and with the Ionian Sea through the three Kitherian straits. The Cretan Sea receives most of the saline waters from the Levantine and less saline waters from the North Aegean (Theocharis *et al.,* 1986; Papageorgiou,1986; Lascaratos and Papageorgiou, 1987). A depression, with an east-west direction, is located in the central area of Cretan Sea, with 1,000 to 2,000 m depth. Kiklades plateau bound that depression to the north at a depth of 400 m. The shelf of the island of Crete, which is the south bound extends at about 5 nautical miles from the northern coast with depths reaching 200 m. Two deeper depressions, reaching the depth of 2,500 m, are located at the eastern part of Cretan Sea. (Georgopoulos et al., 1989).

In the Southern Aegean's upper water column are identified three water masses and three water masses in the intermediate and great depths. The Levantine sea water (LSW), the Black Sea water (BSW) and the Modified Atlantic Water (MAW) are the three water masses of the upper water column. In more details, water masses formed in the region and are similar to the Levantine Intermediate water (LIW) are located from 50dbars = 50m to 250dbars = 250m. However, those are more warm and slightly more saline than LIW's, up to 700m, is the TMW (Transitional Mediterranean Water), which is water from the middle depths of the eastern Mediterranean through the Eastern and Western Cretan Trench and end at depths of 800-2500m deep Cretan Water (CDW) which is locally generated (Lykousis et al. 2002).

Aegean Sea's southern, deeper and larger in volume basin is Cretan Sea and it is used as a reservoir for dissolved oxygen, salt and heat (Georgopoulos et al. 1989). That high salinity causes a net loss of water to the atmosphere (Georgopoulos et al. 2000). The supplies of weathered material from seasonal streams and the complex mesoscale circulation pattern have a strong influence on fluxes in Cretan Sea. That circulation pattern, which is consisted by a cyclone (east) – anticyclone (west) system, control particle transfer in the area and generate a jet of water flowing constantly in a SE and ESE direction (Georgopoulos et al. 2000, Theocharis et al. 1999). The persistence of low concentrations of nutrients, low primary productivity values and phytoplankton densities are some characteristics of open Cretan Sea waters. At those characteristics, are also added the high concentration of dinoflagellates and the formation of pronounced deep chl *a* maxima throughout most of the year (Psarra et al. 2000; Tselepides et al. 2000b). Transmissions take place in winter and cause an intermediate and /or deep-water mass formation. Therefore, in recent years, Transition Mediterranean Water (TMW), has been identified within the upper layer of the S.Aegean Sea . TMW is a distinctive "nutrient (phosphate) rich-oxygen poor" water mass with minimum salinity, which is located at depths up to 700dbar= 700m, coming from the mid-depths of the eastern Mediterranean through the eastern and western Cretan Arc Straits (Lykousis et al. 2002). The productivity of the open waters of the Cretan Sea is influenced by the enrichment of TMW water mass and the double gyre (Souvermetzoglou et al. 1999; Tselepides et al. 2000b).

Cretan Sea is a unique dynamic marine environment that is characterised by distinct seasonal and interannual fluctuations. This is a result of the combination of local characteristics. Those could be an interaction of atmospheric forcing, deep water formation and outflow, the compensating inflow of `nutrient-rich' TMW, the circulation imposed by the mesoscale dipole and the resultant southward and onslope transport of waters and also the unknown influence of down-slope lenses of `spiky water'. (Tselepides et al. 2000b).

Previous studies in the Eastern Mediterranean have shown that coccolithophores are the dominant species of phytoplankton that produce carbonate sediments (Knappertsbusch, 1993; Ziveri et al., 1995; Malniverno et al. 2003) and the main contributor to biogenic particle flux.
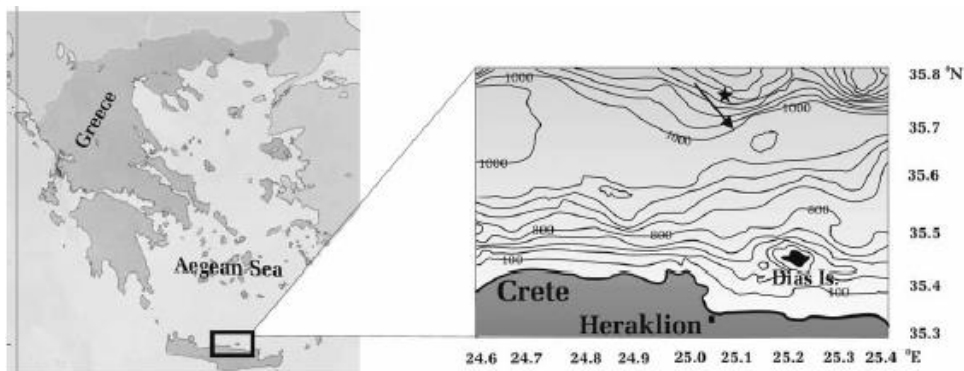
Fig. 7: Sediment trap mooring location in the Cretan Sea (black star). The arrow indicates the general direction of the surface currents (source Triantaphyllou et al., 2004).

2.3. North Aegean-Athos Basin

The Aegean Sea communicates with the Black and Marmara Seas through the Dardanelles Straits, and with the open eastern Mediterranean (Levantine Sea) through the Cretan Straits and is situated between Turkey and Greece. The basin has complicated physical and geographic configuration and exhibits complicated seabed morphology and numerous island complexes (Lykousis et al., 2002).
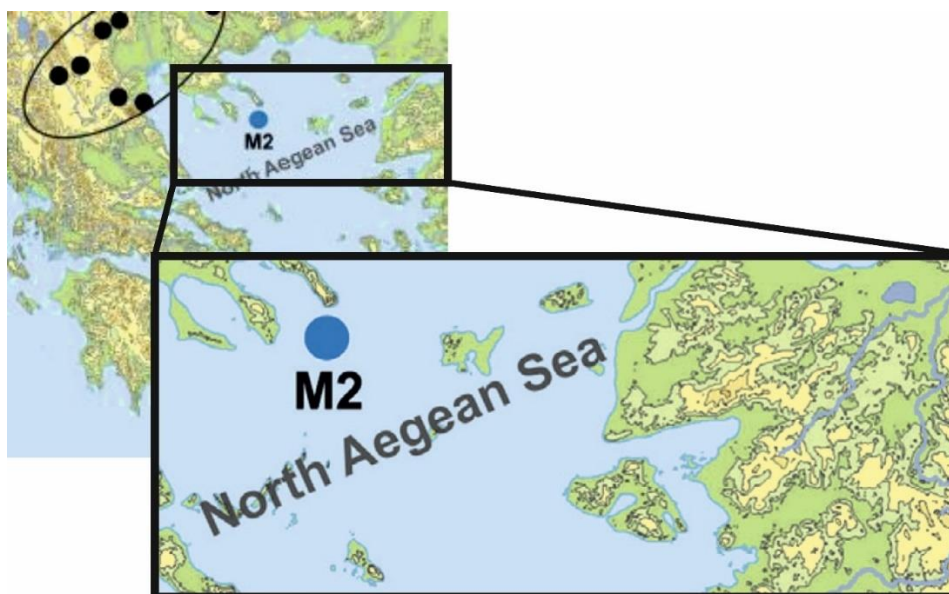
Fig. 8: M2 site location in the North Aegean Sea (source Gogou et al., 2016)

The surface water circulation pattern of the Aegean Sea exhibits temporal and seasonal changes. Black Sea water, colder (9–22 $^{\circ}$C) and less saline (22–33 psu), circulate in the surface through the Dardanelles straits along the east coast of Greece to southwest Aegean Sea, thus cause an increase in the productivity of the water column of the North Aegean Sea, while the South Aegean sub-basin environment is considered as a ''typical oceanic margin'' (Lykousis et al., 2002). Surface waters of Levantine Basin are warm (16–25 $^{\circ}$C) and saline (39.2–39.5 psu) and are circulated toward the north along the eastern Aegean until it meets the outflowing modified by lateral and diapycnal mixing Black Sea water, which flows upward of the first. (Zervakis et al., 2005). Aegean Sea waters are characterised as less oligotrophic and with less nutrients but more oxygen than the nearby Ionian and Levantine Seas (Becacos-Kontos 1977; Lykousis et al. 2002, Souvermezoglou et al. 1999). Several rivers discharge into the Aegean Sea, mostly from the north Hellenic coast and from the east Turkish coast (Fig.9), such as Evros, Nestos and Strymon, and collectively constituting an important source of land-derived organic matter. These rivers supply the Aegean basin with freshwater, as the Black Sea surface water inputs through the Dardanelles do (Poulos et al., 1997; Roussakis et al., 2004). However, the Black Sea water inflow rate displays strong seasonal and interannual variations. This pattern reaches its higher values during mid to late summer and its minimum during winter (Zervakis et al., 2000). Therefore, BSW spreading during winter may result in the stratification of the water column, and as a result influencing dense water formation activity (Zervakis et al., 2000; Zervakis et al., 2004; Velaoras and Lascaratos, 2010; Velaoras et al., 2013). All these facts make north Aegean Sea one of the dense water formation areas in the Mediterranean (e.g., Theocharis and Georgopoulos, 1993; Lascaratos et al., 1999; Zervakis et al., 2000; 2003; Velaoras and Lascaratos, 2005; Gertman et al., 2006; Androulidakis et al., 2012). According to previous studies, carbonate produced by phytoplankton in that area is mainly by coccolithophores (e.g., Ignatiades et al., 2002; Triantaphyllou et al., 2004; Dimiza et al., 2008) with chlorophyll-a concentration values to present a seasonal pattern (maximum values in late winter until early spring and minimum values in summer) (www.seawifs. gsfc.nasa.gov; www.modis.gsfc.nasa.gov).

An alternation of shallow shelves, deep trenches and troughs Consist North Aegean's deep basin. The North Aegean Trough has three depressions; the Mount Athos basin, the N. Sporades basin and the trough between Limnos and Samothraki. Those three deep basins are oriented in a direction of SW -

NE (Figure 9 a,b). A 500m deep sill separate the deep Lemnos basin (1550 m) from the North Sporades (1468m depth) and Athos basins (1149m depth), (Zervakis et al.,2000).
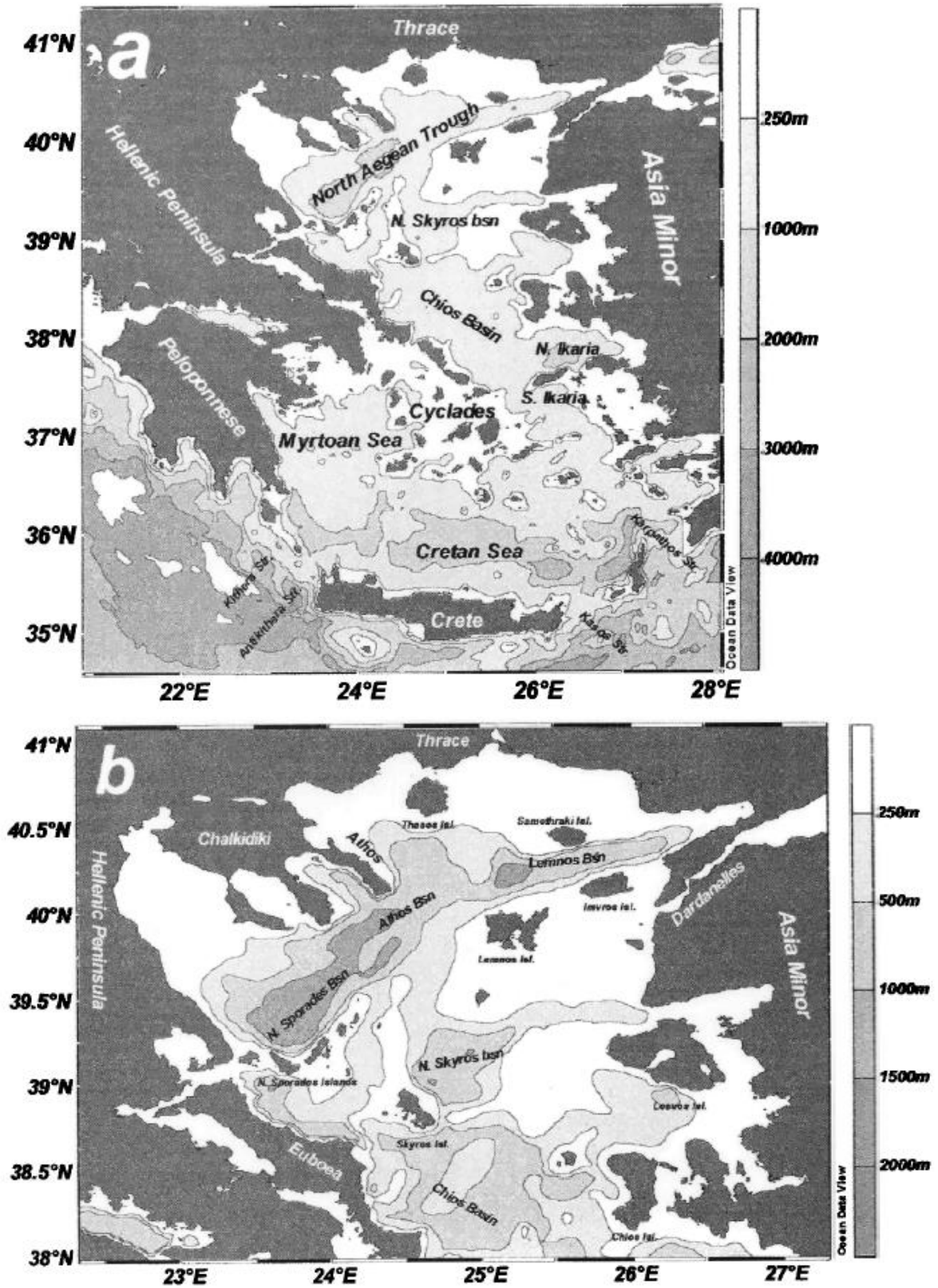

Fig. 9: (a) The major basins of the Aegean Sea. (b) The various subbasins of the North Aegean Sea (source Zervakis et al., 2000).

The structure of the North Aegean's water column is prescribed by the seabed morphology and the presence of fresh and brackish water and a typical winter θ/S profile is showed in Figure 10 (as of 1997). The Black Sea Water (BSW), one of the major water masses of the region, flows through the Dardanelles with a salinity less than 30 psu and forms a surface layer of less than 40 m thickness. This surface layer of BSW is characterised by very low salinity in relation to the Aegean waters and by lower temperatures, especially in winter months. That surface water mass' characteristics are being modified by air-sea interaction and vertical diffusion through mixing with the underlying waters, and the salinity is gradually increased to 38 psu in the region of the Sporades islands (Figure 11). The highly saline and dense water masses of Levantine origin are underlying the lower salinity and density BSW water, which effectively isolate the Levantine water from the atmosphere (Krestenitis et al., 1994). A different pattern is followed below 400 m. At that depth, there is a local formation of saline and extraordinarily dense waters, with slightly different hydrological characteristics per basin, and a limited communication between the basins (Georgopoulos, 2000). North Aegean Deep Waters (DW) is the water of the deepest layers of the various North Aegean suppressions, in spite of the fact that they often possess significantly different O/S characteristics per basin. However, a less saline, colder deep water is formed by BSW water at the northern basins (Zervakis et al., 2000).
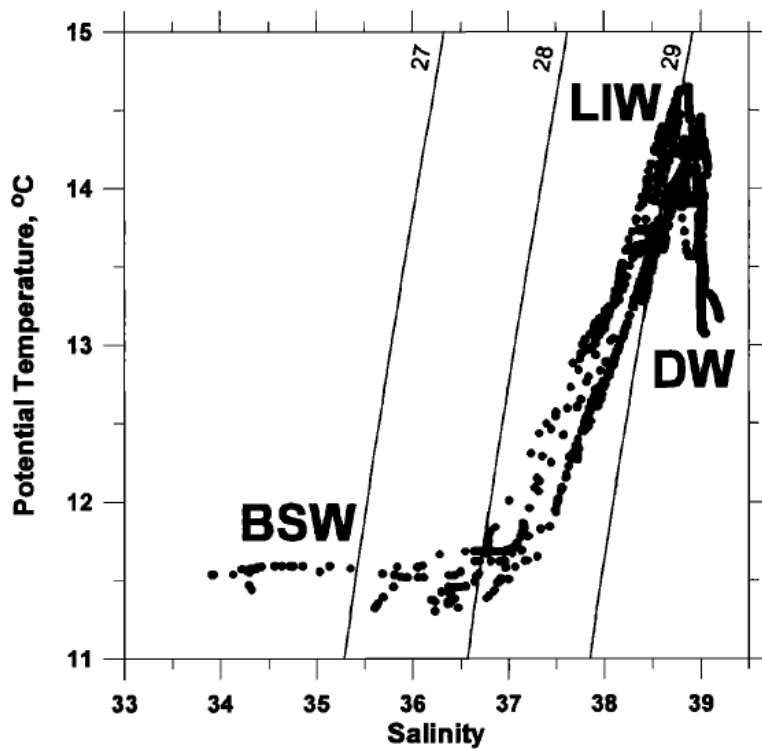

Fig. 10: Representative winter North Aegean θ/S diagram (source Zervakis et al., 2000).
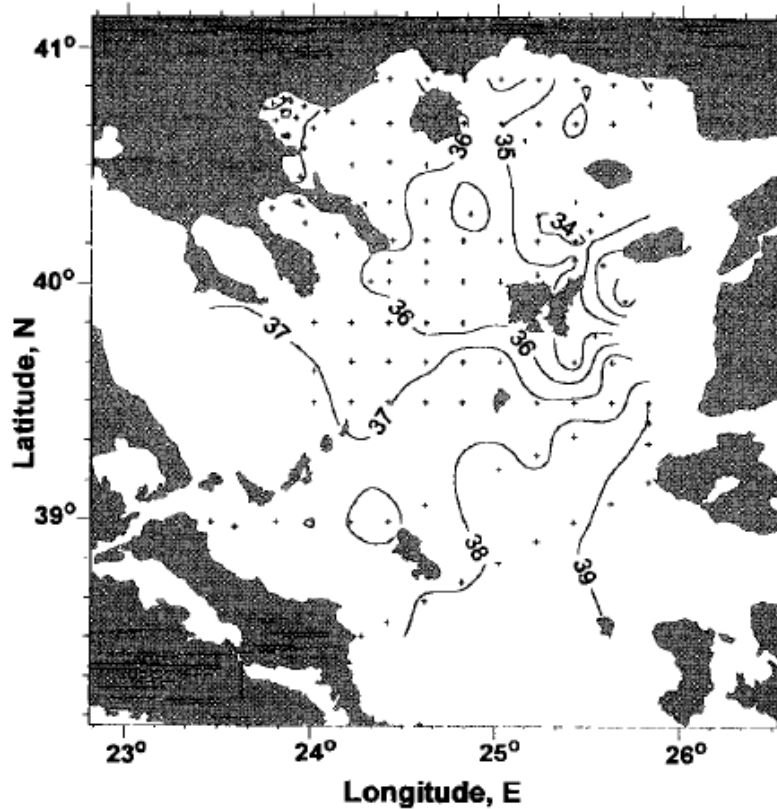
Fig. 11: Surface salinity in the North Aegean Sea (May 1997, source Zervakis et al., 2000).

3. Coccolithophores

Coccolithophores or Calcareous nanoplankton are marine unicellular, flagellate organisms, which are an important component of the marine phytoplankton. The secrete calcareous plates (or discs), from which they are consist, are called coccoliths, and these are the only cell elements that can be preserved in fossil records (Fig. 12). Their contribution to the carbonate in deep-sea sediments is quite important. As they produce organic carbon, carbonate and dimethyl sulphide (Milliman 1993; Westbroek et al. 1993), gases related to the greenhouse effect (Ayers et al., 1991; Prospero et al., 1991), coccolithophores are essentials contributors to marine biochemistry. In addition, some coccolith species produce long-chain organic compounds called alkenones, which are resistant to diagenesis and that is the reason why they are a useful tool in paleoclimatic reconstructions and particularly in SST reconstructions (Palumbo 2012). According to Prahl et al (1988), alkenones display an unsaturation degree, depending to the SST (sea surface temperature). Coccolithophore functions that are related with climate conditions are the calcite production which lead to CO_2 release, their CO_2 sinking by organic carbon production in photosynthesis, and that they produce dimethyl sulphoniopropionate (DMSP), which may be converted into the cloud-generating dimethyl sulphide(DMS) (Westbroek et al., 1993,1994b).The amount of $CaCO_3$ produced, is exported from the water column to the deep-sea, and its dissolution mainly occurs at the sediment-water interface (Westbroek et al., 1993,1994b).

Fig. 12: SEM images of coccolithophore species

3.1. Coccolithophores ecology

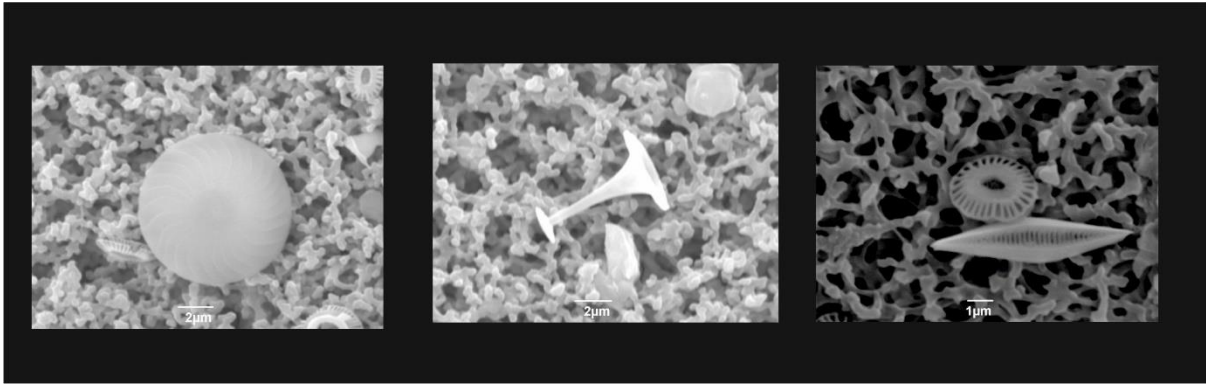In order to carry out the photosynthesis process, coccolithophores live within the photic zone. Fecal pellets and marine snow are responsible for transport coccoliths on the sea and ocean floors (Steinmetz, 1994). Coccoliths have the ability to be preserved in fossil records but with the only limitation not reach the Carbonate Compensation Depth (CCD), because of their carbonate composition.

Throughout geological time, major changes related to coccolithophores spatial and temporal distribution took place (Brand, 1994) as a result of environmental changes and genetic alterations within species, with the majority of present representatives of coccolithophore species preferring nutrient-poor, stratified, warm, offshore waters. Nutrient supplies and temperature are the most important factors that control coccolithophores ecological responses (Palumbo, 2012). The stratified waters of the temperate and tropical regions of the world are the most common habitat of coccolithophore species (Brand, 1994) and in the subtropical oceanic gyres is detected the current highest diversity of coccolithophores (Hulburt, 1963, 1964). On the opposite hand, in tropical oceanic waters, a minimum of diversity is observed and subpolar oceanic and coastal waters residents are only few species, although they can be quite abundant there (Hulburt, 1963).

As it is already mentioned, coccolithophores are found in the Photic zone. In the subtropical zone, the photic zone reaches the depth of 120 m, whereas this depth decreases at 30m in high latitudes. It is important to learn more about the photic zone in order to understand more about coccolithophores. Three subzones part the Photic zone and each one is characterised by certain coccolithophore species. The first subzone is the Upper Photic Zone (UPZ) and is located from surface (0 m) to the depth of 80 m. Some of the coccolithophore species that characterize the UPZ are *Rhabdosphaera clavigera*, *Discosphaera tubifera*, *Neosphaera coccolithomorpha*, *Umbellosphaera* spp., *Acanthoica quattrospina*, *Ceratolithus cristatus* (Winter et al., 1994). The next subzone is the Middle Photic Zone (MPZ) between the depths 80-120 m and it is not easily carachterized by a discrete flora. However, MPZ often contains high abundances of a few species also found in the other zones as, in particular, *Umbellosphaera tenuis*, *Syracosphaera* spp. (Winter et al., 1994). The deeper subzone is the Lower Photic Zone (LPZ) is mainly represented by *Florisphaera profunda* (Winter et al., 1994). However, it is noticed that some species don't show depth preferences, e.g. *Helicosphaera* spp. (Winter et al., 1994).

The following description concerns the ecological and paleoecological preferences of the major coccolithophores species used in this study.

Emiliania huxleyi (Table 2 a-d): The strong presence of the species in marine ecosystems of Aegean Sea is highlighted especially during the winter-early spring period (Triantaphyllou et al., 2004; Dimiza

2006; Dimiza et al., 2008). However, this species is one of the most opportunistic species between coccolithophores, as it has the ability to flourish in both eutrophic and oligotrophic conditions (Bard, 1994). This is a species that is resistant to a wide range of temperatures and salinity (Okada & McIntyre, 1979; Bukry1974; Roth & Colbourn,1982; Okada & Wells, 1997). However, high frequencies of this species recorded during the Younger Dryas cold event (Sprovieri et al., 2003; Di Stefano & Incarbona, 2004) supporting the immediate response to incidents of sudden cooling.

Rhabdosphaera clavigera (Table 3e)**:** The presence of Rhabdopshaeracea family representatives is important on marine ecosystems of the Aegean Sea (Triantaphyllou et al., 2004; Dimiza, 2006; Dimiza et al., 2008). *Rhabdosphaera clavigera* displays the higher rates of the Rhabdopshaeracea family*,* which higher contents are observed during the summer period (Dimiza et al., 2008). This species is characteristic for the upper euphotic zone of modern environments (Honjo & ,1974; Winter et al., 1994; Tayhashi & Okada, 2000) while high concentrations of the species caracterise warm oligotrophic waters (Roth & Colbourn, 1982; Flores et al., 1997; Sprovieri et al., 2003).

Algirosphaera robusta (Table 2 g-h)**:** This species lives in the deep euphotic zone of tropical to transitional conditions (Okada and Honjo, 1973; Okada and McIntyre, 1979; Reid, 1980; Knappertsbusch, 1993; Takahashi and Okada, 2000). When it is in less deep waters (Jordan and Winter, 2000; Malinverno et al., 2003b; Dimiza et al., 2008) is linked with periods of stratification of the water column (Broerse et al. (2000a, b). This species is also associated with a limited increase in the concentration of nutrients (Broerse et al., 2000a). High frequency of *A. robusta* is found in non-coastal areas (Sprengel et al., 2002). Usually, it is a minor component of the total coccolithophore flux (Ziveri et al., 2000b; Malinverno et al2009). However, in seasonal basis, it may be an important species in oligotrophic conditions (Triantaphyllou et al., 2004 Malinverno et al., 2009)

Discosphaera tubifera (Table 4 c-d)**:** A species with high abundance in Eastern Mediterranean Sea (Knappertsbusch, 1993; Malinverno et al., 2003a). Its maximum abundance is presented in oligotrophic subtropical areas (Okada and McIntyre, 1977; Nishida, 1979; Kleijne et al., 1989; Young, 1994).

***Helicosphaera* spp. (mainly *H. carteri*)** (Table 3a)**:**   This genus characterises warm waters with high productivity and low nutrient content (Ziveri et al., 2004; Haidar & Thierstein, 1997). Moreover, the existence of high frequency of this genus shows inflow of fresh water (Triantaphyllou et al., 2009 a, b).

Florisphaera profunda (Table 4 a-b)**:** It is an important component of Mediterranean marine ecosystems, especially during summer and it characterise the deep euphotic of tropical-subtropical waters (Castradori, 1993; Young, 1994; Triantaphyllou et al., 2004; Dimiza et al., 2008; Ziveri et al., 2000; Andruleit & Rogalla, 2002; Triantaphyllou et al., 2009a, b, 2010) a fact that is reflected in its limitation to the deeper layers of the water column (Triantaphyllou et al., 2004; Dimiza 2006; Dimiza et al., 2008). This species is usually referred under the Deep Chlorophyll Maximum (DCM), as it prefers low temperature and low illumination combined with high nutrient content (Young, 1994; Cortes et al., 1997; Negri et al., 1999; Andruleit & Rogalla, 2002; Giunta et al., 2003; Triantaphyllou et al., 2004; Dimiza et al., 2008). Relatively of this species confirm stratified water column combined with the presence of nutricline in the deep euphotic zone (Molfino & McIntyre, 1990; Sbaffi et al., 2001; Colmenero-Hidalgo et al., 2004; Triantaphyllou et al., 2004; Dimiza et al., 2008). Moreover, high relative frequencies of this species characterise waters with high productivity (Barcena et al., 2004), while reduced relative frequencies are linked with enhanced phenomenon of the intrusion of cold deep water to the upper layers of the water column (Ziveri & Thunell, 2000).

***Syracosphaera* spp.** (Table 3b)**:** This is a complex group of species which do not appear to present any specific biogeographical distribution (Okada & Mc Intyre, 1979). Representatives of the genus is considered to prefer environments with intermediate / normal conditions (Young, 1994). However, in many cases (Giraudeau, 1992; Andruleit & Rogalla 2002) this genus is favored by high concentrations

of nutrients in coastal areas. Many refereces link its high concentrations with warm waters (π.χ. Giunta et al., 2003; Principato et al., 2003), while low salinity is an important factor for its increasing abundance (Flores et al., 1997; Colmenero-Hidalco et al., 2004). *Syracosphaera pulchra* abundance characterise tropical-subtropical regions with oligotrophic-mesotrophic waters (Ziveri et al., 2004; Crudeli et al., 2006; Principato et al., 2006). This species is an indicator for warm waters which display maximum values during interglacial periods with major outbreaks during deglaciation (Flores et al., 1999).

Calcidiscus **spp.** (Table 2 e-f)**:** This genus is considered to survive under a wider range of temperature conditions (Okada & Mcintyre, 1979). However, according to some references (Winter et al., 1994; Wells & Okada, 1997) its presence is linked to warm subtropical waters. According to Triantaphyllou et al. (2009a), this genus was present in the warm waters of SE Aegean Sea. On the contrary, Jordan et al. (1997) support its negative correlation with temperature. According to Flores et al. (1999) high concentrations was occurred during the last phase of deglaciation.

Umbilicosphaera **spp. (mainly** *U. sibogae***)** (Table 3c)**:** It is thought as an indicator for warm tropical waters (Wells & Okada, 1997; Flores et al., 1999; Tayhashi & Okada, 2000) most preferably in waters with high nutrient content (Andruleit & Rogalla 2002). This genus is positive correlated with a decrease of salinity (Shipe et al., 2002) and according to Flores et al. (1999) the maximum concentrations was occurred during the last phase of deglaciation.

Umbellosphaera tenuis (Table 3d)**:** High relative frequencies of this species characterise tropical-subtropical areas with oligotrophic warm (Cortes et al., 2001; Andruleit et al.; 2003; Giunta et al., 2003), while its abundance in the warm waters of SE Aegean Sea is attested by Triantaphyllou et al. (2009a).

Holococcoliths: This group prefers the upper euphotic zone (Haidar &Thierstein, 2001). During the summer period, they are abundant in oligotrophic marine environments of Mediterranean Sea (Kleijne et al., 1989; Kleijne et al 1991; Cros, 2001; Triantaphyllou et al., 2002; Dimiza et al., 2008) and also, according to Dimiza et al. (2008), holococcoliths are abundant in warm oligotrophic waters of central Aegean Sea.

Reworked species (Table 3f)**:** They are mainly provided by the increased provision of terrestrial material and they provide useful paleoceanographic information (Flores et al., 1997; Colmenero-Hidalgo et al., 2004).
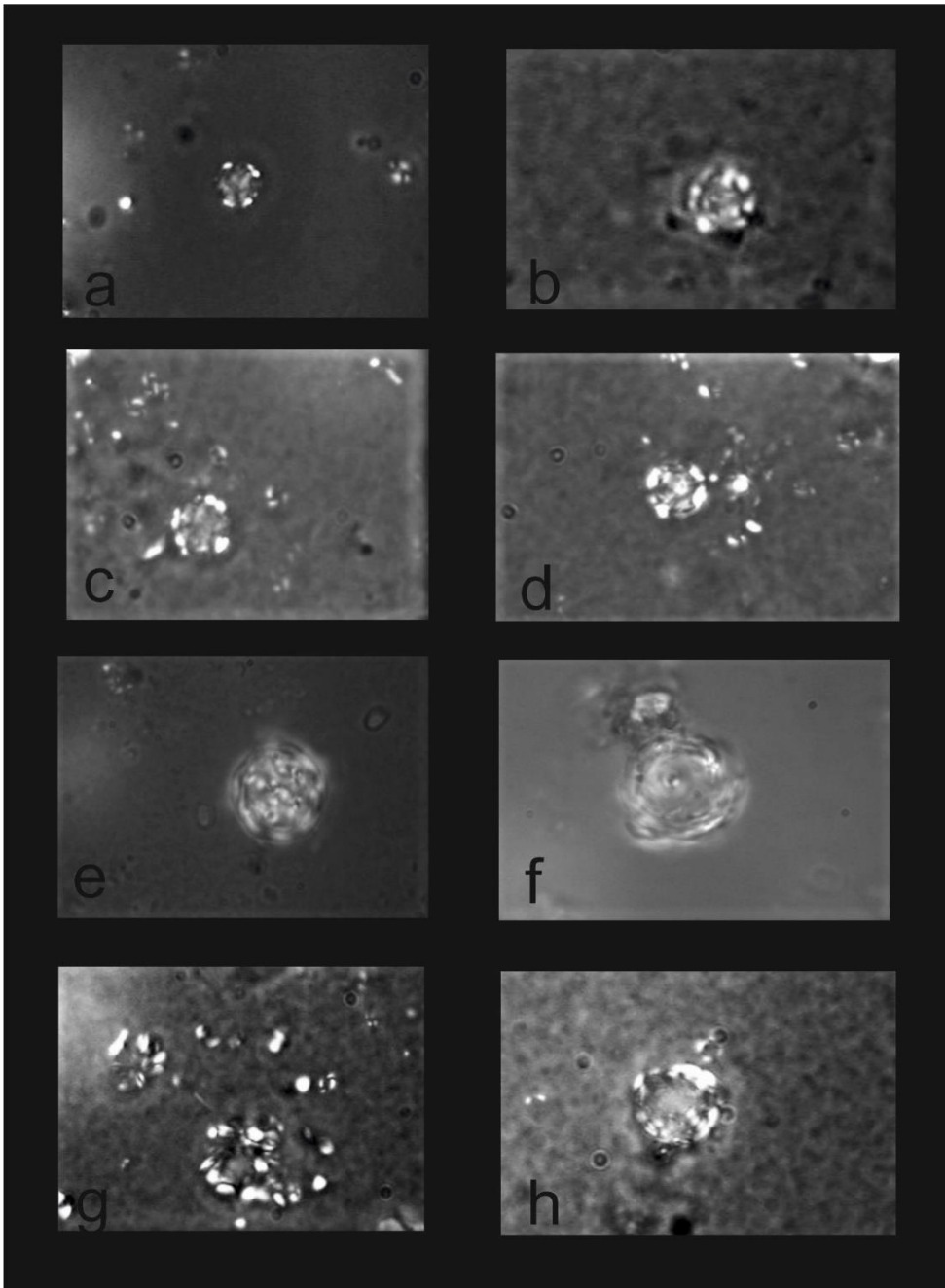
Table 2: Coccolithophore species (images taken from Light Microscope): a-d: *Emiliania huxleyi* coccosphere, e-f: *Calcidiscus leptoporus* coccosphere, g-h: *Algirosphaera robusta* coccosphere

Table 3: Coccolithophore species (images taken from Light Microscope): a: *Helicosphaera carteri* coccosphere, b: *Syracosphaera pulchra* coccosphere, c: *Umbilicosphaera sibogae* coccosphere d: *Umbellosphaera tenuis* coccosphere e: *Rabdosphaera clavigera* coccosphere f: reworked species (*Discoaster* spp.)
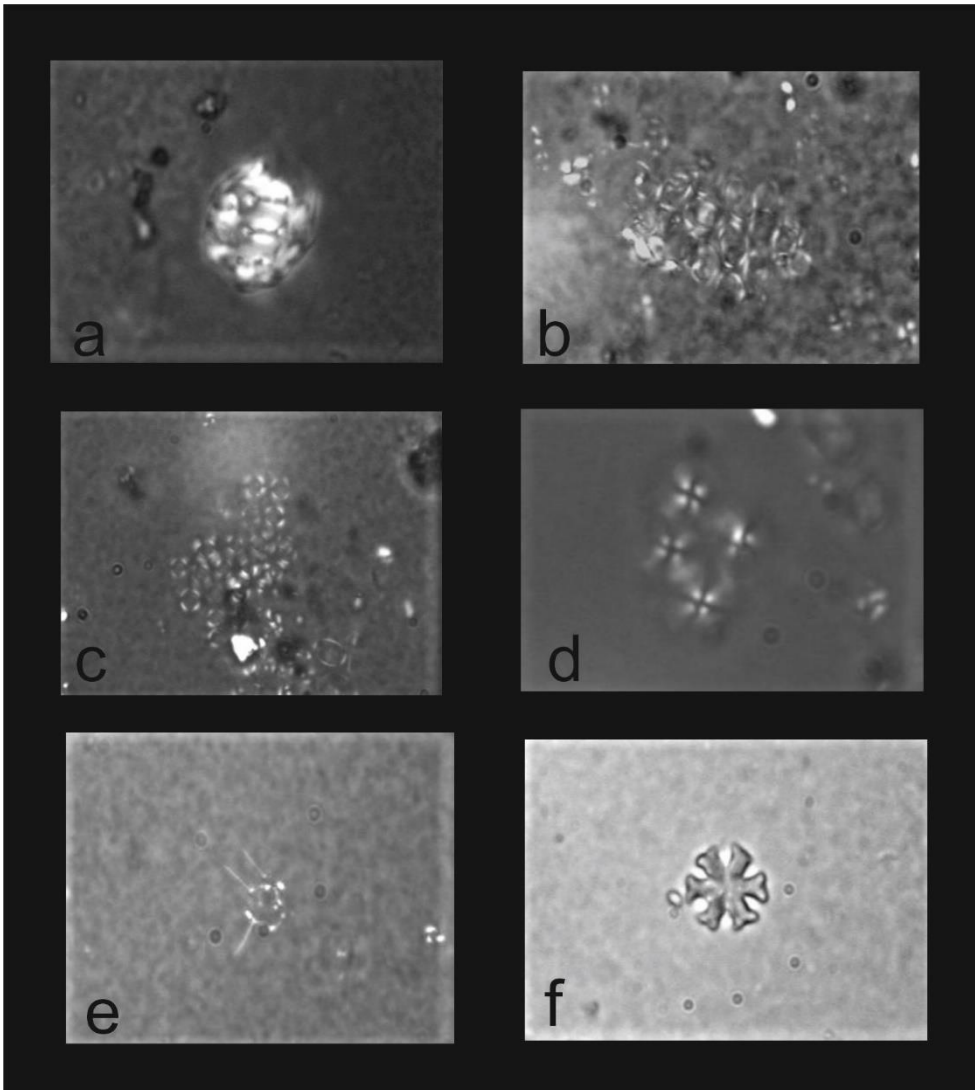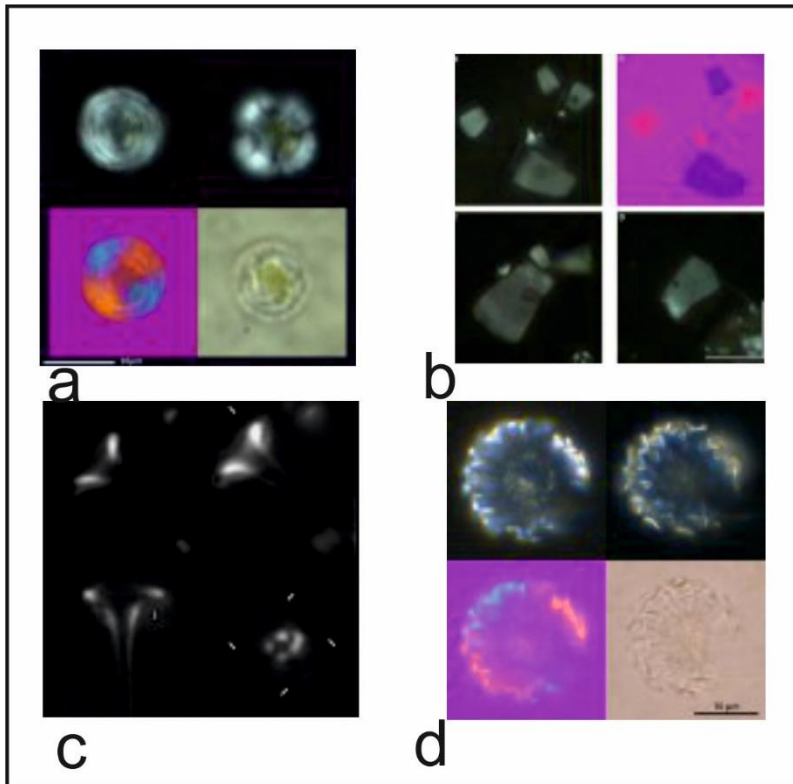
Table 4: Coccolithophore species (images taken from Light Microscope): a: *Florisphaera profunda* coccosphere (source: www.microtax.org), b: *Florisphaera profunda* coccolith (source: www.microtax.org), c: *Discosphaera tubifera* coccolith (source: www.microtax.org), d: *Discosphaera tubifera* coccosphere (source: www.microtax.org)

3.2. Coccolithophores impact to the environment

Coccolithophores are sensitive indicators of environmental conditions, because, as one of the main groups of marine producers, they respond to any changes on salinity, nutrients, temperature and availability of sunlight (McIntyre and Bé, 1967; Samtleben and Schröder, 1992; Giradeau, 1992a, b; Giradeau et al., 1993; Winter and Siesser, 1994; Baumann and Freitag, 2004). This is the reason why studying modern coccolithophores ecology and biogeography is so important to paleoenvironmental and paleoclimatic reconstructions.

Coccolithophore's direct response to any changes in these parameters, makes them a useful tool to identify possible fluctuations to climate and surface-water. Their contribution in the CO_2/O_2 exchange between the ocean and the atmosphere is considerably important, as they combine effects on both the biological and the carbonate pump (Baumann and Freitag, 2004).

According to Brand (1994), coccolithophores has the ability to modify their environment, except from responding to it. Coccolithophores, as the most productive calcifying organisms on earth, has a key role in the marine carbon cycle by forming their calcite skeletons in the surface layers and then sink to deeper layers. They have the ability to modify the upper-ocean alkalinity and display immediate effects on the air/sea CO_2 exchange (Palumbo 2012). According to many studies in E. Mediterranean Sea, the phytoplankton group producing carbonate that dominate in the area is coccolithophores and even their strong seasonal variability, they contribute al lot to biogenic particle export production (Knappertsbusch 1993; Ziveri et al. 1995; Malinverno et al. 2003). Other studies reveal the fact that

coccolithophores' productivity and distribution are highly susceptible to any changes of CO_2 in the environmental, either from acidification that occurs in surface layers of water column or through the increasing upper-ocean thermal stratification (Rost and Riebesell, 2004). Photosynthesis in the sunlit upper mixed layer, which fixes the inorganic carbon, combined with the vertical export of part of organic carbon leads to a drawdown of CO_2 in the surface ocean (Palumbo, 2012). Moreover, particulate organic carbon's remineralisation during its sinking to deeper layers, releases organically bound CO_2 and as result it is accumulated in that depth (Rost and Riebesell, 2004). This procedure, called organic carbon pump, leads to a net draw down of CO_2 from the atmosphere into the ocean. On the opossite hand, the reversed outcome on air/sea CO_2 exchange happened, as a net release of CO_2 to the atmosphere is caused by the production and export of calcium carbonate (Rost and Riebesell, 2004). The flux of CO_2 between the surface ocean and the overlying atmosphere is controled by the rain ratio, which is the ratio of particulate inorganic to organic carbon in exported biogenic matter and represent the relative strength of the two biological carbon pumps mentioned before (Rost and Riebesell, 2004). In addition, dimethysulfoniopropionate is used for osmoregulation and leads to the excretion of dimethylsulfide and is mainly produced by coccolithophores, combained with other prymnesiophytes and dinoflagellates in contrast of the rest phytoplankton groups that contribute less (Brand, 1994). It is thought that coccolithophores may have an impact to earth's climate, due to their production of dimethylsulfide, during their bloom periods. The reason is because the gas mentioned above is oxidized to sulphate aerosols in the atmosphere, which constitute the most important nuclei in the atmosphere over the ocean promoting cloud condensation, fact that increases the Earth's albedo (Brand 1994, Palumbo 2012).

As already mentioned, atmosphere and ocean interact as one independent system, so any changes may have occurred in the oceanic carbon cycle has important influences on atmospheric CO_2 levels. Marine calcium carbonate cycle is under biological control because it is mainly produced by benthic organisms, coccolithophores and foraminifera in the open sea surface waters. pCO2 changes in glacial/interglacial transition are mainly forced by variations in carbonate dissolution/ preservation, as atmospheric models have shown (Palumbo 2012). Coccolithophore productivity alterations have a minor impact on the global climate, but dissolution of $CaCO_3$ in sediments related with them contribute to create a buffer of atmospheric CO_2 on the time scales of thousands of years (Archer, 1994).

3.3. Coccolith biometry

The dominant coccolithophore species in world oceans is *Emiliania huxleyi*, which stands out for its high abundance and for the fact that is extremely widespread (Winter et al., 1994; Young, 1994; Fig. 13). Conditions such as temperature, salinity and availability of nutrients (e.g., Watabe and Wilbur, 1966; Paasche and Brubak, 1994; Paasche, 1998, 2002; Bollmann and Herrle, 2007) is observed to cause variation in *E. huxleyi* coccolith size and morphology (Young and Westbroek, 1991). According to Triantaphyllou et al. (2010), the increasing trend in atmospheric CO_2 partial pressure causes changes in the seawater carbonate chemistry, which lead to a decrease in *E. huxleyi* cellular PIC/POC ratio and cause malformations of the coccoliths (Riebesell et al., 2000). As a result, these consequences could be opposed to the marine carbon cycle, i.e. changes in ocean alkalinity, changes in photosynthesis cause arising in air/sea CO_2 exchange , calcification and shifts in the dominance of coccolithophores (Rost and Riebesell, 2004).

In the Aegean Sea, it is observed a tendency in which *E. huxleyi* display larger coccospheres and bigger coccoliths with heavier calcification in the central area when sea surface temperature is decreased. In a heavy calcified coccolith inner tube elements begin to merge and lose their individual identity, fact that cause an apparent fusion of the tube elements with the inner ends of the rays of

the distal shield (Triantaphyllou et al., 2010). Triantaphyllou et al. (2010) documented that coccolith and coccosphere size is negatively correlated to temperature. Specimens of *E. huxleyi* heavily calcified have been displayed from cold waters (McIntyre and Be, 1967; Roth and Berger, 1975; Burns, 1977; Jordan, 1988). On the contrary, other studies report the opposite fact (Watabe and Wilbur, 1966; Beaufort and Heussner, 2001) or others do not indicate a correlation between the degree of calcification and temperature (Young and Westbroek, 1991). However, according to Sorrosa et al. (2005), recent culture experiments have pointed out that when temperatures are low there is a combination between suppressed coccolithophore cell division and induced cell enlargement and stimulated calcification.

Chlorophyll maxima are positive correlated with an increase in the size of *E. huxleyi* coccospheres and coccoliths in the Aegean Sea, reflecting highest coccolithophore productivity and low temperatures and on the opposite hand, smaller and less calcified specimens occurred when the temperature is higher during the summer low productivity period. (e.g., Triantaphyllou et al., 2004, 2010; Dimiza et al., 2008).

Salinity has been suggested to play an important role in E. huxleyi morphology, with reduced values associated with size decrease (Green et al., 1998; Bollmann and Herrle, 2007), However, a recent global survey has shown that the calcification state of *E. huxleyi* is not related to salinity (Beaufort et al., 2011), which is also confirmed by data of Triantaphyllou et al., (2010). However, the salinity variability displayed in the Aegean Sea is so small to account for any significant variation in coccolith size (Green et al., 1998; Bollman and Herrle, 2007).

Nutrient available content affect calcification of *E. huxleyi.* This could be done in by an increase in coccolith weight associated with higher nutrient conditions and produced during coccolithophore blooms (Beaufort et al., 2007) and also when phosphate limitation is observed, despite slower growth (Kayano and Shiraiwa, 2009; Müller et al., 2008; Satoh et al., 2009).
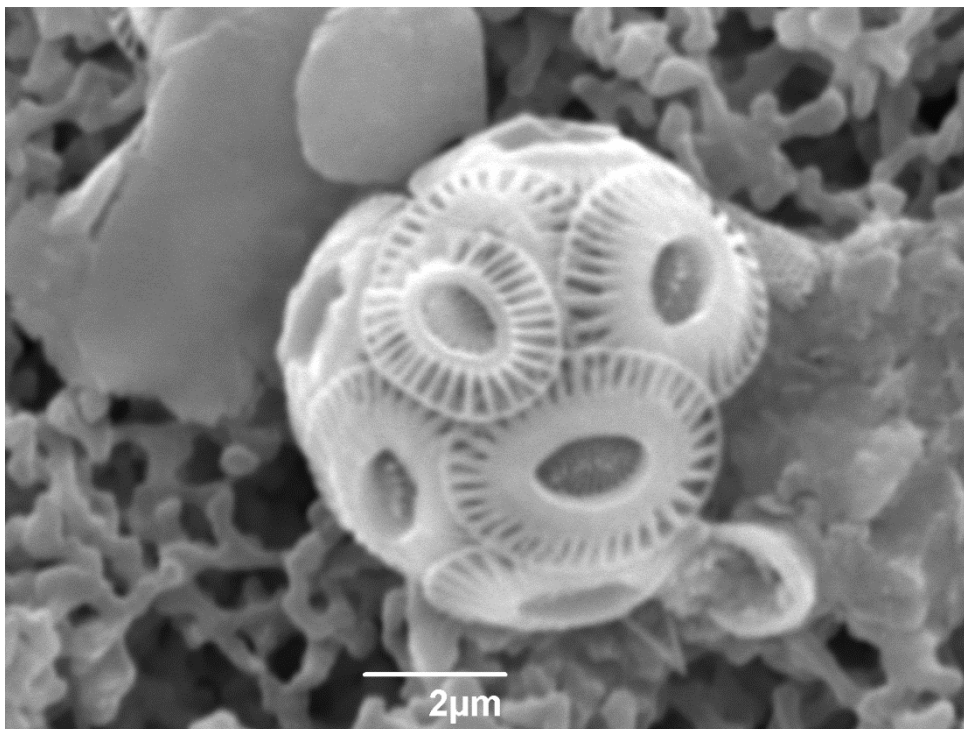

Fig.13: *E. huxleyi* coccosphere (SEM image)

3.4. Flux and sediment traps

Flux is a term to describe the rate of transferred material from one reservoir to another, or one physical or chemical state to another. Estimates made by fluxes are substantial prerequisites for models of biogeochemical processes. Sediment traps are the prime technology for marine flux studies (Broerse, 2000).

Sediment traps are devices that are usually deployed at different depths in anchored vertical arrays and passively collect particles settling through the water column over intervals ranging from a few days to more than a year. The rotation of a set collecting cups allow to take continuous measurements by an open-close time schedule that can be set at regular or variable intervals (Broerse, 2000) (Figs. 14,15). The use sediment traps make possible direct measurements of the water column flux of matter and as a result to quantify some important components of the global biochemical cycles (Ziveri, 1999).

Sediment traps are time-series mechanism that allows the study of seasonal fluctuations of particle fluxes. The term ''export production'' can be used instead of ''flux'' when particle fluxes reflect changes in productivity in the overlying surface waters (Broerse, 2000). However, suspended or advected particles may influence he productivity signal in sediment traps deployed near the sea floor or near shelf areas. Moreover, complex water movements around and within the sediment trap and tilting of the vertical array may affect the trapping efficiency, as well as swimmers microbial growth and sample degradation that lead to a reduced reliability of recorded particle fluxes (Honjo, 1996a).

Sediment traps collect coccolithophores that are between the living assemblages (biocoenoses) in the euphotic zone and the sedimented assemblages (thanatocoenoses) on the seafloor. Therefore, sediment trap sampling provides not only flux estimates but also important information about alteration processes, such as dissolution and fragmentation (Broerse, 2000).
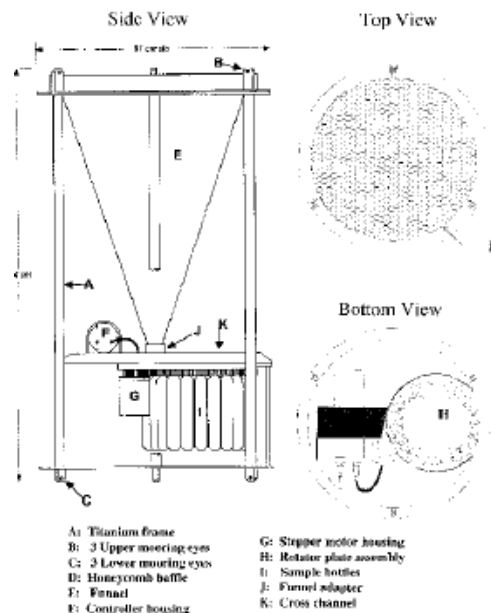
Fig. 14: Sediment Trap Line Drawing (source Mc Lane Time Series Sediment Trap User Manual).
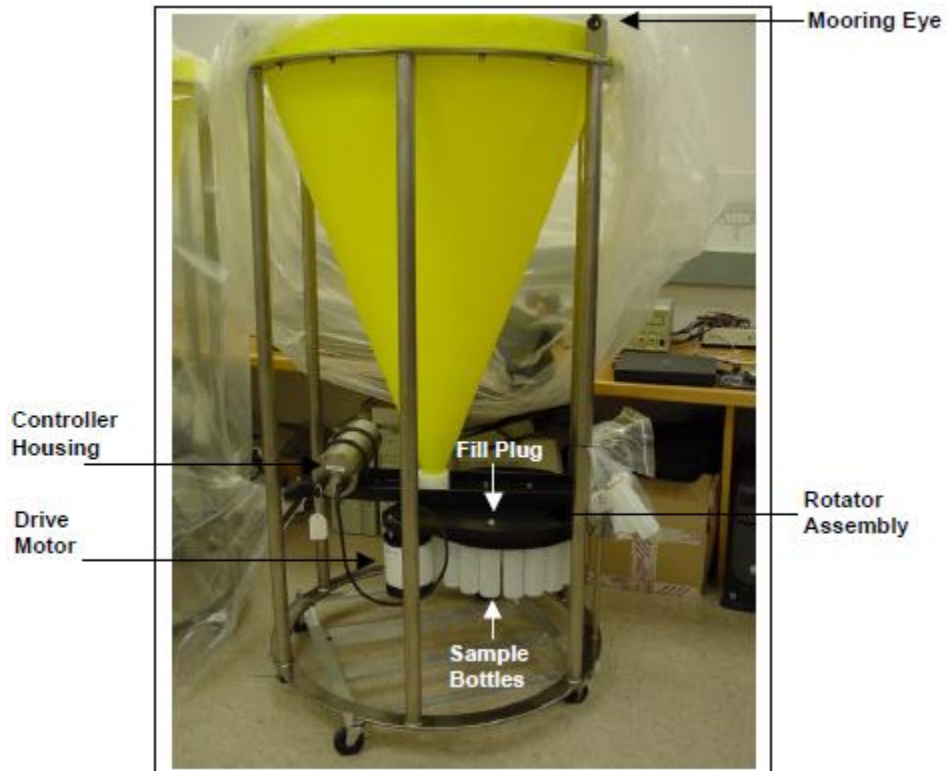
Fig. 15: Sediment Trap Full View (source Mc Lane Time Series Sediment Trap User Manual).

4. Materials and methods

4.1. Sediment traps

This study, is an attempt to estimate seasonal and interannual variability of coccolithophore fluxes, which can be accomplished by time series provided by sediment trap samples. Several sediment traps (PPS3/3 Technicap, 0.125m^2 collecting area, 12 receiving cups) were deployed at three different areas of the NE Mediterranean (N. Aegean Sea, Ionian Sea, and Cretan Sea) and in different depths and periods of the year in order to collect that database (Tables 5-7).

Sediment trap mooring location	North Aegean Sea (M2 site)	
Depth from sea surface	500m	
Sample	Start sampling date	Sampling duration
M2IA1	16 Oct 2014	16
M2IA2	1 Nov 2014	15
M2IA3	16 Nov 2014	15
M2IA4	1 Dec 2014	15
M2IA5	16 Dec 2014	16
M2IA6	1 Jan 2015	15
M2IA7	16 Jan 2015	16
M2IA8	1 Feb 2015	15
M2IA9	16 Feb 2015	13
M2IA11	16 Mar 2015	16
M2IA12	1 Apr 2015	15
M2IIA1	1 Jun 2015	15
M2IIA2	16 Jun 2015	15
M2IIA3	1 Jul 2015	15
M2IIA4	16 Jul 2015	16
M2IIA5	1 Aug 2015	15
M2IIA7	1 Sep 2015	15
M2IIA8	16 Sep 2015	15
M2IIA9	1 Oct 2015	15
M2IIA10	16 Oct 2015	15
M2IIA11	1 Nov 2015	15

Table 5: Samples and sampling interval at the sediment trap mooring location in the North Aegean Sea (M2 site).

Sediment trap mooring location		Ionian Sea (Nestor site)
Depth from sea surface		2000m
Sample	Start sampling date	Sampling duration
KMSXVC1	16 Oct 2014	16
KMSXVC3	16 Nov 2014	15
KMSXVC4	1 Dec 2014	15
KMSXVC5	16 Dec 2014	16
KMSXVC6	1 Jan 2015	15
KMSXVC7	16 Jan 2015	16
KMSXVC8	1 Feb 2015	15
KMSXVC9	16 Feb 2015	13
KMSXVC10	1 Mar 2015	15
KMSXVC11	16 Mar 2015	16
KMSXVC12	1 Apr 2015	15
KMSXVIC1	1 Jun 2015	15
KMSXVIC2	16 Jun 2015	15
KMSXVIC3	1 Jul 2015	15
KMSXVIC4	16 Jul 2015	16
KMSXVIC5	1 Aug 2015	15
KMSXVIC7	1 Sep 2015	15

Table 6: Samples and sampling interval at the sediment trap mooring location in the Ionian Sea (NESTOR site).

Sediment trap mooring location		Cretan Sea (M3 site)
Depth from sea surface		1550m
Sample	Start sampling date	Sampling duration
M3AVIIB6	1 Jan 2015	16
M3AVIIB7	15 Jan 2015	15
M3AVIIB8	1 Feb 2015	16
M3AVIIB9	15 Feb 2015	15
M3AVIIB10	1 Mar 2015	16
M3AVIIB11	15 Mar 2015	15
M3AVIIB12	1 Apr 2015	16
M3AVIIIB1	1 Aug 2015	15
M3AVIIIB2	16 Aug 2015	16
M3AVIIIB3	1 Sep 2015	15
M3AVIIIB4	16 Sep 2015	15
M3AVIIIB5	1 Oct 2015	15
M3AVIIIB6	16 Oct 2015	16
M3AVIIIB7	1 Nov 2015	15
M3AVIIIB8	16 Nov 2015	15
M3AVIIIB10	16 Dec 2015	15

Table 7: Samples and sampling interval at the sediment trap mooring location in the Cretan Sea (M3 site).

4.2. Coccolithophore sediment trap sample preparation and flux measurements

For coccosphere analysis, each sample was first split into equal fractions by the use of a McLane rotary wet splitter, with a less than 4% deviation between aliquots. Rinse water that was used in splitting and sieving was prepared from prefiltered distilled water, buffered with sodium tetraborate (pH 8). Using a vacuum pump, aliquots were filtered onto a Millipore cellulose filter (47 mm diameter, 0.45 μm pore size), rinsed with buffered distilled water, dried in oven and stored in plastic petri dishes. For coccolith sample preparation each aliquot from the above coccosphere's sample process was split one more time. In order to eliminate macro aggregates, organic material was removed from the samples following the process described in Bairbakhish et al. 1999. Then the aliquots were sieved over a 32μm mesh and rinsed with buffered distilled water. Afterwards, the <32μm fraction was filtered onto a Millipore cellulose filter (47 mm diameter, 0.45 μm pore size) and rinsed with buffered distilled water, using a vacuum pump. The produced filters were oven dried at 40°C, stored in petri dishes and a piece of each filter was placed on a smear slide with a drop of immersion oil. Then, the filters were studied in a light or scanning electron microscope.

For studying coccoliths and coccosphere fluxes from sediment traps, a small sub-sample (or split) of the wet sample was taken and was concentrated it onto a filter by the process described before. In order to determine coccosphere fluxes, a piece of $20mm^2$ of each filter was analyzed using a polarized light optical Leica DMLSP microscope (LM) at 1250x. For coccolith fluxes, the investigated filtration area $2mm^2$. All species were counted in the first $1mm^2$ and then continued up to $2mm^2$, excluding the specimens of *Emiliania huxleyi*. In order to calculate the fluxes, counted specimens were extrapolated to the entire effective filtration area and total sample, duration days and trap aperture area, according to the following equation:

Ziveri et al. (1999):

F = N × Af × S / af × Ast × T

where F=flux (specimens-m^{-2}-day^{-1}), N=number of counted specimens, Af=effective filtration area (mm^2), S=split factor, af=investigated filtration area (mm^2), Ast=sediment-trap aperture area (m^2), T=sample collecting time (days).

4.3. *E. huxleyi* coccolith biometry

In order to carry out morphological measurements on *E. huxleyi* coccoliths a piece of each filter was attached to a copper electron microscope stub by a double sided adhesive tape and afterwards coated with gold. Then, each sample was scanned in Jeol JSM 6360 Scanning Electron Microscope (National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment) and took 40 pictures of *E. huxleyi* coccoliths at 10000x. All images should be from flat-lying coccoliths seen in distal view.

On each coccolith 8 parameters were measured: Coccolith length (CL), Coccolith width (CW), Element number, Element width, Tube width, Inner tube cycle thickness at the long axis (INTL), Relative tube width (= 2 x tube width/ CW) and Relative element width (= 2x element width/ CL). Each coccolith

was measured for the length and width by dragging an ellipse around the coccolith perimeter. The rest of the parameters were measured by the ImageJ software following the biometric approaches of Young et al. (2014b).

5. Results

5.1. North Aegean

All coccolithophore species identified in the North Aegean sediment trap samples are listed in Table 12.

Total coccosphere fluxes in the North Aegean Sea (June- December 2011, 500 m water column depth) followed a seasonal pattern (Triantaphyllou et al., 2011, 2014, Fig. 16), with monthly fluctuations. Highest values occurred during early summer (late June: 2.54×10^5 coccospheres/m^2/day and late July: 2.47×10^5 coccospheres/m^2/day) and early winter (December: 2.91×10^5 coccospheres/m^2/day). The minimum flux value is recorded during early July (0.11×10^5 coccospheres/m^2/day). Coccosphere data were not provided for the interval January to May 2011.
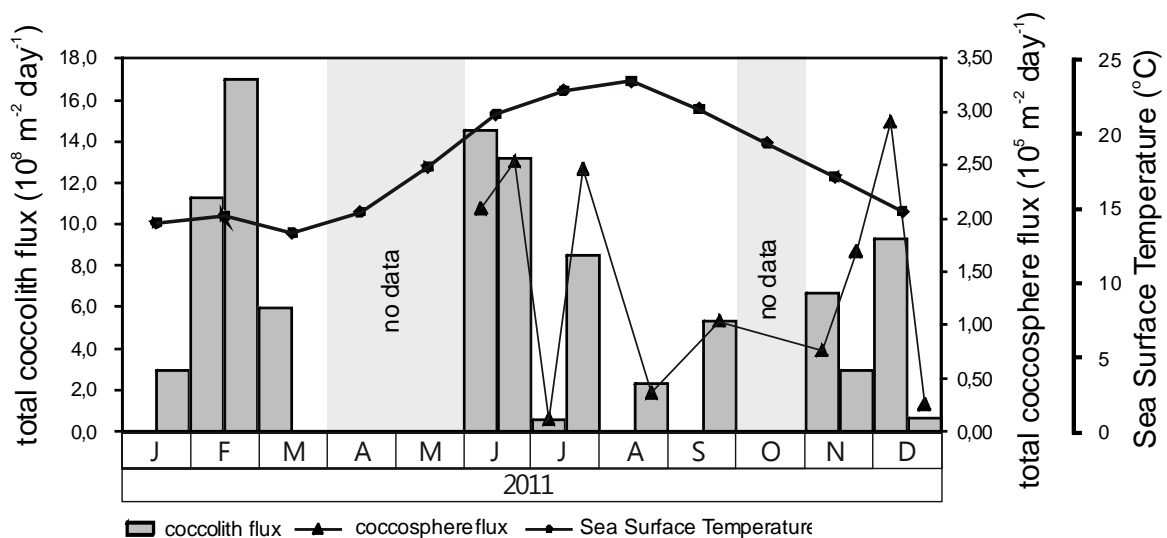
Fig. 16: Total coccosphere and coccolith fluxes in the North Aegean Sea sediment trap for the time interval January 2011-December 2011 (Triantaphyllou et al., 2011, 2014)

Similarly, the coccolithophore export production in the North Aegean Sea (500 m water column depth) for the period between October 2014 to November 2015 (present study) is characterized by a seasonal pattern (Fig. 18), with highest values occurring during late winter-early spring (February-March). The maximum value is recorded at late February 2015 (85.6×10^5 coccospheres/m^2/day), whereas the rest of the year displays lower values with a minor peak in late July (10.3×10^5 coccospheres/m^2/day). However, there are considerable data gaps in late spring and late summer (Fig. 18).

During 2011, *E. huxleyi* displayed a flux peak in late June (2.48 x 10^5 coccospheres/m^2/day; Fig. 17). The second major peak during this time interval occurred in early December (2.45 x 10^5 coccospheres/m^2/day; Fig. 17). Although there are no available coccosphere data for the first semester of 2011, the coccolith flux of the species suggest a major peak in February 2011 (12.7 x 10^8 coccoliths/m^2/day). *Emiliania huxleyi* is the dominant species also for the sediment trap interval 2014-15 (97.44% of the total coccosphere flux in January 2015, Table 8), with coccosphere flux following the general trend of total coccolithophore export production. The highest productivity season of this species is recorded from February to March (maximum flux in late February 2015: 79.2 x 10^5 coccospheres/m^2/day; Fig. 18), whereas the absolute abundance in June 2015 is 12.6 x 10^5 coccospheres/m^2/day; Fig. 18).

The species that also contribute to total coccosphere flux of the North Aegean Sea in 2011 and 2015 are *Syracosphaera pulchra, Algirosphaera robusta* and *Umbilicosphaera sibogae*; the presence of *Coronosphaera mediterranea, Helicosphaera carteri, Calcidiscus leptoporus, Calciosolenia* spp*., Umbellosphaera tenuis, Rhabdosphaera clavigera* and *Rabdospahaera xiphos* are practically negligible as they contribute to the assemblages very sporadically and with abundances <0.9%*. Syracosphaera pulchra* displayed peak in both coccosphere and coccolith flux in late June 2011 (0.16 x 10^5 coccospheres/m^2/day and 30.4 x 10^8 coccoliths/m^2/day, respectively; Fig. 17) followed by a second peak in early December (0.14 x 10^5 coccospheres/m^2/day; Fig. 17). Following a similar trend, it also represented 56% of the total coccosphere flux in November 2014 (Table 8), however maximum flux has been recorded in early June 2015 (maximum flux: 3.36 x 10^5 coccospheres/m^2/day; Fig. 18).

Algirosphaera robusta (4.76% of the total coccosphere flux in November 2015, Table 8) displayed the maximum peak during late November (0.49 x 10^5 coccospheres/m^2/day; Fig. 18).

Umbilicosphaera sibogae represented 6.67% of the total coccosphere flux in September 2015 (Table 8). However, maximum flux has been recorded in early June (maximum flux: 0.42 x 10^5 coccospheres/m^2/day; Fig. 18). Interestingly, it has showed the maximum coccolith flux in November 2011 (8.94 x 10^5 coccoliths/m^2/day; Fig. 17).

Florisphaera profunda maximum flux is recorded in early June 2011 (0.19 x 10^5 coccospheres/m^2/day; Fig. 17), fact that is in correspondence with the *F. profunda* coccolith flux during the same month (4.35 x 10^8 coccoliths/m^2/day; Fig. 17). In the 2014-15 sampling, *F. profunda* coccospheres have not been recorded.

Rhabdosphaera spp. displayed two major peaks in coccolith fluxes during the investigated time period of 2011. The maximum value displayed in early November 2011 (0.294 x 10^8 coccoliths/ m^2/day; Fig. 17) followed by late June (0.268 x 10^8 coccoliths/m^2/day; Fig. 17).

			A. robusta		*U. sibogae*

month	sample		*E. huxleyi*			*S. pulchra*		
	2011	2014-15	2011	2014-15	2014-15	2011	2014-15	2014-15
Oct	*No data*	M2IA1	-	81.25	0.00	-	18.75	0.00
Nov	*No data*	M2IA2	-	36.00	0.00	-	56.00	0.00
Nov	*No data*	M2IA3	-	45.24	4.76	-	23.81	0.00
Dec	*No data*	M2IA4	-	79.49	2.56	-	15.38	0.00
Dec	*No data*	M2IA5	-	87.23	0.00	-	8.51	0.00
Jan	*No data*	M2IA6	-	93.75	0.00	-	3.13	0.00
Jan	*No data*	M2IA7	-	97.44	0.00	-	2.56	0.00
Feb	*No data*	M2IA8	-	92.45	0.00	-	5.66	0.00
Feb	*No data*	M2IA9	-	92.51	0.44	-	1.76	0.44
Mar	*No data*	M2IA11	-	93.75	0.00	-	0.00	0.00
Apr	*No data*	M2IA12	-	90.00	2.00	-	0.00	2.00
Jun	AM3A2	M2IIA1	81.82	75.00	0.00	0.00	20.00	2.50
Jun	AM3A3	M2IIA2	93.75	56.25	0.00	0.00	18.75	0.00
Jul	AM3A4	M2IIA3	78.57	76.92	0.00	0.00	7.69	0.00
Jul	AM3A5	M2IIA4	78.26	83.33	0.00	4.35	13.33	0.00
Aug	AM3A6	M2IIA5	62.5	58.33	0.00	0.00	20.83	0.00
Aug	*No data*	*No data*	-	-	-	-	-	-
Sept	*No data*	M2IIA7	-	40.00	0.00	-	33.33	6.67
Sept	AM3A7	M2IIA8	76.47	60.00	0.00	0.00	16.67	3.33
Oct	*No data*	M2IIA9	-	86.96	0.00	-	8.70	4.35
Oct	*No data*	M2IIA10	-	82.35	0.00	-	17.65	0.00
Nov	AM3A9	M2IIA11	42.86	76.92	3.85	0.00	3.85	0.00
Nov	AM3A10	*No data*	84.21	-	-	0.00	-	-
Dec	AM3A11	*No data*	75.61	-	-	4.88	-	-
Dec	AM3A12	*No data*	83.33	-	-	0.00	-	-
	Average		75.74	75.48	0.65	0.92	14.11	0.92

Table 8: Coccosphere relative abundance (%) of the recorded species in the North Aegean Sea sediment trap (2011 and 2014-15)
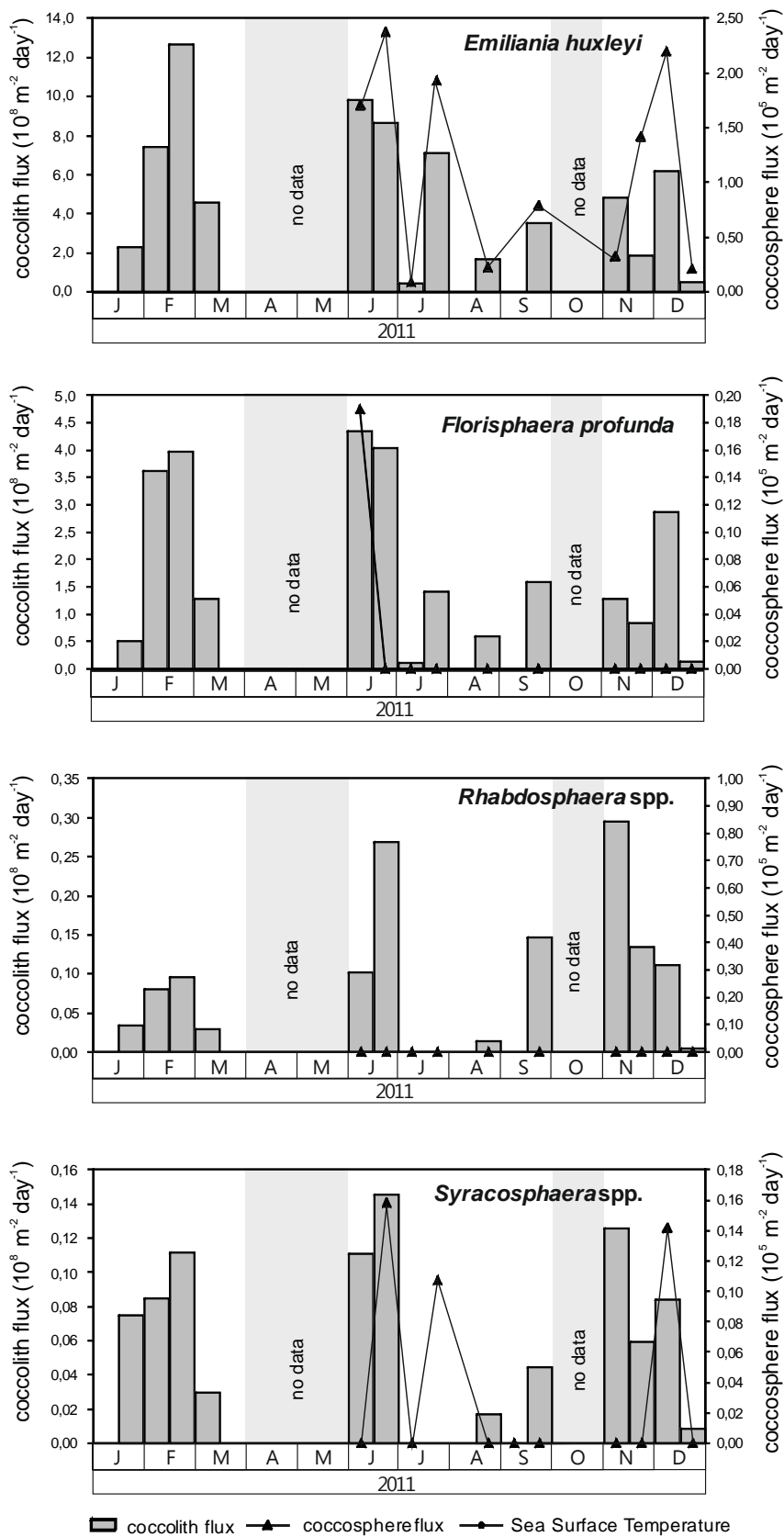
Fig. 17: Species coccosphere and coccolith fluxes in the North Aegean Sea sediment trap for the time interval January2011-December 2011 (Triantaphyllou et al., 2011, 2014)
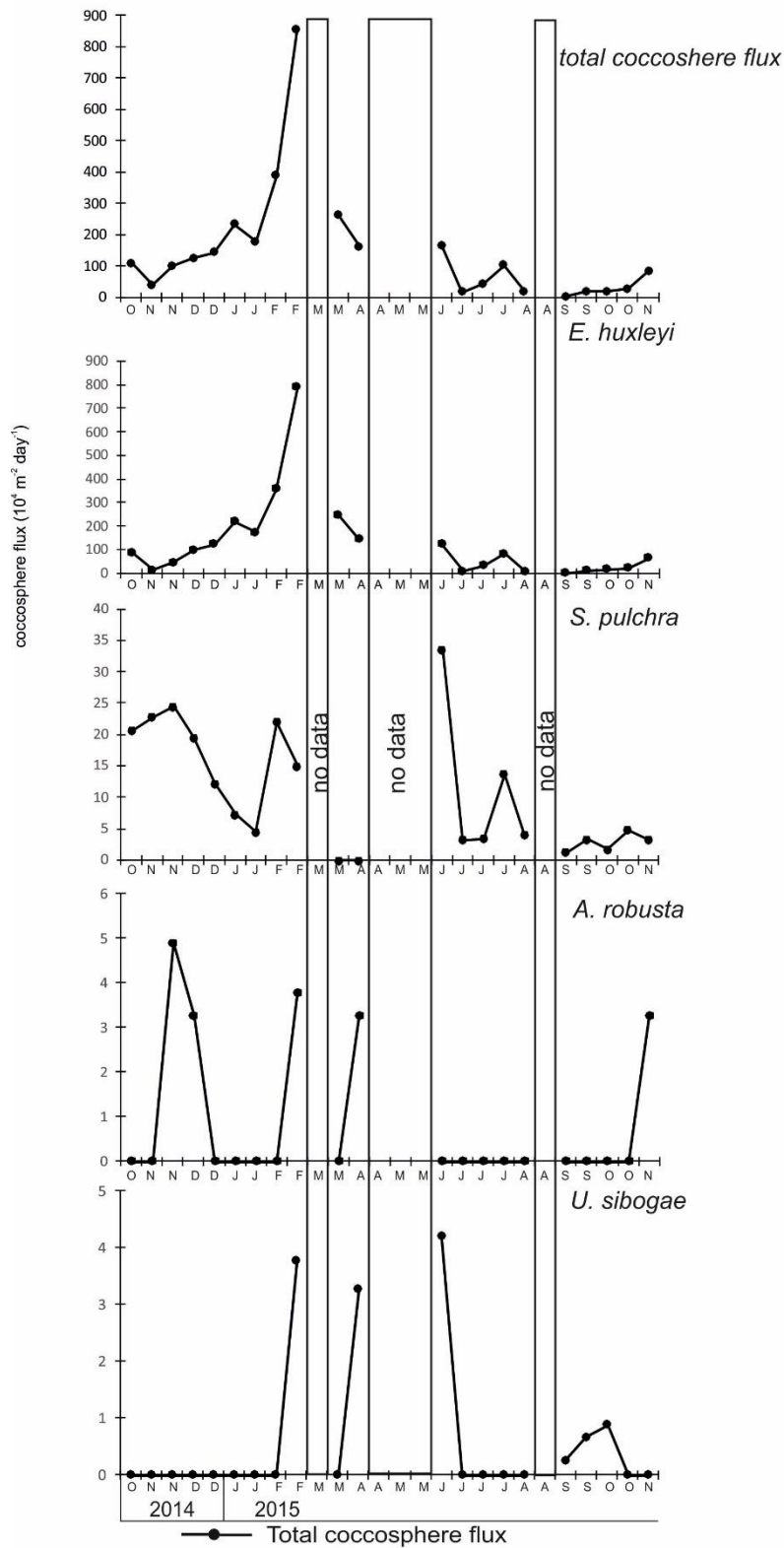
Fig. 18: Total coccosphere flux and species coccosphere fluxes in the North Aegean Sea sediment trap for the time interval October 2014-November 2015

5.2. Ionian Sea (NESTOR site)

The coccolithophore species identified in the Ionian Sea sediment trap samples are listed in Table 12.

Total coccosphere fluxes in the Ionian Sea (June 2010- August 2012, 2000 m water column depth) displayed higher values at certain time intervals (Fig. 19). Lack of coccosphere data in many time periods make the description incomplete. The highest value during the investigated time intervals occurred during late May 2012 (14.3 x 10^5 coccospheres/m^2/day; Fig.19), followed by early May 2012 (12.7 x 10^5 coccospheres/m^2/day; Fig. 19). The minimum flux value is recorded during late January 2011 (0.173 x 10^5 coccospheres/m^2/day; Fig. 19).

Coccosphere export production in the Ionian Sea (October 2014- September 2015, 2000 m water column depth) displayed a seasonal pattern (Fig. 20) with an increase in winter - summer (early February-early June). The total coccolithophore export production was characterized by two main high flux periods. The first was recorded from late January 2015 till early April 2015 and the second was between early June 2015 and early July 2015, with the highest total coccosphere flux peak occurring within 16-31 March 2015 (maximum flux: 8.12 x 10^5 coccospheres/m^2/day; Fig. 20). A minor peak between those high flux periods was recorded at early April 2015. The total coccosphere export production was generally low from late October 2014 till early January 2015.

Coccosphere assemblages in the Ionian Sea (2010-2012 and 2014-2015) were dominated by high abundances of *Emiliania huxleyi*. The species that also contributed to the total coccosphere flux are *Syracosphaera pulchra, Umbilicosphaera sibogae, Algirosphaera robusta, Coronosphaera mediterranea* and *Helicosphaera carteri.* Other less significant species with abundances 1<% are *Calcidiscus leptoporus, Pontosphaera* spp*., Rhabdosphaera clavigera, Umbellosphaera tenuis* and *Calciosolenia* spp.

Emiliania huxleyi displayed the major flux peak of 2010-2012 during late May 2012 (7.79 x 10^5 coccospheres/m^2/day; Fig. 19)*. E. huxleyi* (87.50% of the total coccosphere flux in late November 2014, Table 9) coccosphere flux displayed a similar pattern with total coccolithophore export production of 2014-2015(Fig. 20), with the two high productivity seasons observed from late January 2015 till early April 2015 and between early June 2015 to early July 2015. The major *E. huxleyi* coccosphere flux peak occurred during late March 2015 (maximum flux: 5.21 x 10^5 coccospheres/m^2/day; Fig. 20). The period between late October 2014 till early January 2015 was characterized by low *E. huxleyi* coccosphere flux values and the rest of the year displayed fluctuations of moderate flux values (Fig. 20).

Syracosphaera pulchra maximum flux is recorded in late May 2012 (4.02 x 10^5 coccospheres/m^2/day; Fig. 19). *S. pulchra* (30% of the total coccosphere flux in early January 2015, Table 9) demonstrated two major peaks in coccosphere fluxes during the investigated time period of 2014-2015. The maximum value displayed in early June (0.76 x 10^5 coccospheres/m^2/day; Fig. 20) was followed by late February 2015 peak (0.62 x 10^5 coccospheres /m^2/day; Fig. 20).

Algirosphaera robusta higher values of the period 2010-2012 occurred during spring 2012 with the higher peak occurring in late March (0.5 x 10^5 coccospheres/m^2/day; Fig. 19). *A. robusta* coccosphere flux (46.15% of the total coccosphere flux in late February 2015, Table 9), reached maximum values at late February 2015 (maximum flux: 3.01 x 10^5 coccospheres/m^2/day; Fig. 20), a value considerably higher than the other major species' fluxes, followed by a second peak at late June 2015(1.85 x 10^5 coccospheres/m^2/day; Fig. 20).

Umbilicosphaera sibogae major peak during 2010-2012 was displayed during late May 2012 (0.75 x 10^5 coccospheres/m^2/day; Fig. 19)*.* An important component of the minor species (42.86% of the total coccosphere flux in early July 2015, Table 9) during early July 2015- early September 2015 is *U. sibogae* (Fig. 20), with the major peak displayed during June 2015 (0.98 x 10^5 coccospheres/m^2/day; Fig. 20).

Coronosphaera mediterranea displayed the higher peak of 2010-2012 period during early May 2012 (0.55 x 10^5 coccospheres/m^2/day; Fig. 19). *C. mediterranea* (15% of the total coccosphere flux in late December 2014, Table 9) demonstrated a flux peak in early February 2015 (0.33 x 10^5 coccospheres/m^2/day; Fig. 20). Other major peaks during this time interval occurred in February 2015 and in late March (0.25 x 10^5 coccospheres/m^2/day and 0.23 x 10^5 coccospheres/m^2/day respectively; Fig. 20)

Helicosphaera carteri presented the maximum peak during late July 2012 (1.33 x 10^5 coccospheres/m^2/day; Fig. 19). *H. carteri* (6.49% of the total coccosphere flux in early April 2015, Table 9) displayed the major flux peak during early June 2015 (0.22 x 10^5 coccospheres/m^2/day, Fig. 20) followed by a second peak in early April 2015 (0.18 x 10^5 coccospheres/m^2/day, Fig. 20).
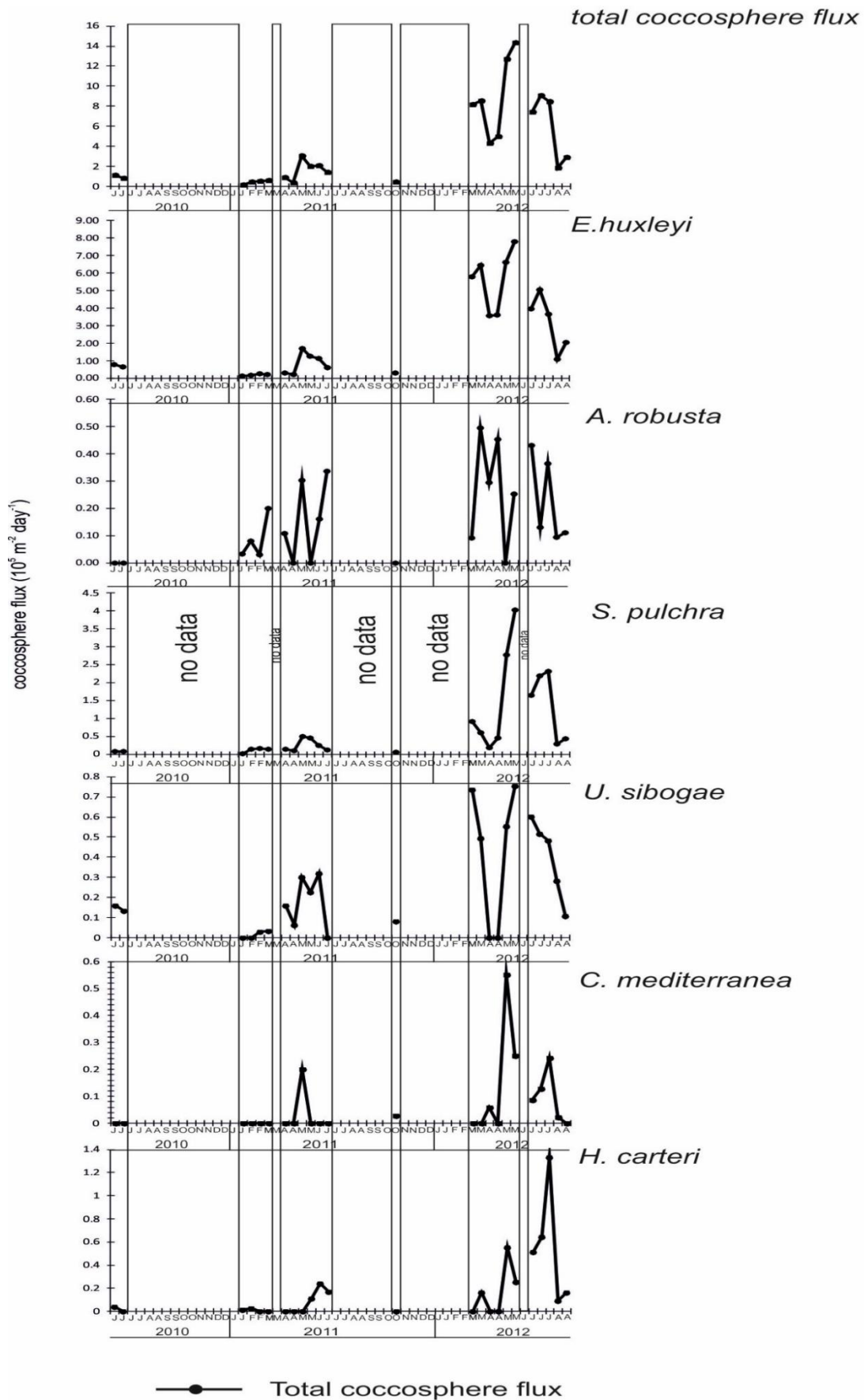
Fig.19: Total coccosphere and species coccosphere fluxes in the Ionian Sea (NESTOR site) sediment trap for the time interval June 2010-August 2012.
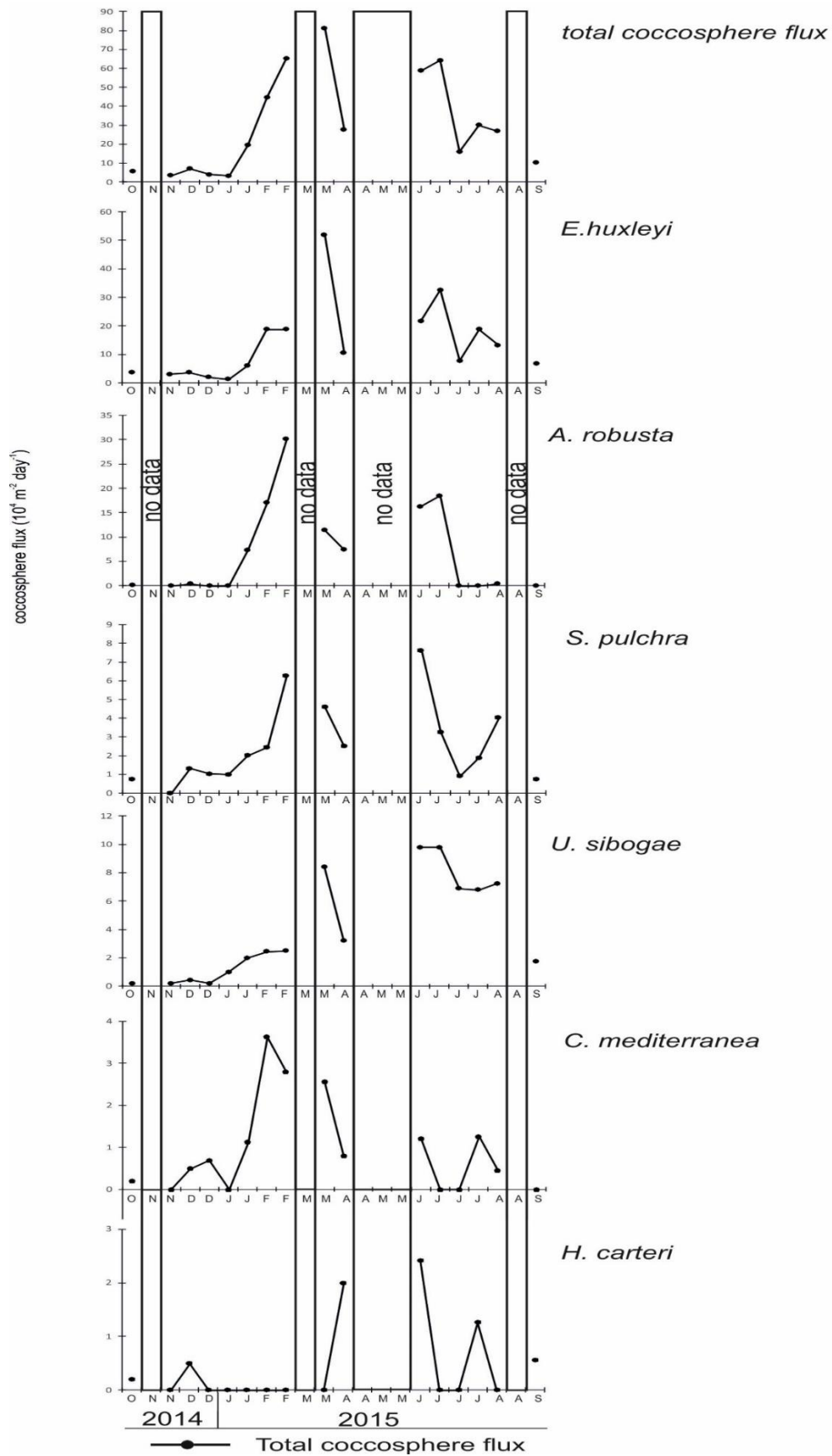
Fig.20: Total coccosphere and species coccosphere fluxes in the Ionian Sea (NESTOR site) sediment trap for the time interval October 2014- September 2015.

sample	E. huxleyi	S. pulchra	A. robusta	C. mediterranea	U. sibogae	H.carteri
KMSXVC1	67.74	12.90	3.23	3.23	3.23	3.23
KMSXVC3	87.50	0.00	0.00	0.00	6.25	0.00
KMSXVC4	53.13	18.75	6.25	6.25	6.25	6.25
KMSXVC5	50.00	25.00	0.00	15.00	5.00	0.00
KMSXVC6	40.00	30.00	0.00	0.00	30.00	0.00
KMSXVC7	31.03	10.34	37.93	5.17	10.34	0.00
KMSXVC8	41.82	5.45	38.18	7.27	5.45	0.00
KMSXVC9	28.85	9.62	46.15	3.85	3.85	0.00
KMSXVC11	64.15	5.66	14.15	2.83	10.38	0.00
KMSXVC12	38.96	9.09	27.27	2.60	11.69	6.49
KMSXVIC1	37.04	12.96	27.78	1.85	16.67	3.70
KMSXVIC2	50.85	5.08	28.81	0.00	15.25	0.00
KMSXVIC3	48.57	5.71	0.00	0.00	42.86	0.00
KMSXVIC4	62.50	6.25	0.00	3.75	22.50	3.75
KMSXVIC5	49.25	14.93	1.49	1.49	26.87	0.00
KMSXVIC7	65.85	7.32	0.00	0.00	17.07	4.88
Average	51.08	11.19	14.45	3.33	14.60	1.77

Table 9: Coccosphere relative abundance (%) of the recorded species in the Ionian Sea (NESTOR site) sediment trap (October 2014- September 2015)

5.3. Cretan Sea

The coccolithophore species identified in the Cretan Sea sediment trap samples are listed in Tables 12 and 13.

The total coccolithophore fluxes in the Cretan Sea sediment trap for the time interval January 2001 – February 2002 (1700m depth) displayed a seasonal pattern (Fig. 21) with highest peak occurring in early April (4×10^5 coccospheres/m^2/day; Fig. 21).

The coccolithophore export production recorded in the Cretan Sea during January 2015 to December 2015 (1550m water column depth) exhibited a moderate seasonal pattern with the only major increase recorded in the early spring (early to late March). The total coccolithophore export production was generally low, with the coccosphere flux peak recorded in late March 2015 (maximum flux: 33.7×10^5 coccospheres/m^2/day; Fig. 24). Before and after that high productivity season, coccosphere flux values were relatively low, however data were not sufficient due to sampling gap. The total coccolith flux pattern observed was similar to the total coccosphere flux (Fig. 24). The high coccolith flux period was during March 2015 and reached a maximum value at late March 2015 (maximum flux: 19.46×10^8 coccoliths/m^2/day; Fig. 24). The period during January 2015 to February 2015 was characterized by low but gradually increasing values (Fig. 24). From the end of July 2015 till November 2015, the total coccolith flux was decreasing with small fluctuations (Fig. 24).

During the investigated time interval of 2001-2002 *Emiliania huxleyi* was the most dominant species of the assemblages. Highest values of the species displayed in early March 2001 (1.71×10^5 coccospheres/m^2/day; Fig.22), followed by February 2002 (1.11×10^5 coccospheres/m^2/day; Fig.22).

Both coccolith and coccosphere sinking assemblages were characterized by high abundances of *Emiliania huxleyi* (100% of the total coccosphere flux in late September 2015 and 68.78% of the total coccolith flux in late March 2015; Tables 10, 11). *E. huxleyi* coccosphere flux displayed a similar pattern to the total coccolithophore export production (Fig. 24), with highest values occurring during early spring (late March- early April) and a major peak at late March 2015 (maximum flux: 13.1 x 10^5 coccospheres/m^2/day; Fig.24). The rest of the year had regular lower values of coccosphere flux. *E. huxleyi* coccolith flux followed the general trend of total coccolith flux (Fig. 24). The period between late December 2014 to late February 2015 and from early August 2015 till late December 2015 was characterized by low *E. huxleyi* coccolith flux values. *E. huxleyi* coccolith flux displayed a similar pattern to the species coccosphere flux (Fig. 24), with the highest productivity season recorded from early to late March. The highest values occurred in late March 2015 (maximum flux: 13.38 x 10^8 coccoliths/m^2/day; Fig. 24).

Species that also contributed to the total coccosphere flux of the period January 2001- February 2002 (Figs. 21-23) and January 2015- December 2015 (Figs. 24;25, Table10) are *Syracosphaera pulchra, Umbilicosphaera sibogae, Calcidiscus leptoporus , Coronosphaera mediterranea* and *Algirosphaera robusta*. In coccolith flux, major components are the species *Florisphaera profunda, Rhabdosphaera clavigera, Syracosphaera pulchra, Umbilicosphaera sibogae* and *Calciosolenia* spp., *Calcidiscus leptoporus* and *Coronosphaera mediterranea* (Figs. 21-25; Table 11). The presence of *Helicosphaera carteri, Umbellosphaera tenuis, Discosphaera tubifera, Pontosphaera* spp., *Scysphosphaera* spp. and *Gladiolithus flabelatus is* insignificant to the coccosphere and coccolith assemblages, as their abundance is <5% of coccosphere (Table 10) and <0.4% of coccolith (Table 11) fluxes.

Syracosphaera pulchra displayed one major peak during 2001-2002 recorded in late April (1.24 x 10^5 coccospheres/m^2/day; Fig. 23). The same species showed (20% of the total coccosphere flux and 6.40% of the total coccolith flux in early January 2015; Tables 10, 11) the higher values in spring 2015 with the maximum peak for both coccospheres and coccoliths in late March 2015 (1.63 x 10^5 coccospheres/m^2/day and 0.41 x 10^8 coccoliths/m^2/day; Fig. 24)
Algirosphaera robusta higher coccosphere flux displayed in early February 2001 (1.44 x 10^5 coccospheres/m^2/day; Fig. 22). The species (35.71% of the total coccosphere flux in late February and late September 2015; Table 10) revealed the maximum peak during early April 2015 (0.55 x 10^5 coccospheres/m^2/day; Fig. 24).
Umbilicosphaera sibogae (62.5% of the total coccosphere flux in late August 2015 and 6.52% of the total coccolith flux in early August 2015; Tables 10, 11 and coccosphere flux (Fig. 24)), reached maximum values at late March (maximum flux: 10.13 x 10^5 coccospheres/m^2/day), considerably higher than the other major species' fluxes. The higher coccolith flux of the species occurred also in late March (0.62 x 10^8 coccoliths/m^2/day; Fig. 24).
Calcidiscus leptoporus revealed high values during early spring (Late April 2001) with the maximum flux recorded to be 0.32 x 10^5 coccospheres/m^2/day (Fig 23). *C. leptoporus* (100% of the total coccosphere flux in late November 2015 and 0.83% of the total coccolith flux in late December 2015; Tables 10, 11) displayed high coccosphere and coccolith values during spring 2015 with higher peak in late March 2015 (1.36 x 10^5 coccospheres/m^2/day and 0.1 x 10^8 coccoliths/m^2/day; Fig. 24)
One important component of the coccosphere and coccolith flux species is *Coronosphaera mediterranea* (16% of the total coccosphere flux in early November 2015 and 0.89% of the total coccolith flux in early September 2015; Tables 10, 11), with a major peak occurred at late March 2015 (maximum flux: 2.61 x 10^5 coccospheres/m^2/day and 0.13 x 10^8 coccoliths/m^2/day; Fig. 25).
Florisphaera profunda coccolith flux (46.18% of the total coccolith flux in early February 2015; Table 11), has considerably higher values concerning species coccolith fluxes, with the highest peak at late March 2015 (maximum flux: 3.46 x 10^8 coccoliths/m^2/day; Fig. 25).

Calciosolenia spp. (3.63% of the total coccolith flux in late March 2015; Table 11) reached the maximum value in late March 2015 (0.71 x 10^8 coccoliths/m^2/day; Fig. 25)
Rhabdosphaera clavigera higher values during the period 2001-2002 was recorded in early February (0.05 x 10^5 coccospheres/m^2/day; Fig. 22). *R. clavigera* (5.57% of the total coccolith flux in early September 2015; Table 11) displayed the highest value during late March 2015 (0.26x 10^8 coccoliths/m^2/day; Fig. 25). *R. clavigera* also presented high values during late summer- early autumn 2015, although without reaching the March peak.

sample	*E. huxleyi*	*S. pulchra*	*C. leptoporus*	*U. sibogae*	*C. mediterranea*	*A.robusta*
M3AVIIB6	45.00	20.00	0.00	0.00	5.00	0.00
M3AVIIB7	50.00	8.33	0.00	0.00	4.17	0.00
M3AVIIB8	59.09	9.09	4.55	9.09	4.55	4.55
M3AVIIB9	28.57	14.29	7.14	14.29	0.00	35.71
M3AVIIB10	81.82	9.09	0.00	9.09	0.00	0.00
M3AVIIB11	38.83	4.85	4.85	30.10	7.77	0.00
M3AVIIB12	55.56	0.00	3.70	24.07	7.41	5.56
M3AVIIIB1	52.94	11.76	0.00	17.65	5.88	5.88
M3AVIIIB2	25.00	0.00	12.50	62.50	0.00	0.00
M3AVIIIB3	72.22	5.56	0.00	16.67	5.56	0.00
M3AVIIIB4	100.00	0.00	0.00	0.00	0.00	0.00
M3AVIIIB5	50.00	15.00	5.00	10.00	15.00	0.00
M3AVIIIB6	58.82	11.76	0.00	11.76	11.76	5.88
M3AVIIIB7	60.00	16.00	0.00	8.00	16.00	0.00
M3AVIIIB8	0.00	0.00	100.00	0.00	0.00	0.00
M3AVIIIB10	57.14	0.00	0.00	0.00	0.00	35.71
Average	52.19	7.86	8.61	13.33	5.19	5.83

Table 10: Coccosphere relative abundance (%) of the recorded species in the Cretan Sea sediment trap (January 2015 - December 2015)

sample	E. huxleyi	F. profunda	S. pulchra	U. sibogae	R. clavigera	Calciosolenia spp.	C. leptoporus	C. mediterranea
M3AVIIB6	46.40	35.31	6.40	1.37	4.69	2.63	0.34	0.57
M3AVIIB7	40.54	42.75	4.34	1.75	3.60	2.68	0.37	1.11
M3AVIIB8	41.72	46.18	2.71	0.97	3.39	1.94	0.29	0.77
M3AVIIB9	47.33	36.38	4.17	1.96	3.52	3.00	0.52	0.39
M3AVIIB10	51.59	29.46	4.40	1.83	4.40	3.55	0.37	1.47
M3AVIIB11	68.78	17.76	2.12	3.17	1.36	3.63	0.53	0.68
M3AVIIB12	67.13	19.55	3.36	3.55	1.28	2.57	0.59	0.79
M3AVIIIB1	57.45	24.34	4.52	6.52	2.53	2.26	0.66	0.53
M3AVIIIB2	57.87	22.57	3.62	5.59	4.55	2.90	0.41	0.62
M3AVIIIB3	52.30	23.18	6.32	6.09	5.57	2.75	0.67	0.89
M3AVIIIB4	50.26	32.19	4.67	3.32	4.26	2.18	0.52	0.42
M3AVIIIB5	42.93	40.40	3.45	4.21	4.29	2.19	0.59	0.17
M3AVIIIB6	47.18	38.07	2.14	4.74	3.75	2.32	0.36	0.54
M3AVIIIB7	47.91	37.43	2.62	2.55	4.45	2.68	0.26	0.72
M3AVIIIB8	49.45	32.99	3.50	3.50	4.94	2.81	0.26	1.11
M3AVIIIB10	46.10	35.59	4.68	2.81	4.06	2.91	0.83	0.52
Average	50.93	32.13	3.94	3.37	3.79	2.69	0.47	0.71

Table 11: Coccolith relative abundance (%) of the recorded species in the Cretan Sea sediment trap (January 2015- December 2015)

Fig. 21: Total coccosphere and coccolith fluxes in the Cretan Sea sediment trap for the time interval January2001-February 2002 (Triantaphyllou et al., 2004)

Fig. 22: Species coccosphere and coccolith fluxes in the Cretan Sea sediment trap for the time interval January 2001-February 2002 (Triantaphyllou et al., 2004)
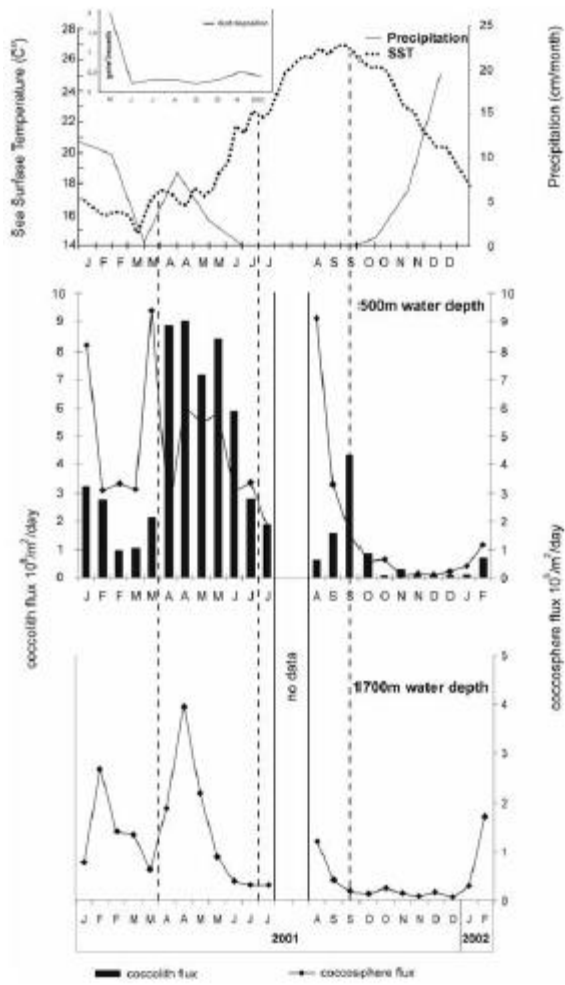
Fig. 23: Species coccosphere and coccolith fluxes in the Cretan Sea sediment trap for the time interval January2001-February 2002 (Triantaphyllou et al., 2004)

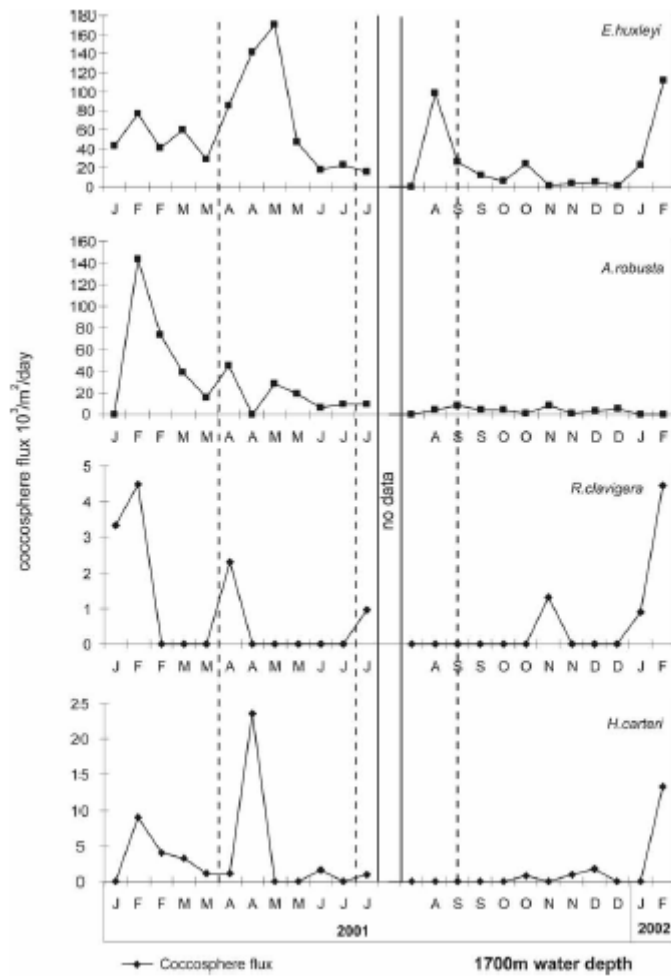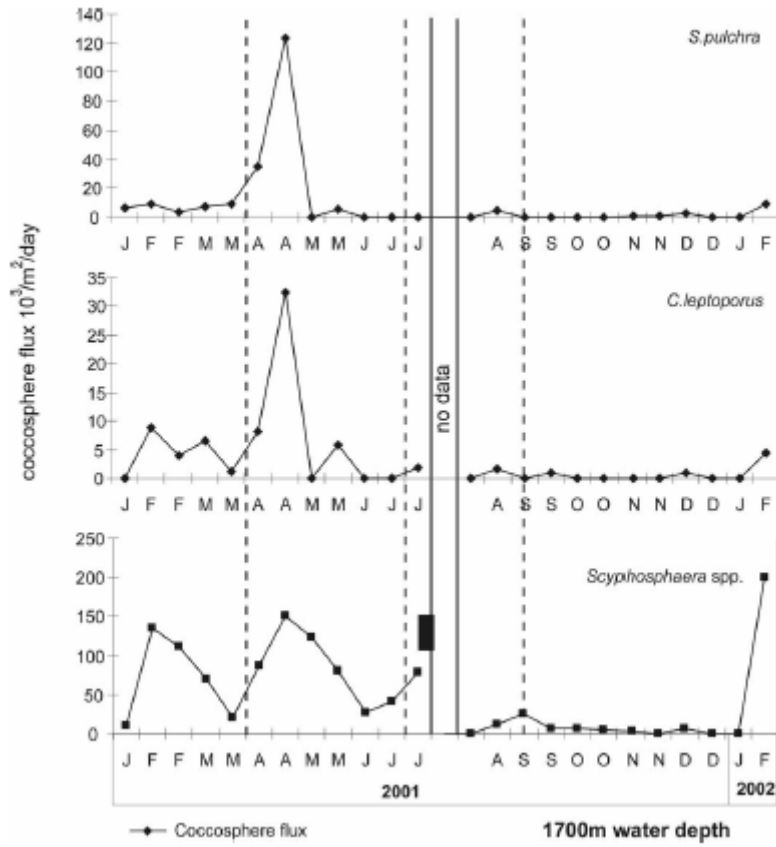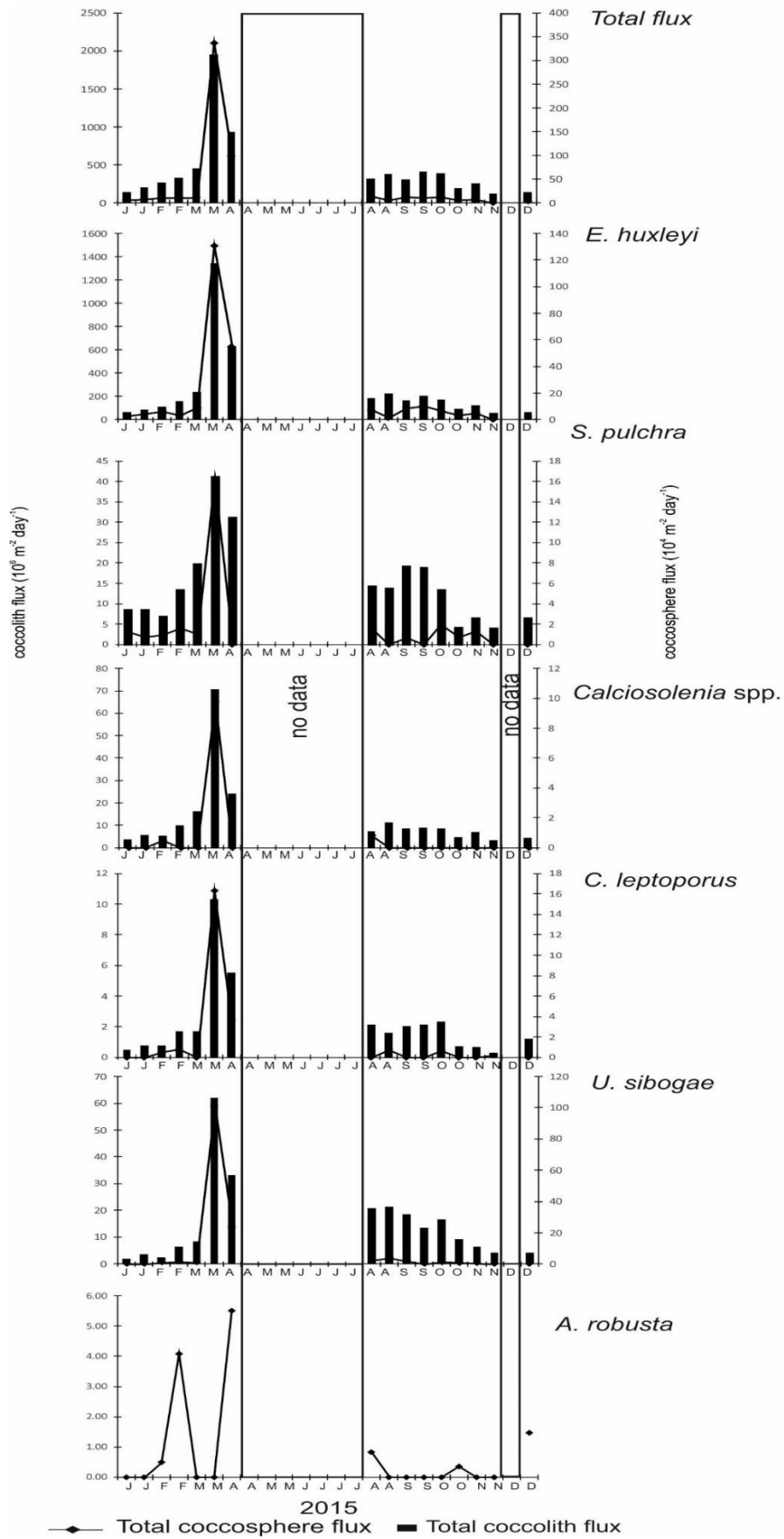Fig. 24: Species coccosphere and coccolith fluxes in the Cretan Sea sediment trap for the time interval January 2015-December 2015.
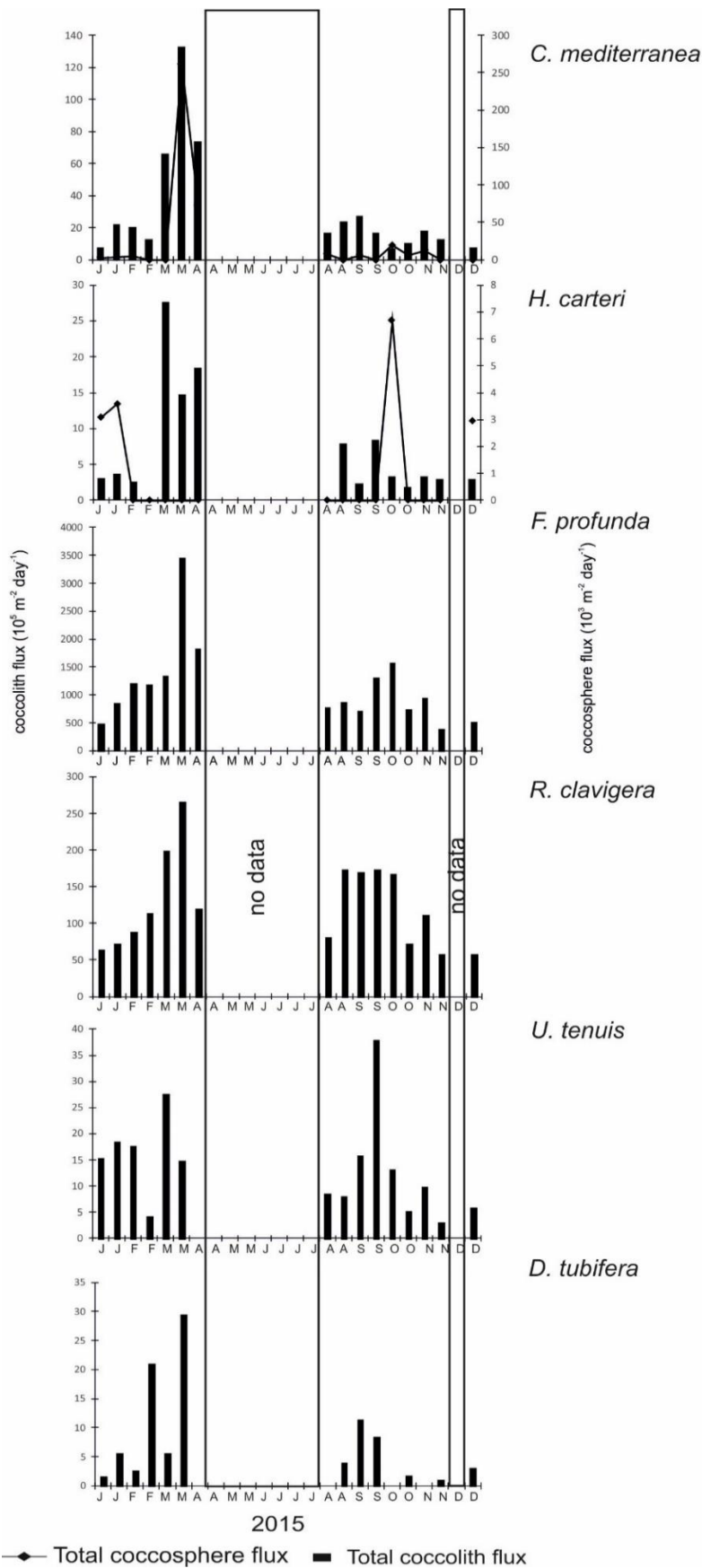
Fig. 25: Species coccosphere and coccolith fluxes in the Cretan Sea sediment trap for the time interval January 2015-December 2015 (minor species).

North Aegean	Ionian Sea	Cretan Sea
Algirosphaera robusta	*Algirosphaera robusta*	*Algirosphaera robusta*
Calcidiscus leptoporus	*Calcidiscus leptoporus*	*Calcidiscus leptoporus*
Calciosolenia spp.	*Calciosolenia* spp.	*Calciosolenia* spp.
Coronosphaera mediterranea	*Coronosphaera mediterranea*	*Coronosphaera mediterranea*
Emiliania huxleyi	*Emiliania huxleyi*	*Emiliania huxleyi*
Helicosphaera carterri	*Helicosphaera carteri*	*Helicosphaera carteri*
Pontosphaera spp.	*Pontosphaera* spp	*Pontosphaera* spp
Rhabdosphaera clavigera	*Rhabdosphaera clavigera*	*Syracosphaera pulchra*
Rhabdosphaera xiphos	*Syracosphaera pulchra*	*Thoracosphaera heimi*
Syracosphaera pulchra	*Thoracosphaera heimi*	*Umbilicosphaera sibogae*
Thoracosphaera heimi	*Umbilicosphaera sibogae*	
Umbilicosphaera sibogae		
Umbellosphaera tenuis		

Table 12: List of coccolithophore species (coccospheres and calcareous dinoflagellates) recorded in the studied sediment trap samples

Cretan Sea
Braarudosphaera bigelowii
Calcidiscus leptoporus
Calciosolenia spp.
Ceratolithus spp.
Coronosphaera mediterranea
Discosphaera tubifera
Emiliania huxleyi
Florisphaera profunda
Gladiolithus flabelatus
Helicosphaera carteri
Holococcoliths
Pontosphaera spp..
Rhabdosphaera clavigera
Scyphosphaera spp.
Syracosphaera pulchra
Umbellosphaera tenuis
Umbilicosphaera sibogae

Table 13: List of dominant coccolithophore species (coccoliths) recorded in the Cretan Sea sediment trap

6. Discussion

6.1. Time series data: comparative description of fluxes annual trend and seasonality of the assemblages

The three investigated areas, as well as most areas of the eastern Mediterranean Sea, are characterized by a seasonal surface productivity typical of subtropical–temperate zones (Malinverno et al., 2009). Production displayed its maxima in late winter–spring, during the water column mixing phase, which is in correspondence with the interval of increased rainfall. Seasonal ecological shifts can alter the composition of coccolithophore assemblages, as tracked by coccolith export production, with consequent impacts on the carbonate system (Ziveri et al., 2007). In the present study, coccosphere fluxes are studied, mostly as their occurrence reveals direct surface water productivity; intact coccospheres disintegrate relatively rapidly after the cell dies, whereas coccoliths may bear multiple signals, as they may have been resuspended and redeposited from the shelf into the deep sea, through currents and winds (Ziveri et al., 2000).

The following comparative description of coccolithophore export production in the N. Aegean, SE Ionian and Cretan Seas reveal an increasing trend during the last years (in total 2001-2015). Overall all three investigated areas, display higher flux values within time, with the highest values occurring during 2015. The extreme peak recorded in the Ionian Sea during 2012, is not practically affecting the increasing trend of export production during the years, related to large scale processes and oceanographic changes (Gogou et al., 2016).

6.1.1. North Aegean Sea

The dataset provided by the North Aegean mooring in 2014-2015 sampling, is featured by an outstanding peak (8.56×10^6 coccospheres/m^2/day) in late February (Fig. 18). This late winter-early spring peak has also been observed in the North Aegean water column coccolithophore assemblages (March 2014) by Karatsolis et al. (2016), marking a positive correlation with nutrients associated with significant export from the surface BSW layer. Although there are no available data for February 2011 concerning coccosphere fluxes (Fig. 16), a similar peak of total coccolith flux in the same month (Triantaphyllou et al., 2014), suggests highly productive conditions for the certain time interval. The period between early June to early August is featured by higher values during 2015 than the same period in 2011, with exception of late June, when the total coccosphere fluxes are almost similar (2.54×10^5 coccospheres/m^2/day and 1.71×10^5 coccospheres/m^2/day, in 2011 and 2015 respectively; Fig. 28). In early November, the highest total coccosphere flux is recorded in 2015 (0.85×10^6 coccospheres/m^2/day), followed by the year 2014 (0.41×10^6 coccospheres/m^2/day); the lowest values were documented in 2011 (0.76×10^5 coccospheres/m^2/day) (Fig. 28). In addition, the total coccosphere fluxes in between November to December 2014 are higher than those of 2011 for the same time period (Fig. 28). Overall, coccosphere fluxes expose an increasing trend during 2011-2015, as this is recorded at least within the time intervals of June - August, September and November.
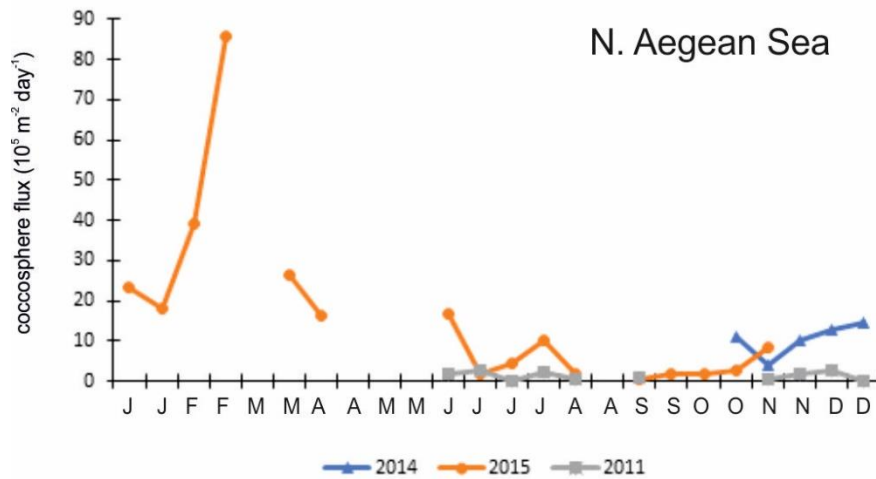
Fig 28: Total coccosphere fluxes in the N. Aegean Sea during 2011-2014-2015
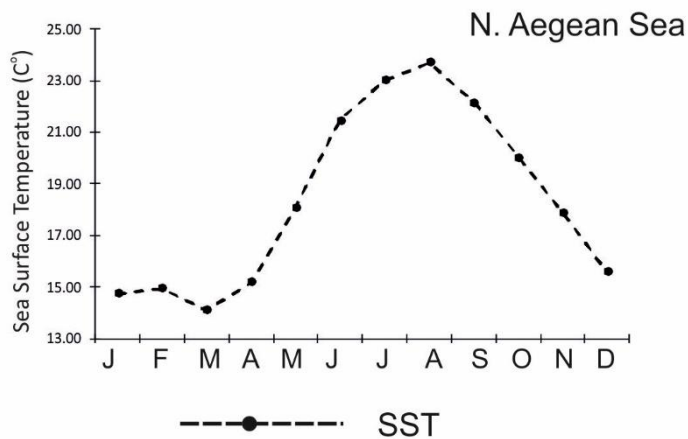
Fig. 29: Sea Surface Temperature (^{o}C) in N. Aegean Sea in 2015

The increased flux values during late winter- early spring mostly represent the seasonal peak of *E. huxleyi*, the most abundant coccolithophore species (Fig. 18; Table 8). This species also prevails throughout the year 2011 (Triantaphyllou et al., 2013, 2014; Fig. 17), at the same sediment trap location and depth. *Emiliania huxleyi* is a typical opportunistic species, resistant to a wide range of conditions, as temperature and salinity (e.g., Okada & McIntyre, 1979; Bukry1974; Roth & Colbourn, 1982; Okada & Wells, 1997; Malinverno et al., 2009) and dominates the Aegean water column particularly within the winter period (e.g., Dimiza et al., 2008, 2015). Therefore, the relatively low summer total coccosphere flux values (July 2011, 2015) reflect the low coccosphere flux of *E. huxleyi* during this time interval in the Aegean Sea (Triantaphyllou et al., 2002; Dimiza et al., 2008, 2015; Karatsolis et al., 2016) suggesting the influence of low mineral nutrients related to a metabolically active community in the BSW surface masses (Karatsolis et al., 2016). As there are no coccosphere data for the species major peak in February from the 2011 sampling, the available values of the secondary peak in June presume for a slight increase in coccosphere fluxes within 2015 (Fig. 28).

Syracosphaera pulchra (average coccosphere abundance 14.11%; Table 8) shows a seasonal signal with higher values in October-November 2014, early February, early June and late July 2015 (Figs. 17,18), following the total coccosphere flux (Fig. 18) in association to the SST increase (Fig. 29). It is a tropical subtropical species, which seems to have an oligotrophic distribution (Ziveri et al. 2004; Crudeli et al., 2006; Principato et al., 2006; Triantaphyllou et al., 2004) and according to Flores et al. (1999) it is an indicator of waters with high temperatures. This is a fact that is confirmed by the SST increasing values at the interval of high *S. pulchra*'s coccosphere fluxes. This seasonal pattern is similar to the one observed in 2011, in which *S. pulchra* displayed high values during late June (although in much less absolute abundances, Fig. 17), and is supported by analogous observations for the ecological preference of the species in the Aegean Sea water column (Dimiza et al., 2008, 2015; Karatsolis et al., 2016). According to Dimiza et al. (2008), *S. pulchra* is commonly concentrated during the warm season of the Eastern Mediterranean waters.

Algirosphaera robusta (average coccosphere abundance 0.65%; Table 8) was recorded only during November and December 2014 and February, April and November 2015 (Fig. 18). Higher fluxes of this species during the year 2015 are associated with the lower SST interval (February to early April; Fig. 29), but it reached maximum values during November till December 2014, as *A. robusta* is generally related with increased nutrients in the deeper photic zone and periods of stratification of the water column (Broerse et al., 2000a, b). In the North Aegean site, this is related to the proximity to the coastline, which provides nutrients through the riverine input during this time interval. Although Sprengel et al. (2002) supported a preference of *A. robusta* for open pelagic rather than coast-influenced settings, our data add to Dimiza et al. (2008) and Malinverno et al. (2009) evidence for its preference to nearshore sites. According to Dimiza et al. (2015), this species as an indicator for relatively cold and eutrophic conditions (Kleijne 1993), displays maximum relative abundances in the North Aegean lower photic zone during the cold period, fact also confirmed by our study.

Concerning the species *Umbilicosphaera sibogae* (average coccosphere abundance 0.92%; Table 8), it is found to follow the SST increase (Fig. 29). The observed peaks in late February, April, June (Fig. 18) correspond to the beginning of SST increase (Fig. 29), as this species is considered an indicator of tropical and warm waters (Wells & Okada, 1997; Flores et al., 1999; Tayhashi & Okada, 2000).

6.1.2. Ionian Sea

A comparison of total coccosphere fluxes has been made from the same sediment trap deployment (NESTOR site, 2000 m depth) between the years 2010-2012 and 2014-2015. Lack of data on different months of each year makes that comparison incomplete. However, the recorded maximum values are similar in between the studied years, with major peak of total coccosphere flux to be observed at early to mid-spring (Fig. 30). The total coccosphere flux of the investigated time period was higher in 2012 than 2015 (Fig. 30), with an exception occurring in late March, when the values were almost identical (late March 2015: 8.12 x 10^5 coccospheres/m^2/day, late March 2012: 8.52 x 10^5 coccospheres/m^2/day; Figs. 19, 20). The recorded data show that in early summer (the second half of June), the year with the highest coccosphere flux is 2012 (7.41 x 10^5 coccospheres/m^2/day; Fig. 19), followed by 2015 (6.43 x 10^5 coccospheres/m^2/day; Fig. 20) and 2011 (1.39 x 10^5 coccospheres/m^2/day; Fig. 19), whereas the lowest value occurred at 2010 (0.84 x 10^5 coccospheres/m^2/day; Fig. 19). The coccosphere flux pattern follows that of the temporal distribution of total mass flux, which exhibited strong seasonal patterns, with higher fluxes recorded mainly in late winter/early spring followed by a second, more pronounced flux maximum period in late spring/summer and significantly lower fluxes in autumn/winter (Gogou et al., 2016). The time period late November-early December in the Ionian Sea coincides with deeply oligotrophic conditions of the area. During this interval, the summer thermocline is still maintained but a surface mixed layer is

already developed, as a result of the presence of strong autumn winds, with lower temperatures then the summer season (mean SST around 19^OC) (Malinverno et al., 2002). Primary productivity in the Ionian Sea, displays high seasonal variability with maximum rates observed during the winter/ spring convective mixing period, similarly to previous studies (e.g., D'Ortenzio and Ribera d'Alcala, 2009; Patara et al., 2009). In the NESTOR time-series, the seasonal variability coincides with relative increases in organic carbon and opal export during late winter/early spring, being possibly related to the development of siliceous blooms in the euphotic zone (Gogou et al., 2016). In late spring/ summer period (May-July), carbonate producing species (coccolithophores) gain more importance as primary producers, as it is witnessed by the increase in the carbonate contents (Gogou et al., 2016) and coccolithophore export (Malinverno et al., 2014; present study). A mid summer (July) peak may represent the more favourable conditions for TEP- enhanced phytoplankton aggregation which are attended by higher particle fluxes (Patara et al., 2009).

According to Stavrakakis et al. (2013) the total mass flux maxima at various depths demonstrated considerable interannual variability in vertical distributions despite some similarities in the seasonal patterns. The mass flux variability played crucial role to the gradual increase of winter mass flux almost at all depths, followed by an evident analogous increase (with some exceptions) in spring and summer mass flux, with such an interannual changing flux patterns to be explained by the reinforcement of processes which produce and/or transfer particulate matter in the area (Stavrakakis et al., 2013). The increase of fluxes from 2006 to 2010 could possibly be related to the general circulation patterns at the NESTOR site, which displays strong interannual variability (Stavrakakis et al., 2013). The large scale anticyclonic circulation recorded during the 1980s and early 1990s was limited during mid-late 1990s in the southern part and changed to a cyclonic circulation in the northern Ionian Sea (Gacic et al., 2011). After 2006, the Ionian circulation was changed back into anticyclonic, as indicated by changes in the salinity and nutrient in the south Adriatic (Civitarese et al., 2010). As a result, an upwelling of the nutricline was caused in the periphery of the anticyclonic gyre and the weakening or even the absence of the Pelops gyre and, as nearby observational buoy of the Poseidon system revealed, NESTOR site is found at the edge of this anticyclone (Stavrakakis et al., 2013). Stavrakakis et al. (2013) suggest that the remarkable enhancement of the fluxes from 2008 was linked to the intensity of the intrusion in the upper layer of high salinity intermediate waters of Levantine/Cretan origin, whose upward movement could favor upwelling of nutrients and enrichment of the upper layer, thus triggering surface productivity and the enhancement of downward particle fluxes. Finally, during spring 2012, an outstanding increase of all biogenic fluxes was recorded, when atmospheric conditions including particularly strong cold and dry northerly winds triggered intense winter convection mixing (Gogou et al., 2016). In the study of Gogou et al. (2016), multi-biogeochemical parameters demonstrate that the combination of oceanographic changes and large scale processes had a decisive role controlling the ecological and biogeochemical functioning of the Ionian Sea on seasonal and interannual scales

Overall, coccosphere fluxes in the Ionian Sea demonstrate an increasing trend during 2010-2015, as it is recorded at the various investigated time intervals during June 2010- September 2015. According to Gogou et al. 2016 atmospheric conditions involving particularly strong cold and dry northerly winds triggered intense convection mixing winter causing the mentioned increased biogenic fluxes in spring 2012. Thus, this fact is an isolated event that cannot affect the observed increasing flux trend.
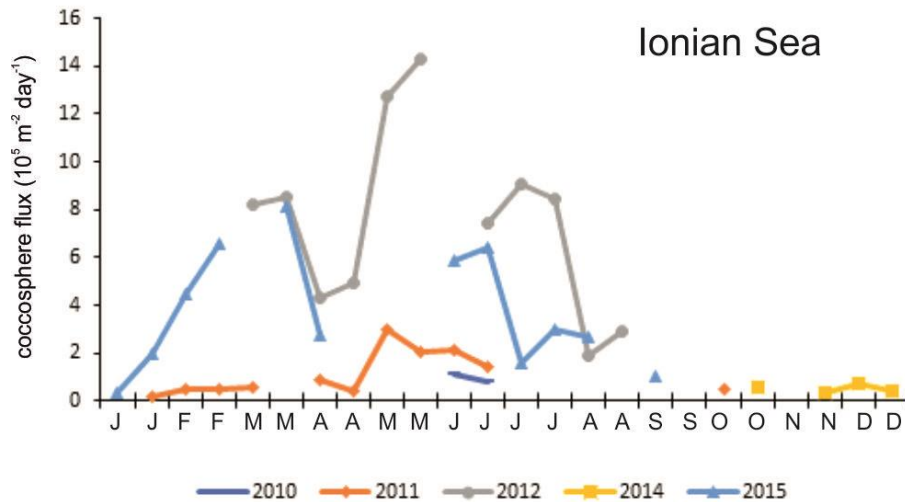
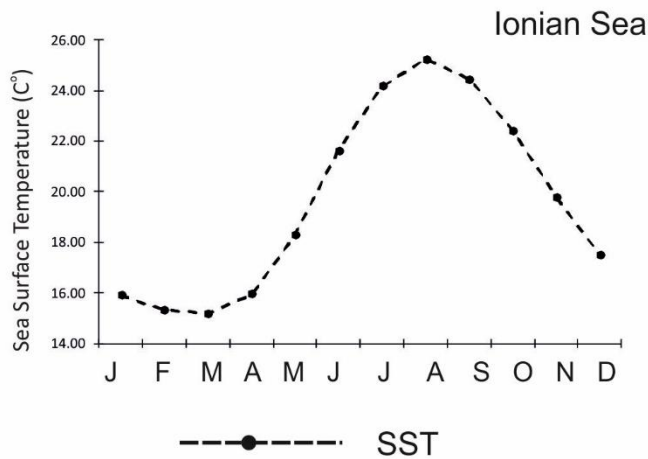Fig 30: Total coccosphere fluxes in Ionian Sea during 2010-2011-2012-2014-2015

Fig. 31: Sea Surface Temperature (^{o}C) in Ionian Sea (NESTOR site) in 2015

The high peaks observed in March (2012, 2015) and early summer (May-June; peak in 2012), efficiently respond to the increase in the *E. huxleyi* abundance. Being the dominant coccolithophore species, *E. huxleyi* prevails throughout the year 2015 in the coccolithophore assemblages of NESTOR site sediment trap (average coccosphere abundance 51.08%; Table 9). This opportunistic species is resistant to a wide range of conditions, being most abundant in the surface layers but it is also found in relative deeper layers of the photic zone (Okada & McIntyre, 1979; Bukry, 1974; Roth & Colbourn, 1982; Okada & Wells, 1997; Malinverno et al., 2009). *E. huxleyi* flux pattern is following that of total coccosphere flux, and is in accordance with the fluxes calculated for the 2010-2012 time interval (Fig.19). Higher values occur during late winter- early spring, with the major peak at the end of March 2015; followed by decrease in coccosphere flux within April (Fig. 20). The observed pattern is similar to what has been recorded in the same interval of the year 2012. Then, high values occurred in June and at early August with a minimum value between them (July). That reduction in between those two peaks is also observed at the same months of 2012 (Figs. 19, 20). Obviously the coccolithophore productivity as shown by coccosphere fluxes is negatively correlated to SST (Fig. 31).

Syracosphaera pulchra is a tropical subtropical species which seems to have an oligotrophic distribution (Ziveri et al., 2004). *S. pulchra* 's (average coccosphere abundance 11.19%; Table 9) pattern of 2015 shows a seasonal signal comparable to that of the same species of 2011-2012 (Figs. 19, 20) with higher values recorded during late spring- summer. Malinverno et al. (2014) mentioned a marked flux increase of the species especially during spring (late April–May). According to Dimiza et al. (2008), *S. pulchra* is one of the less opportunistic species and is considered to indicate intermediate environments with moderate nutrient conditions.

Algirosphaera robusta inhabits the deep euphotic zone of tropical to intermediate conditions (Okada and Honjo, 1973; Okada and McIntyre, 1979; Reid, 1980; Knappertsbusch, 1993; Takahashi and Okada, 2000). In 2015, *A. robusta* 's (average coccosphere abundance 14.45%; Table 9) higher values of 2015 occurred during late February till early April (Fig. 20), which corresponds to the lowest SST time period (Fig. 16), and June. A similar seasonal pattern was recorded during 2012 (Fig. 19). The increased abundance of *A. robusta* could imply a period of stratification of the water column (Broerse et al. (2000 a, b). However, similarly to our results, the species has been found more abundant during fall-winter during the period of maximum rainfall in the South Cretan Margin (Malinverno et al., 2009), though being present throughout the whole seasonal cycle. It seems that this is a feature for the eastern Mediterranean region; the significant peak of *A. robusta* takes place during winter, when the surface mixed layer is deeper and nutrients are likely more easily diffused to the lower photic zone from deeper water layers. It is considered as a deep dwelling species, even if it sometimes is present in the surface waters, reaching maximum abundance at slightly shallower depths (Malinverno et al., 2002).

Umbilicosphaera sibogae is considered as an indicator of tropical and warm waters (Wells & Okada, 1997; Flores et al., 1999; Tayhashi & Okada, 2000). During the year 2015, *U. sibogae* (average coccosphere abundance 14.6%; Table 9) responded positively to the increase of SST at the interval June-August (Fig. 31), when the highest values of the species were recorded. An abundance increment has also been observed during the high productivity season (late February-March), implying relatively high nutrients and low salinity (Andruleit & Rogalla 2002; Shipe et al., 2002). Similarly, *U. sibogae* exhibited a flux increase especially during spring (late April–May), as recorded by Malinverno et al. (2014). The same seasonal pattern was displayed during 2011-2012, revealing a tendency for warmer water conditions (Fig. 19).

In addition, coccosphere flux of *Coronosphaera mediterranea* (average coccosphere abundance 3.33%, Table 9) reached its higher values during February-March and June-July 2015 (Fig. 20), mostly following the high productivity season (late February-March). *C. mediterranea* demonstrated a similar flux peak during late spring (May; Fig. 19) 2011 and 2012. According to Malinverno et al. (2009) *Coronosphaera* species are usually abundant in July, but can also increase sporadically during fall to spring time (mainly November and late March) and among the minor species, they have higher relative abundance during fall and winter. In addition, this species usually considered as typical from low-nutrient high-temperature areas (Nishida, 1979; Okada and McIntyre, 1977) and periods (Haidar and Thierstein, 2001; Okada and McIntyre, 1979; Triantaphyllou et al., 2004). Whenever found with species as *R. clavigera, U. tenuis and D. tubifera* it may document a well-developed surface community, thriving in a stratified upper water column, likely resulting in gradual nutrient depletion in the photic zone (Malinverno et al., 2009).

Helicosphaera carteri (average coccosphere abundance 1.77%, Table 9) reached maximum values during early June 2015 followed by a second peak in early April 2015 (Fig. 20), in accordance to high SST values (Fig. 31). The species high peak of 2012 was also recorded during the warm period (late July 2012; Fig.19), probably associated with inflow of fresh water (Triantaphyllou et al., 2009 a, b). In general, *H. carteri* characterises warm waters with high productivity and low nutrient content (Ziveri

et al., 2004; Haidar & Thierstein, 1997). According to Malinverno et al. (2014), the species displays a slight flux increase during the period late April-May, responding to the seasonality of available nutrients in the photic zone, caused either by water column mixing or due to an increase in fresh-water input, related to higher precipitation (Malinverno et al., 2009).

6.1.3. Cretan Sea

Sediment traps in Cretan Sea provide data of coccosphere sinking assemblages at 1700 m and 1550 m depth, during years 2001-2002 (Triantaphyllou et al., 2004) and 2014-2015 (present study). Total coccosphere flux values in January and February 2015 are almost identical for the years presented (Fig. 32). The highest productivity season was recorded in early March 2015 (33.7×10^5 coccospheres/m^2/day), followed by early April 2015 (9.93×10^5 coccospheres/m^2/day). The high peak of March-April 2015 is in contrast with March 2001, where the values were much lower; 2001's major peak was recorded in late April (Triantaphyllou et al., 2004), showing a 30-days delay between 2015 and 2001 highest productivity season. From August till December the values of total coccosphere fluxes of both years are very similar.

Data of coccolith sinking assemblages at 1550 m and 500 m were provided by the same sediment trap in the Cretan Sea at the years 2014-2015 and 2001-2002 respectively. It can be easily observed in Fig. 33 that the coccolith flux pattern varied between the years 2001 and 2015. From January till the end of February 2015 the coccolith flux was gradually increasing with the major peak recorded in March (Fig. 25). In the same period of 2001 sampling the values were much lower (Fig. 33) (Triantaphyllou et al., 2004). A similar winter peak was recorded in the shallower trap (500m), but with a delay of a month; highest values occurred in early April (8.85×10^8 coccoliths/m^2/day), nevertheless still much lower than what has been observed in 2015. Between August and December 2001, the fluxes   were lower than those of 2015, with the only exception in late September (2001: 4.34×10^8 coccoliths/m^2/day and 2015: 4.05×10^8 coccoliths/m^2/day) (Triantaphyllou et al., 2004). However, the difference in depth between the two datasets must be considered, as it may cause inaccuracies in the comparison.

The late March peak in coccosphere flux of our study (Fig. 25) is also detected in the wider area, as observed by Malinverno et al. (2009) in the South Cretan Margin.

Overall, coccosphere fluxes follow an increasing trend during 2001-2015, as this is verified during the investigated time intervals (Figs 32, 33).
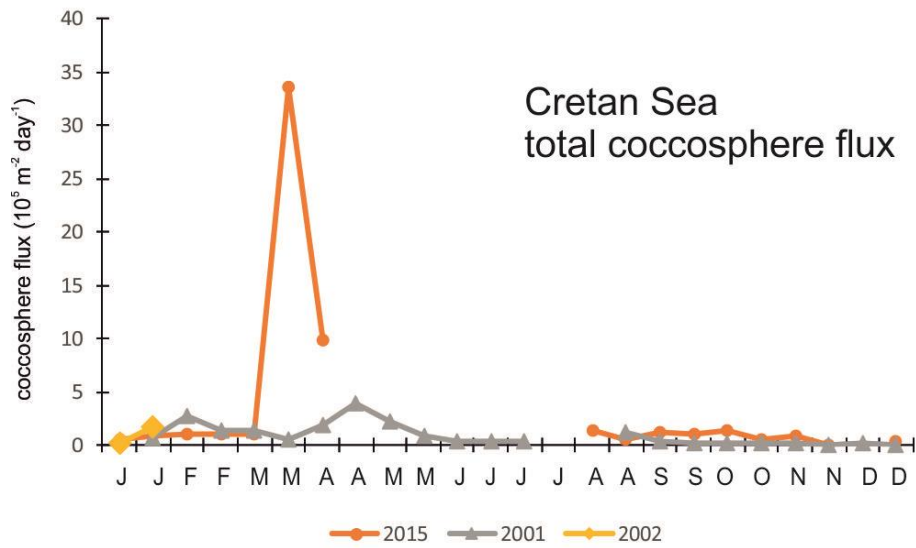
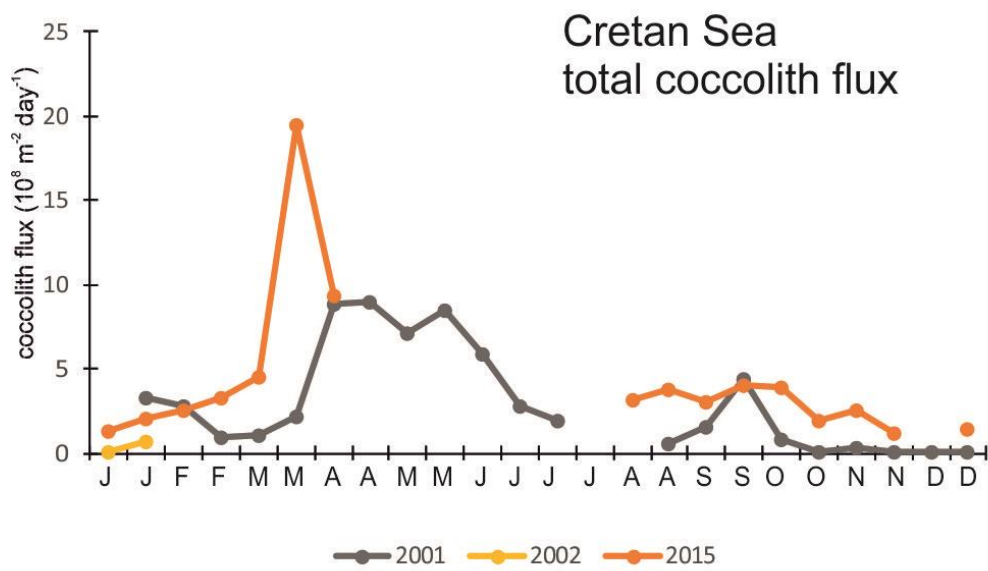Fig 32: Total coccosphere fluxes in Cretan Sea during 2001-2002-2014-2015

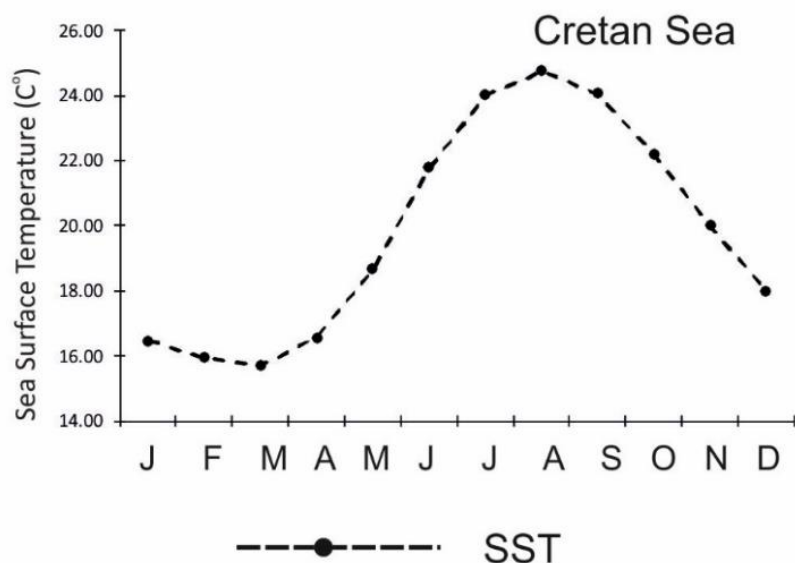Fig 33: Total coccolith fluxes in Cretan Sea during 2001-2002-2014-2015

Fig. 34: Sea Surface Temperature ($^{\circ}$C) in Cretan Sea in 2015

Sediment trap coccolithophore assemblages in the Cretan Sea are dominated by two species; *Emiliania huxleyi* (average coccosphere abundance 52.19%, average coccolith abundance 50.93%; Tables 10, 11) and *Florisphaera profunda* (average coccolith abundance 32.13%; Table 11). This is observed in both 2014-2015 and 2001-2002 samplings in the area (Triantaphyllou et al., 2004). The major peak recorded in March 2015 reflects the high fluxes recorded for both major species, *E. huxleyi* and *F. profunda.*

The strong presence of *E. huxleyi* in Aegean's marine ecosystems has been pointed up especially during the late winter-early spring period (Triantaphyllou et al., 2004; Dimiza, 2006; Dimiza et al., 2008). The high N/P ratio (Tselepides et al., 1993; Tselepides et al., 2000b) that is presented in the Cretan Sea combined with the resistance of the species to a variety of conditions, may enhances the dominance of *E. huxleyi* in the coccolithophore assemblages. In early March 2015, both coccosphere and coccolith fluxes of *E. huxleyi* displayed the maximum peak (Fig. 25). However, there is a difference during 2001-2002, as *E.huxleyi* displayed the higher values in May, in the deep trap (1700 m); and in the shallower trap of 500 m the higher values were recorded in August for coccospheres and in April for coccoliths. The peak of *E. huxleyi* in March 2015 responds positively to the high productivity season (late winter- early spring), and corresponds to the lower SST values recorded in 2015 (Fig. 34). Similarly, *E. huxleyi* is more abundant, relative to all other species, during spring (peak flux in middle–late March) and early summer (June) in the South Cretan Margin (Malinverno et al., 2009). The species high flux during early spring–early summer is a rapid response to the increased nutrient supply to the photic zone, following the deep water column mixing (Triantaphyllou et al., 20014; Malinverno et al., 2009).

Syracosphaera pulchra (average coccosphere abundance 7.86%, average coccolith abundance 3.94%; Tables 10, 11) higher peaks occurred during the end of winter (late March 2015; Fig. 25), in the high coccolithophore productivity season, in association to the SST increase (Fig. 34). During 2002, *S. pulchra* displayed a similar pattern with high values recorded during the period early spring -early summer both in 500 m and 1700 m depth (Triantaphyllou et al., 2004). In general, *S. pulchra* flourishes in tropical-subtropical regions with oligotrophic to mesotrophic waters (Ziveri et al., 2004; Crudeli et al., 2006; Principato et al., 2006) and low salinities (Flores et al., 1997; Colmenero-Hidalco

et al., 2004). Our data are in an agreement with Malinverno et al. (2009), who indicated that *S. pulchra* corresponds to the interval of maximum rainfall and water column mixing.

Algirosphaera robusta (average coccosphere abundance 5.83%; Table 10) displayed a considerably high value among the minor species fluxes during different intervals the whole year, with the major peak occurred in late February, in agreement to Malinverno et al. (2009). However, in Malinverno et al. (2009), *A.robusta* displayed high values during the whole year and in some specific periods seemed to become even dominant over *E. huxleyi*. High frequency of *A. robusta* is found in non-coastal areas (Sprengel et al., 2002). This species is also associated with a limited increase in the concentration of nutrients (Broerse et al., 2000a) and it may be an important species in oligotrophic conditions (Triantaphyllou et al., 2004; Malinverno et al., 2009). Unlike the findings of Triantaphyllou et al. (2004) in the Cretan Sea during 2001, and similarly to Broerse et al. (2000b) in the NE Atlantic, *A. robus*ta is increasing together with *F. profunda* in the Cretan Sea during 2015, definitely pointing to the development of a seasonal nutricline*.

Umbilicosphaera sibogae is a proxy of tropical and warm waters, rich in nutrients and increased salinity (Wells & Okada, 1997; Flores et al., 1999; Tayhashi & Okada, 2000; Andruleit & Rogalla, 2002; Shipe et al., 2002). *U. sibogae* (average coccosphere abundance 13.33%, average coccolith abundance 3.37%; Tables 10, 11) displayed the same seasonal pattern to the total coccolith and coccosphere flux (Fig 25), with higher values recorded in March 2015, and also in summer only for coccolith flux. This peak is the same in comparison with 2002 sediment trap assemblages from 500 m depth, where the peak occurred in March, June and August. Those data confirm that *U. sibogae* responds efficiently to the increase of SST (Fig. 34). In accordance with Malinverno et al. (2009), *U. sibogae* exhibits an increase during the interval of high total coccosphere flux (March) and responds positively to the increased nutrient availability that follows the seasonal water column mixing, revealing a tendency for mesotrophic to eutrophic conditions.

Coronosphaera mediterranea (average coccosphere abundance 5.19%, average coccolith abundance 0.71%; Tables 10, 11) revealed a seasonal pattern with higher values occurring during late winter 2015 (late March; Fig. 27), and a second peak during late September 2015. According to Malinverno et al. (2009), *Coronosphaera* species are usually abundant in July, but can also get sporadically increased during fall to spring time (mainly November and late March); among the minor species, they present higher relative abundance during fall and winter.

Florisphaera profunda is restricted to the light-limited, lower euphotic zone of the tropical and subtropical environments (Okada and Honjo, 1973; Winter et al., 1994; Sprengel et al., 2000; Kinkel et al., 2000). This species has proven to be a very reliable proxy to locate the nutricline-thermocline level in those environments (Molfino and McIntyre, 1996; Sprengel et al., 2000). Its high abundance confirms the presence of stratification of the deep water column layers (Molfino & McIntyre, 1990; Sbaffi et al., 2001; Colmenero-Hidalgo et al., 2004; Triantaphyllou et al., 2004; Dimiza et al., 2008). *F. profunda* coccolith flux is in correspondence with the total coccolith flux (Fig. 26), displaying the major peak during early March 2015. The simultaneous high abundance of this deep water species with *E. huxleyi* could imply the coccolithophore production throughout all the layers of water column. High values of *F. profunda* also occurred during late September- early October 2015, i.e. during the same period with the 2002 major flux of this species in the sediment trap of 500 m (Triantaphyllou et al., 2004).

Rhabdosphaera clavigera displays a seasonal trend (Fig. 26). It is a warm water species of the upper water column (Okada and McIntyre, 1979). *R. clavigera* higher concentrations (average coccolith

abundance 3.79%) (Table 11) are related with higher SST (early spring to early autumn), with the major peak occurred in late March 2015 (Fig 34), in accordance to Triantaphyllou et al. (2004) findings. *Rhabdosphaera* spp. indicates intermediate environments with normal nutrient conditions (Young, 1994; Triantaphyllou et al., 2002) and its high values are related to warm oligotrophic waters (Roth & Colbourn, 1982; Flores et al., 1997; Sprovieri et al., 2003). *R. clavigera* displays usually higher flux values and relative abundance in summer, as confirmed by Malinverno et al. (2009).

Calcidiscus leptoporus (average coccosphere abundance 8.61%, average coccolith abundance 0.47%; Tables 10, 11) flux peak occurred in March and early autumn 2015 (Fig. 25). This species shows a seasonal pattern, with its higher peak occurring in the high coccolithophore productivity season in association to the SST increase (late March-late summer; Fig. 34). *C. leptoporus* revealed a similar pattern with high values recorded during the period early spring -early summer 2002 in both depths (500 m and 1700 m, Triantaphyllou et al., 2004). Generally, it is considered being a species that thrives in a wide range of temperatures (Okada & Mcintyre, 1979). However, according to Triantaphyllou et al. (2009a) this species existence is confirmed in the warm waters of the SE Aegean Sea.

6.2. Total coccosphere flux trends in the Aegean and Ionian Seas

Total coccosphere fluxes of the three traps displayed a similar seasonal pattern (Fig. 35). An increase in the values was observed at mid to late winter, with the higher peak at mid winter- early spring, i.e. during the mixing period of the water column, which also coincides with the period of increased precipitation (Malinverno et al., 2009). The rest of the investigated interval was characterized by much lower values, with some less important fluctuations. In the N. Aegean Sea, there was also a minor peak occurring at the end of July, but yet not compared to late winter's major peak, which mostly reflects the seasonal peak of *E. huxleyi*. It can be easily observed (Fig. 35) that N. Aegean's total coccosphere flux was considerably higher than those recorded in the Ionian and Cretan Seas. Such differences are basically related to the colder and less saline Black Sea water inputs through the Dardanelles straits enhancing the productivity of the water column of the North Aegean Sea compared to the other two areas, while the South Aegean sub-basin environment is considered as a ''typical oceanic margin'' (Lykousis et al., 2002). In addition, several rivers discharge into the N. Aegean Sea, mostly from the north Hellenic coast and from the east Turkish coast, such as Evros, Nestos and Strymon, and collectively constituting an important source of land-derived organic matter. These rivers supply the N. Aegean basin with freshwater, as the Black Sea surface water inputs through the Dardanelles do (Poulos et al., 1997; Roussakis et al., 2004). Thus, N. Aegean export production is constantly higher compared to the other two regions.

According to Triantaphyllou et al. (2004), the coccolithophore productivity pattern in the Cretan Sea, during 2001-2002, displays the maximum values in March, mostly due to the fertilization in the upper photic zone from the intrusion of the Transition Mediterranean Water from the east. The same pattern is also observed in the present study, referring to the year 2015. Aegean Sea waters are characterised as less oligotrophic and with less nutrients but more oxygen than the nearby Ionian and Levantine Seas (Becacos-Kontos 1977; Lykousis et al. 2002, Souvermezoglou et al. 1999). However, the Ionian Sea displays the same seasonal pattern with the export production maxima occurred during late winter-early spring (Fig. 35) which is in an agreement with the convective mixing period (Stavrakakis et al., 2013). This feature was also revealed in the previous time-series data from the same region (2010-2012). The maximum values of the primary productivity in both Cretan and Ionian Seas occurred during winter/spring convective mixing period (present study; Bosc et al., 2004;

D'Ortenzio and Ribera d'Alcala, 2009) and are in agreement with the relative increases in organic carbon and opal export and the simultaneous increase in the fluxes of planktonic biomarkers. (Gogou et al., 2016). Lithogenic inputs are a common feature that characterize both Ionian and Cretan Seas. The insertion of (bio)lithogenic material through the atmosphere is proven to be an important source of particles to the Ionian Sea (Malinverno et al., 2014).

The export production and fluxes in a north - south transect, are strongly dependent on the nutrient influx, the vertical mixing and/or the influence of episodic dust input events. These immense events affect the fluxes and control coccolithophore variability of the Ionian and Cretan Seas. According to Malinverno et al. (2014) dust input is believed to contribute to new production (Guerzoni et al., 1999; Herut et al., 2005; Krom et al., 2004; Schulz et al., 2012), even though its role in effectively fertilizing the surface waters of the eastern Mediterranean is under discussion (Eker-Develi et al., 2006; Herut et al., 1999; Krom et al., 1991, 2005). The particle flux in the ocean is mainly influenced by the upper water column biological processes as well as the aeolian and riverine inputs, which mostly correspond to coccolithophore production and Saharan dust input, concerning the E. Mediterranean Sea (Ziveri et al., 2000). In general, the Mediterranean Sea receives massive airborne plumes of desert dust from Sahara during the whole year (Bergametti et al., 1989; Moulin et al., 1997). According to Triantaphyllou et al. (2004), during winter/early spring episodes of intense vertical mixing take place that re-supply the euphotic zone with nutrients transferred from deeper waters. This leads to the fertilization of the photic zone, which is crucial for the Eastern Mediterranean, being depleted of nutrients and phosphorus-limited (Zohary and Robarts, 1998). However, the dust deposition might also contribute to higher P concentrations in the upper water column (Rutten et al., 2000). In P-controlled systems such as the eastern Mediterranean, *E. huxleyi* is expected to be the most abundant coccolithophore species, as it is an excellent phosphorus contender (Riegman et al., 1998, Ziveri et al., 2000). Moreover, according to Triantaphyllou et al. (2004) and Ziveri et al. (2000) the coccolithophore productivity pattern may possibly be enhanced by the Saharan dust input in the water column in the Cretan Sea and other parts of the Eastern Mediterranean. Differences between the dry and wet dust deposition can balance the fact that dust concentrations in the Mediterranean atmosphere and chlorophyll concentrations correlate negatively (Ziveri et al., 2000). In fact, actual dust deposition is affected by precipitation, as wet dust deposition contributes 65-80% to the total dust deposition (Molinaroli et al., 1993). As precipitation mainly characterise the winter period, it can be assumed that most of the yearly dust deposition in Ionian and Aegean Seas occurs in this period, where the maximum coccolithophore export production also takes place. It must be mentioned that these facts can only be verified by coccolithophore export production fluctuations, as there is a lack of dust data during the time interval of the present study.

Depth variability is also an important factor affecting the recorded fluxes due to the fact that coccolithophores are found in the euphotic zone. The sediment trap located in N. Aegean Sea (500m) is the shallowest compared to those from Ionian (2000 m) and Cretan (1550 m) Seas and it is expected to have higher flux values in shallower sediment traps (in agreement to our data showed in Fig. 35), as the surface water productivity is more realistically reflected up to these depths.

The inference of the comparison of the three different areas is a north to south decreasing coccosphere export production trend, being a result of the varied oceanographic regimes between the studied sites.
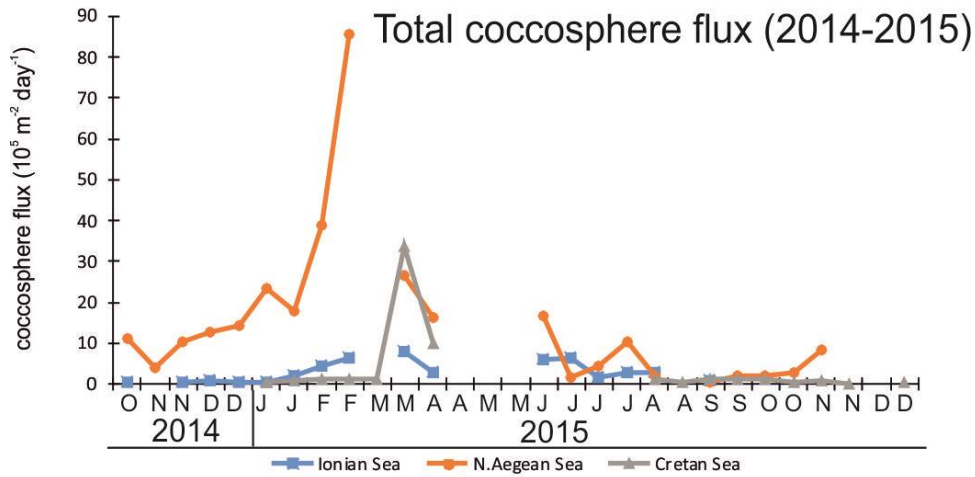
Fig. 35: Total coccosphere fluxes of the three investigated areas during 2014-2015

7. *Emiliania huxleyi* biometry: Case study of the Cretan and Ionian Seas

Sample images taken from scanning electron microscope were studied for the morphology of *E. huxleyi* coccolith, the size and the degree of calcification. On each coccolith 8 parameters were measured (Fig. 21): Coccolith length (CL), Coccolith width (CW), Element number, Element width, Tube width, Inner tube cycle thickness at the long axis (INTL), Relative tube width (= 2 x tube width/ CW) and Relative element width (= 2x element width/ CL). Relative tube width is a dimensionless and size independent parameter used to measure the degree of calcification variation (Young et al., 2014b).

Fig. 20: Morphometric parameters measured of an *Emiliania huxleyi* coccolith in distal shield view.

7.1. Results

7.1.1. Ionian Sea during 2015 (2000m water column depth)
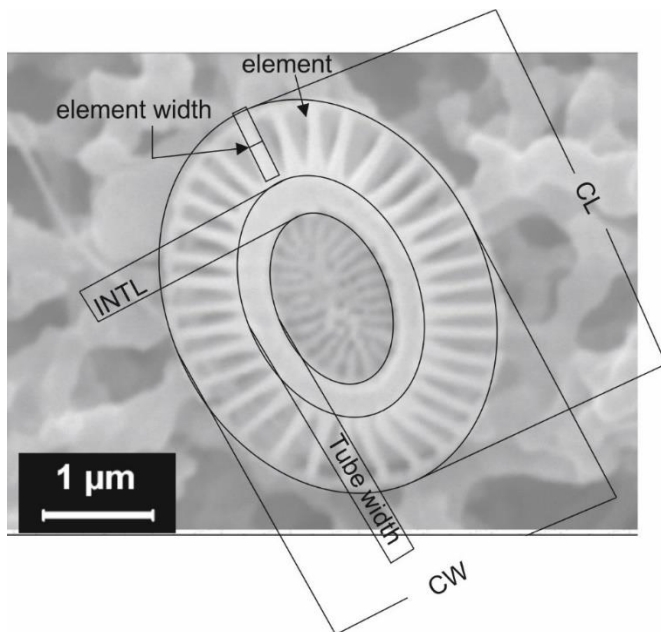
Sediment trap samples, from the depth of 2000 m in the SE Ionian Sea (NESTOR site), were studied for the morphology of *E. huxleyi* coccoliths. A seasonality in the morphological parameters was observed (Figs. 21-23). Coccolith width (CW) and coccolith length (CL) are characterised by monthly fluctuations (Fig. 21). The higher values for both CL and CW occurred in October (CL: 4.21 µm, CW: 3.59 µm; Fig. 21). In June, both parameters reached their minimum value (CL: 3.59 µm, CW: 3.02 µm; Fig. 21). In addition, the number of elements displayed also a seasonal pattern (Fig. 22), with a period of higher values (October 2014 - February 2015, except from November 2014) in which the highest value was recorded (October 2014; Fig. 22), and a second one with lower values (March 2015 – September 2015). The observed pattern of INTL, tube width, relative tube width, element width and relative element width (Fig. 23) demonstrated less degree of seasonality. The two morphological parameters with less seasonal variations were the element width and the relative element width. High values occurred in October (INTL: 0.65 µm, tube width: 0.59 µm, relative tube width: 0.32 µm; Fig.23), January (INTL: 0.63 µm, tube width: 0.58 µm, relative tube width: 0.34 µm; Fig. 23), February (INTL: 0.63 µm, tube width: 0.6 µm, relative tube width: 0.36 µm; Fig. 23), April (INTL: 0.6 µm, tube width: 0.57 µm, relative tube width: 0.34 µm; Fig. 23) and September 2015(INTL: 0.59 µm, tube width: 0.55 µm, relative tube width: 0.35 µm; Fig. 23). The lowest values for INTL, tube width and relative tube width occurred in June 2015 (INTL: 0.52 µm, tube width: 0.46 µm, relative tube width: 0.3 µm; Fig 23).

The mean values of the morphological parameter relative tube width (RTW) were plotted against the Sea Surface Temperature (SST) (Fig.24). It is observed that during the months with low SST, the relative tube width displayed higher values (February 2015:0.36, January 2015:0.34, March 2015:0.34; Fig. 24). Lower values of this parameter were recorded during June 2015 (0.3) and July 2015 (0.3) (Fig.24).

7.1.2. Cretan Sea during 2015 (1550 m water column depth)

Samples taken from a sediment trap in the Cretan Sea (1550 m water column depth) during the period January 2015-December 2015, were studied for the morphology of *E. huxleyi* coccoliths. A seasonal pattern in the morphological parameters was observed (Figs. 21-23). Coccolith length (CL) and coccolith width (CW) are characterised by monthly fluctuations (Fig. 21). The higher values for both CL and CW occurred in August 2015 (CL: 3.77 µm, CW: 3.19 µm; Fig. 21). Their minimum values were recorded with a month of delay; coccolith width minimum value occurred in September 2015 (CL: 3.63 µm, CW: 2.99 µm; Fig. 21) and coccolith length during October 2015 (CL: 3.61 µm, CW: 3.08 µm; Fig. 21). Moreover, the number of elements displayed also seasonal fluctuations (Fig. 22), with the highest value displayed in August 2015 (Fig. 22) and the lowest in April 2015 (Fig. 22). The observed pattern of INTL, tube width, relative tube width, element width and relative element width (Fig. 23) demonstrated much less seasonality. The two morphological parameters with less seasonal variations were the element width and the relative element width (Fig. 23). The maximum peak occurred in April 2015 (INTL: 0.50 µm, tube width: 0.47 µm, relative tube width: 0.30 µm; Fig.23). The lowest values for INTL, tube width and relative tube width occurred in September 2015 (INTL: 0.46 µm, tube width: 0.40 µm, relative tube width: 0.26 µm; Fig.23).

The mean values of the morphological parameter relative tube width (RTW) were plotted against the Sea Surface Temperature (SST) (Fig.24). As It is observed, the highest relative tube width value occurred in April 2015 (RTW: 0.30; Fig. 24), more or less in accordance with the lower SST values.

7.1.3. Cretan Sea during 2001 (1700 m water column depth)

Measurements on *Emiliania huxleyi* 's coccolith morphology have been carried out. The samples were taken from a sediment trap in the Cretan Sea at 1700 m depth and the sampling period was during 2001-2002. The studied morphological parameters display variations according to a seasonal pattern (Figs. 21-23). Coccolith width (CW) and coccolith length(CL) had no strong fluctuation during the year. Their higher values occurred in September (CL: 3.80 µm, CW: 3.15 µm) and March (CL: 3.81 µm, CW: 3.08 µm), followed by April (CL: 3.73 µm, CW: 3.08 µm) (Fig. 21). In December 2001, both parameters reached their minimum value (CL: 3.49 µm, CW: 2.81 µm). In contrast, the number of coccolith elements displayed the opposite pattern, with the major peak recorded in September (Fig. 22) and lower values in January and December 2001. The observed pattern of INTL was identical as recorded by tube width and relative tube width (Fig. 3), with higher values occurring in February 2001 (INTL: 0.6 µm, tube width: 0.55 µm, relative tube width: 0.38µm; Fig.23). After the February peak, values of these three parameters follow a descending trend till August, when they start to increase reaching a high peak in October (INTL: 0.55 µm, tube width: 0.53 µm, relative tube width: 0.34µm; Fig.23). Then, they start decreasing again. In contrast with all the other parameters, element width and relative element width do not show a seasonal pattern, as their values remain almost the same during the year.

The mean values of the parameter relative tube width (RTW) were plotted against the Sea Surface Temperature (SST) (Fig.24). The plot of this morphological parameter revealed that the highest values of relative tube width were recorded during the three colder months of the year, January (RTW: 0.37; Fig.24), February (RTW: 0.38; Fig.24) and March (RTW: 0.33; Fig.24). The lower value was displayed in August (RTW: 0.25; Fig.24), e.g. the second warmer month of the year (26 ^{o}C).

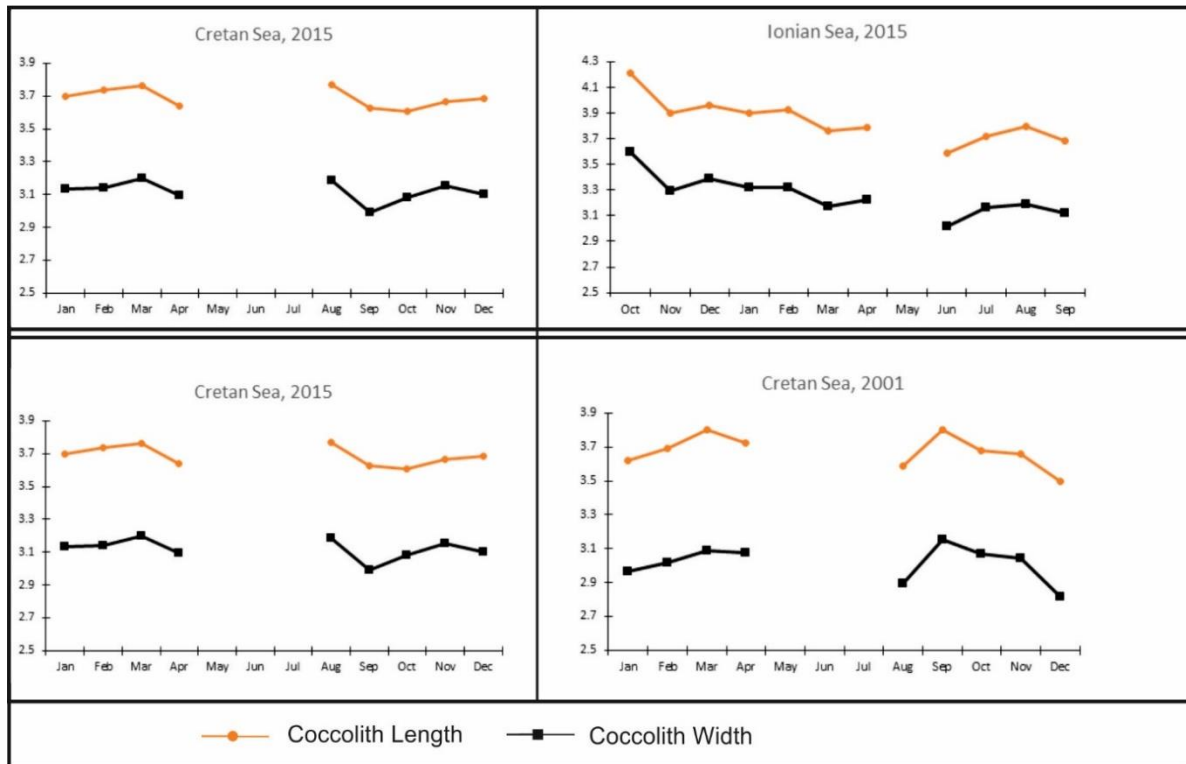Fig.21. Seasonal variations of *E. huxleyi* coccolith length and coccolith width in the Cretan (2001 & 2015) and Ionian (2015) Seas.
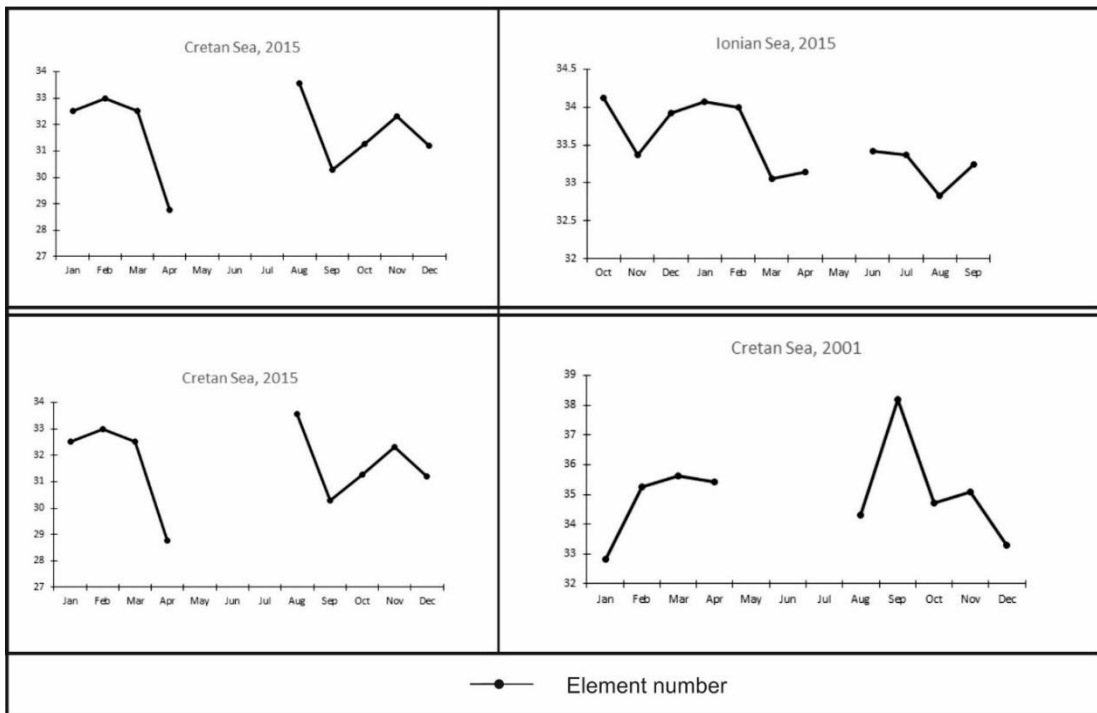
Fig. 22. Seasonal variations on the number of *E. huxleyi* coccolith elements in the Cretan (2001 & 2015) and Ionian (2015) Seas.
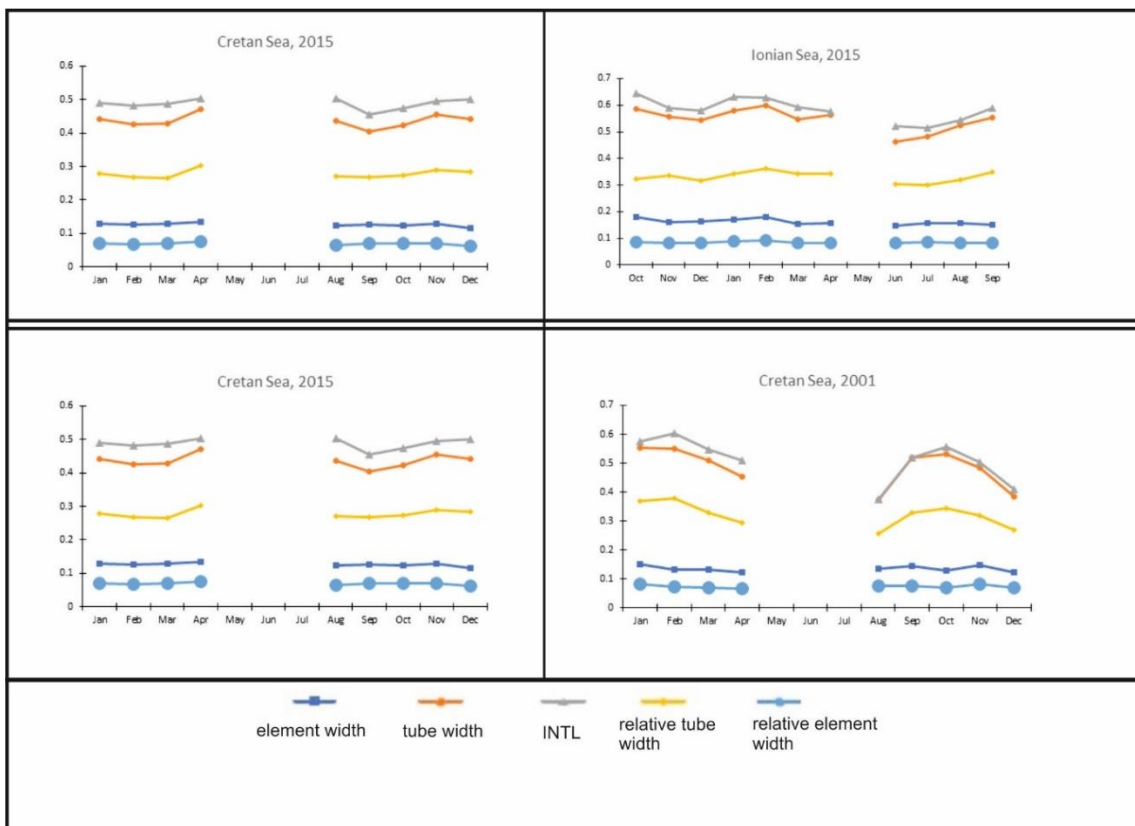

Fig. 23. Seasonal variations of *E. huxleyi* coccolith morphological parameters in the Cretan (2001 & 2015) and Ionian (2015) Seas.
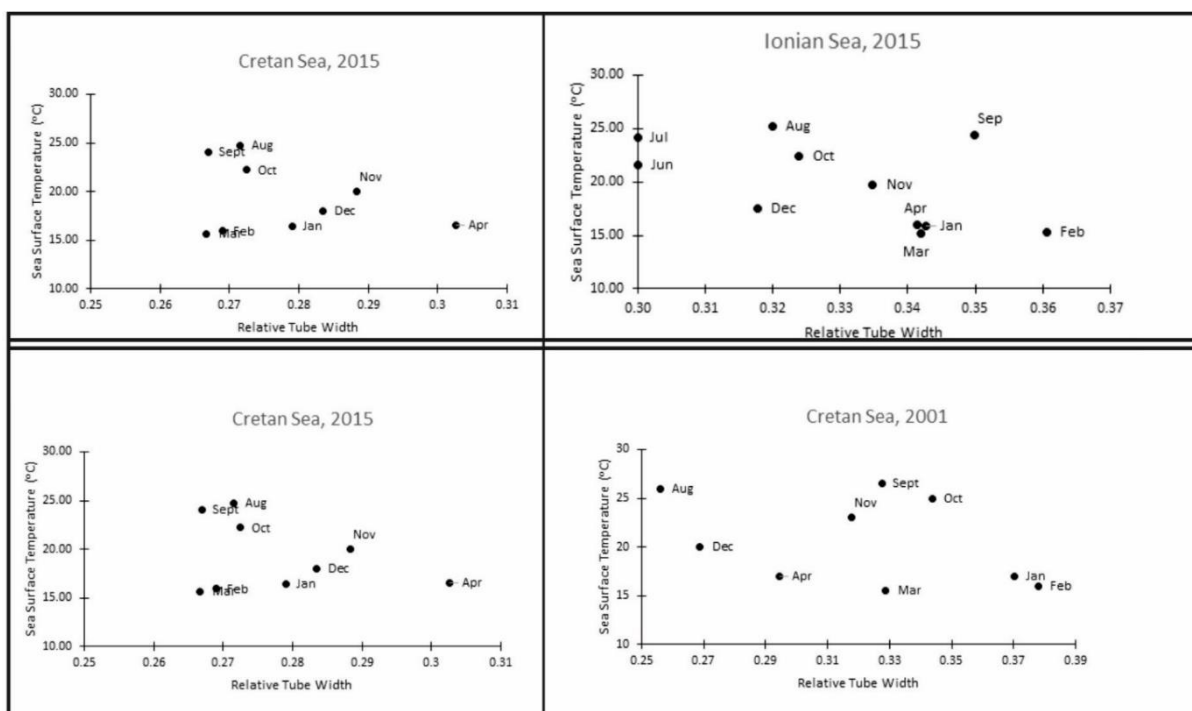
Fig.24. Bivariate plots between *E. huxleyi* coccolith relative tube width and Sea Surface Temperature (SST) in the Cretan (2001 & 2015) and Ionian (2015) Seas.

7.2. Biometry synthesis

A key question in global climate change research is how the ocean ecosystem will be affected by the uptake of anthropogenic CO_2 from the atmosphere in the near future (Meier et al., 2014; Bindoff et al., 2007; Kleypas et al., 2006; Kroeker et al., 2013). Calcifying organisms are the most possibly negative affected by the process of ocean acidification (OA) (Meier et al., 2014). The Mediterranean Sea has undergone acidification since the beginning of industrialization (Meier et al., 2014). The major calcifying phytoplankton group are coccolithophores and a reduction in coccolithophore calcium carbonate production may influence the global carbonate cycle and reduce organic carbon export (Gehlen et al., 2007; Wilson et al., 2012; Meier et al., 2014). Global studies on the variations of coccolith weight over the natural range of CO_2 concentrations in the world's oceans have shown that the increasing CO_2 may cause a decrease in coccolith weight and this effect can also be traced back in sedimentary archives of the last glaciation under natural CO_2 variations (Beaufort et al., 2011; Meier et al., 2014). The increasing atmospheric CO_2 partial pressure cause changes in the seawater carbonate chemistry can lead to decrease of *E. huxleyi* cellular PIC/POC ratio as well as to coccolith malformation (Riebesell et al., 2000) That may cause opposing effects on the marine carbon cycle, i.e. changes in ocean alkalinity, air/sea CO_2 exchange arising from changes in photosynthesis, calcification and shifts in the dominance of coccolithophores (Triantaphyllou et al., 2010; Rost and Riebesell, 2004). In addition, coccoliths that are produced under phosphorus limitation are heavier (bigger) than those produced under phosphorus repleted conditions (Paasche, 1998). Concerning the SE Mediterranean, such conditions are encountered, as it is known to be featured by an eastward increase in the N/P ratio, resulting in an increase in phosphorus limitation (Krom et al., 1991, 1992; Tselepides et al., 2000; Triantaphyllou et al., 2010).

A comparison of the eight morphological parameters [Coccolith length (CL), Coccolith width (CW), element number, element width, tube width, inner tube cycle thickness at the long axis (INTL), relative tube width (= 2 x tube width/ CW) and relative element width (= 2x element width/ CL)] of *E. huxleyi* coccolith between the Cretan and Ionian Seas displayed a fluctuating pattern during the year (Figs. 21-24). CL and CW reached their maximum values in the Ionian Sea during warm period (October 2015; Fig. 21). The same pattern is also observed during the same year (2015) in the Cretan Sea, where the maximum peak of coccolith length and width occurred in August (Fig. 21). That major peak of August during 2015 in the Cretan Sea comes a month earlier than the one recorded in the same area during 2001 (September; Fig. 21). During the exact same months as recorded for coccolith length and width, the number of elements displayed the maximum values in both regions and years (Ionian Sea 2015: October, Cretan Sea 2015: August and Cretan Sea 2001: September; Fig. 22). The five morphological parameters investigated; INTL, tube width, relative tube width, element width and relative element width, followed similar patterns in both Ionian and Cretan Seas (Fig.23), except from the element width and relative element width which did not display significant changes.

The relative tube width, which is a dimensionless and size independent parameter, is preferred among the other morphological parameters to be used as an index of the degree of calcification variation (Young et al., 2014b). Relative tube width (RTW) was plotted against SST (Fig. 24) during 2015, in both Ionian and Cretan Seas. As revealed result, RTW values in the Cretan Sea did not differentiate according to the SST pattern, in contrast to what was observed in the Ionian Sea. In the latter, higher values of relative tube width were recorded during the cold period of the year (January, February) and low values during the months with high SST (June, July) (Fig. 24). However, in the Cretan Sea, the highest value of this parameter was displayed one month later, i.e. during April 2015 and the rest of the months didn't demonstrate such diverse values in respect to the SST (Fig. 24). Apparently, even in this case, the RTW maximum peak occurred in one of the lowest SST months. RTW displayed higher values in the Ionian Sea than in the Cretan Sea during the year 2015 (Fig. 24). Therefore, the pattern observed in the Cretan and Ionian Seas during the year 2015 generally supports the negative correlation between calcification and SST, with heavy calcification in *E. huxleyi* coccolith observed during the cold period of the year. This fact is also suggested by recent culture experiments and field data, which showed that low temperatures suppressed coccolithophore cell division but induced cell enlargement and stimulated calcification (Sorrosa et al., 2005, Triantaphyllou et al., 2010). In particular, Triantaphyllou et al. (2010) documented a tendency of *E. huxleyi* coccospheres from water samples to express bigger coccoliths with heavier calcification in the central area, when the SST is lower. The increase in both coccosphere and coccolith size is observed during chlorophyll maxima, reflecting highest coccolithophore productivity; the observed pattern does not seem to be associated with the phosphate limitation effect or with salinity gradient (Triantaphyllou et al., 2010).

Relative tube width (RTW) demonstrated some differences among the years in the Cretan Sea. During 2001, seasonality was more distinct than 2015. As it is revealed in Fig. 24, during 2001 higher values of relative tube width occurred during the two months of lowest SSTs (February, January) and the lowest value in August, e.g. the month with the highest SST, in accordance with the observed pattern from eater samples (Triantaphyllou et al., 2010). In contrast, during 2015 relative tube width highest value have been shifted to April (Fig. 24), e.g. with a two months delay compared to 2001, but still in the cold period with low SSTs. Overall, the high values of relative tube width in 2015 are corresponding to overcalcified *E. huxleyi* coccoliths during the high coccolithophore productivity season, coupled with low SSTs (Karatsolis et al., 2016; Triantaphyllou et al., 2010). However, the distinct seasonality detected in 2001 RTW values is not clearly observed during 2015. Furthermore, relative tube width demonstrated higher values in 2001 in respect to 2015 (Fig. 24), implying a

reduction of the RTW by the years. A continuous decrease in the average coccolith weight of *E. huxleyi* from 1993 is also detected by Meier et al. (2014). This observed long-term decrease in coccolith weight is possibly a result of the changes in the surface ocean carbonate system (Meier et al., 2014). Changes in *E. huxleyi* calcification are caused by environmental variability, but the outcome of the comparison of Cretan sediment trap samples between 2001 and 2015 is not only restricted to the seasonality. The decrease in relative tube width agrees with the tendency of reduction in the average coccolith calcification, as implied by Meier et al. (2014), and probably is the consequence of a long-term ocean acidification. Moreover, Meier et al. (2014) pointed out that changes in *E. huxleyi* calcification may be linked to global change. In fact, as detected in our study, the shift of the maximum relative tube width values from February (in 2001) to April (in 2015) and the decrease of seasonal fluctuations of this parameter linked to calcification, is most likely an indication of the global warming and the resulting ocean acidification as this is imprinted on the eastern Mediterranean surface waters.

8. Conclusions

In this study, we presented a dataset of coccolithophore export production from three sediment-trap time series, located in the North Aegean, SE Ionian (NESTOR site) and Cretan Seas,
during at least a year-cycle. Moreover, the results of our research were compared to previous time series data from the same sediment traps. Due to relatively high coccosphere fluxes we could analyse the seasonal pattern of coccolithophore export production. The main outcomes of our study can be summarized with the following main conclusions:

• All sediment traps were characterised by seasonal pattern on their coccosphere fluxes.
• *Emiliania huxleyi* was the dominant species in all the investigated locations and total coccosphere flux seasonality was mostly represented by this species seasonal fluctuations.
• Coccosphere fluxes in the North Aegean Sea demonstrate an increasing trend during 2011-2015, as this is recorded at least within the time intervals of June - August, September and November.
• Coccosphere fluxes in the Ionian Sea expose an increasing trend during 2010-2015, as it is recorded at the various investigated time intervals during June 2010-September 2015. Based on observations of Gogou et al. (2016) high fluxes recorded during spring 2012 was an isolated event superimposed on the overall observed increasing flux trend.
• Coccosphere fluxes in the Cretan Sea follow an increasing trend during 2001-2015, as this is verified during the investigated time intervals.
• The inference of the comparison of the three different areas is a north to south decreasing coccosphere export production trend, as a result of the varied oceanographic regimes in the three investigated areas. However, absolute flux values show increasing tendencies through the years.
• Based on relative tube width parameter, there is a negative correlation between calcification and Sea Surface Temperatures, with heavy calcification in E. huxleyi coccolith observed during the cold period of the year (winter- early spring) in both Ionian and Cretan Seas.
• A decrease in relative tube width of E. huxleyi coccoliths was observed in a comparison over time

in the same sediment trap in the Cretan Sea. This fact may be linked to the long-term ocean acidification effects.

• In the sediment trap of the Cretan Sea, a shift from February (in 2001) to April (in 2015) was detected on the maximum value of E. huxleyi coccolith relative tube width, followed by decrease in the seasonal fluctuations of this parameter linked to calcification. This is most likely an indication of the global warming and the resulting ocean acidification as this is imprinted on the eastern Mediterranean surface waters.

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