Οικολογία και ποικιλότητα κοραλλιγενών βιοκοινοτήτων στο Αιγαίο

Ecology and diversity of coralligenous assemblages in the Aegean Sea

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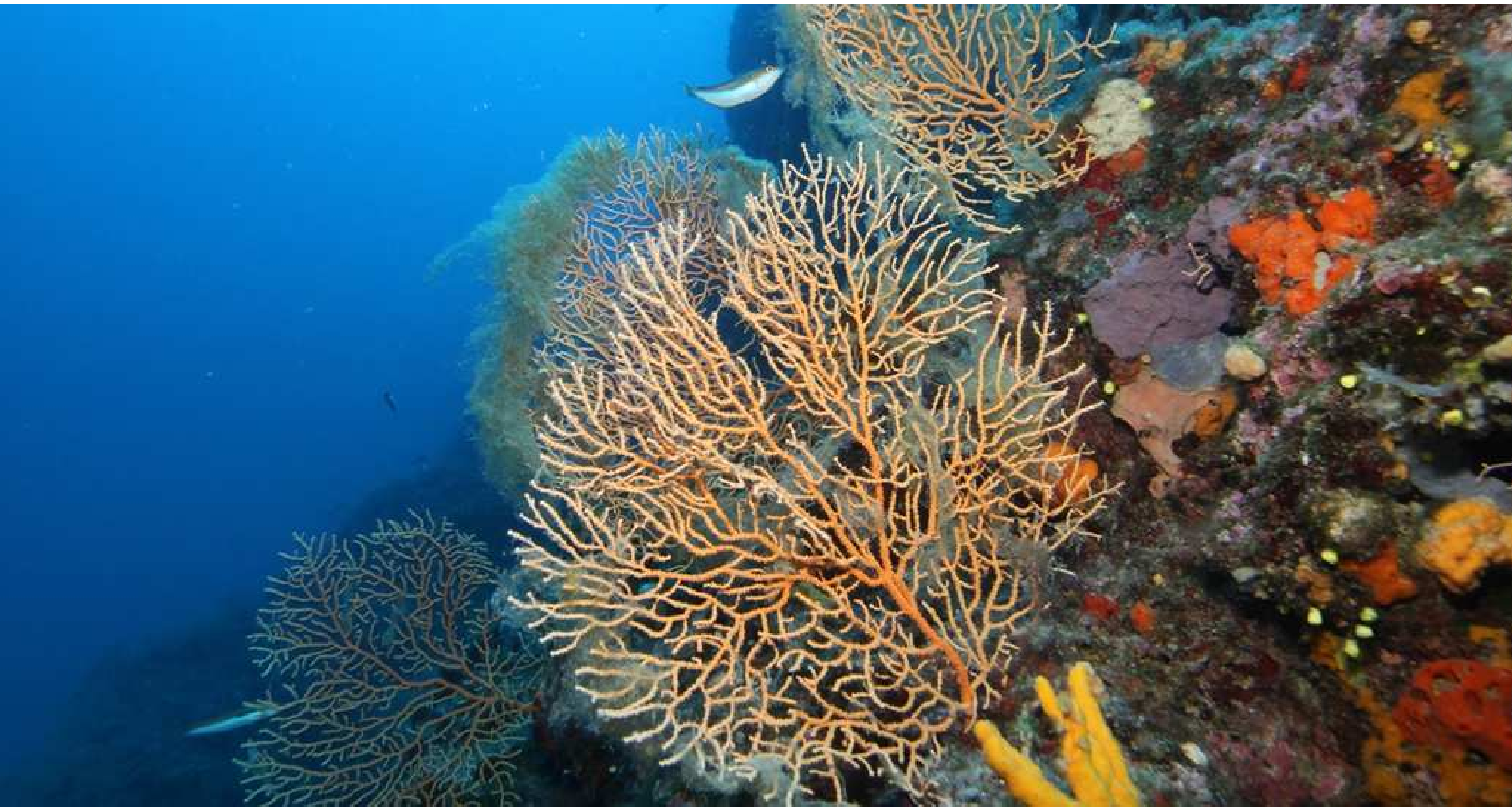
Maria I. Sini

Διδακτορική Διατριβή

PhD Thesis



Οκτώβριος 2015 | October 2015

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Ευχαριστίες

Η ολοκλήρωση του ερευνητικού αυτού έργου σηματοδοτεί ένα σταθμό στο συνεχόμενο ταξίδι μου στη θάλασσα. Όπως κάθε διδακτορική διατριβή έτσι και η δική μου υπήρξε μία μακριά και έντονη διαδρομή, γεμάτη με πολλαπλά πισωγυρίσματα, αμφισβητήσεις και απογοητεύσεις, αλλά και με πολλές ξεχωριστές στιγμές, εμπειρίες και συναισθήματα που με γέμισαν δύναμη και θάρρος, δίνοντας ολοένα και περισσότερο νόημα στη δύσκολή αυτή αποστολή στο βυθό. Φυσικά τίποτα απ' όλα αυτά δεν θα ήταν εφικτό χωρίς τους φίλους και συνεργάτες που βρέθηκαν στο πλάι μου και με στήριξαν ποικιλοτρόπως με τις γνώσεις, το ενδιαφέρον, την αγάπη, την αφοσίωση τους, συχνά ακόμα και με την τρέλα τους! Σας ευχαριστώ όλους από τα βάθη της καρδιάς μου για τον ξεχωριστό τρόπο που μου σταθήκατε και βοηθήσατε να γίνει αυτό το όνειρο πραγματικότητα.

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Τον Στέλιο Κατσανεβάκη, για τις πρόσφατες αλλά πολλά υποσχόμενες συνεργασίες μας.

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Τους τετράποδους φίλους μου. Τη Μωρέλια για τις βόλτες μας…την πιο γλυκιά υποχρέωση, που ιδίως τους τελευταίους μήνες ήταν το μόνο πράγμα που με έφερνε έστω και για λίγο έξω από το σπίτι και μακριά από τον υπολογιστή. Την Πινέλω, και την Πάνκο που εμφανίστηκε την τελευταία στιγμή αλλά η συμβολή της στη διάθεση και ψυχολογία μου στα τελευταία στάδια υπήρξε πολύ σημαντική.

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Η δουλειά αυτή είναι αφιερωμένη
Στον Δώρη
Στη Βαγγελιώ, στη Θάλεια, στο Βασίλη, στη Μωρέλια
Στο Διάπορο και σε όλα τα όμορφα πλάσματα του
Στη θάλασσα και σε όλους όσους ονειρεύονται δίπλα της και αγωνίζονται για την προστασία της

Photo Credits:

Thanos Dalianis: p.12 Fig 3f / p.85 Fig 7a

Vasilis Georvasileiou: p.12 Fig 3a / p.40 Fig 2a / p.67 left image

Panagiotis Papadellis: p.12 Fig 3d,e / p.15 Fig. 5a/ p.63 / p.85 Fig 7b / p.89

Elina Samara: p.12 Fig 3c

Cover image: Coralligenous assemblage featuring a *Eunicella cavolini* facies at Palios reef, NE Lesvos, Aegean (at a depth of 40 m). Photograph taken by Panagiotis Papadellis

All other photographs were taken by Maria Sini

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Ελληνικές Περιλήψεις – Greek Abstracts

Περίληψη

Οι κοραλλιγενείς βιοκοινότητες συγκροτούν έναν από τους πιο χαρακτηριστικούς τύπους οικοτόπου σκληρού υποστρώματος της Μεσογείου. Αναπτύσσονται σε σκιερές συνθήκες, και δημιουργούν ασβεστολιθικές δομές (κοραλλιγενείς σχηματισμοί) μέσω των αλλεπάλληλων αποθέσεων ενασβεστωμένων ροδοφυκών (κυρίως του γένους Corallinacea και Peyssonneliacea), καθώς και άλλων βενθικών οργανισμών όπως ανθόζωα, βρυόζωα, σπόγγοι και πολύχαιτοι. Οι κοραλλιγενείς βιοκοινότητες χαρακτηρίζονται από έντονη δομική πολυπλοκότητα, αποτελούν πυρήνες βιοποικιλότητας, και παρέχουν πληθώρα φυσικών αγαθών. Ωστόσο, είναι ιδιαίτερα ευπαθείς σε ανθρωπογενείς πιέσεις, καθώς πολλοί από τους οργανισμούς που συμμετέχουν στη δημιουργία και διατήρηση των βιογενών αυτών σχηματισμών είναι είδη μακρόβια, με αργούς ρυθμούς ανάπτυξης, και περιορισμένη δυνατότητα ανάκαμψης. Παρά την οικολογική τους σημασία, λίγα είναι γνωστά σχετικά με την παρουσία, την κοινοτική σύνθεση και την κατάσταση διατήρησης των κοραλλιγενών βιοκοινοτήτων. Η σχετική πληροφορία παραμένει εξαιρετικά αποσπασματική, και περιορίζεται κατά κύριο λόγο σε μελέτες που αφορούν στη ΒΔ λεκάνη της Μεσογείου. Η ανάγκη για συστηματική καταγραφή και αξιολόγηση της οικολογικής κατάστασης των κοραλλιγενών βιοκοινοτήτων διατυπώθηκε για πρώτη φορά στο «*Σχέδιο Δράσης για την προστασία των κοραλλιγενών και άλλων ασβεστιτικών βιο-σχηματισμών της Μεσογείου*» στα πλαίσια της Σύμβασης της Βαρκελώνης για τη Μεσογειακή Βιοποικιλότητα (UNEP-MAP-RAC/SPA 2008). Το Σχέδιο Δράσης ανέδειξε την αξία των κοραλλιγενών βιοκοινοτήτων, προσδιόρισε τις κύριες πιέσεις και δυνητικές απειλές, και τόνισε την ανάγκη συλλογής πρωτογενών δεδομένων αναφοράς σχετικά με την κατανομή, τη σύνθεση, την ποικιλότητα, και τη δυναμική τους.

Σκοπός της Διδακτορικής Διατριβής είναι η μελέτη της βιοποικιλότητας των κοραλλιγενών βιοκοινοτήτων του Αιγαίου, και η διερεύνηση της οικολογίας των πληθυσμών της κίτρινης γοργονίας *Eunicella cavolini*, ένα είδος που δημιουργεί μία από τις πλέον χαρακτηριστικές φάσεις της ευρύτερης κοραλλιγενούς βιοκοινότητας. Συγκεκριμένοι ερευνητικοί στόχοι της Διδακτορικής Διατριβής είναι: α) η καταγραφή της γεωγραφικής εξάπλωσης των κοραλλιγενών σχηματισμών και των πληθυσμών της *E. cavolini* στη Μεσόγειο, β) η μελέτη των χωρικών προτύπων δομής και ποικιλότητας των κοραλλιγενών βιοκοινοτήτων σε διαφορετικές περιοχές του Αιγαίου, γ) η διερεύνηση των δημογραφικών χαρακτηριστικών των πληθυσμών της κίτρινης γοργονίας *E. cavolini* στο Αιγαίο και σε άλλες περιοχές της Μεσογείου, και δ) η περιγραφή του ρυθμού ανάπτυξης και των χαρακτηριστικών αναπαραγωγής της *E. cavolini*. Για την επίτευξη των επιμέρους ερευνητικών στόχων, σχεδιάστηκε και υλοποιήθηκε μία σειρά από διαφορετικές, αλλά αλληλοσυνδεόμενες μελέτες, αξιοποιώντας κατάλληλες περιγραφικές και πειραματικές μεθοδολογικές προσεγγίσεις. Συγκεκριμένα, μελετήθηκαν 3 αντιπροσωπευτικές γεωγραφικές περιοχές του Αιγαίου (Πήλιο, Χαλκιδική και Λέσβος) μέσω επιστημονικής κατάδυσης SCUBA σε βάθη έως και 45 m. Για την επιτόπια καταγραφή των κοραλλιγενών βιοκοινοτήτων χρησιμοποιήθηκαν συστηματικά μεθοδολογικά πρωτόκολλα μέσω φωτογραφικών και οπτικών μεθόδων, και σχεδιάστηκαν νέα εργαλεία και λογισμικά για την εξαγωγή ποσοτικής πληροφορίας από τα βαθμονομημένα φωτογραφικά δείγματα. Συμπληρωματικές εργαστηριακές αναλύσεις βιολογικών δειγμάτων επέτρεψαν τον προσδιορισμό χαρακτηριστικών ειδών, και τη διερεύνηση των αναπαραγωγικών χαρακτηριστικών της *E. cavolini*. Τα δεδομένα αναλύθηκαν συνδιαστικά με στοιχεία από άλλες περιοχές της Μεσογείου μέσω συνεργασιών και

κοινών δημοσιεύσεων με ειδικούς επιστήμονες και Ερευνητικά Ινστιτούτα του εξωτερικού.

Η αποτύπωση της γεωγραφικής εξάπλωσης των κοραλλιγενών σχηματισμών (Κεφάλαιο 1) και των πληθυσμών της *E. cavolini* (Κεφάλαιο 3) σε Μεσογειακό επίπεδο έγινε βάσει πληροφορίας που συγκεντρώθηκε μετά από εκτενή επισκόπηση της διαθέσιμης βιβλιογραφίας και άλλων πηγών δεδομένων, καθώς και από προσωπικές παρατηρήσεις επιστημόνων και δυτών. Τα αποτελέσματα ανέδειξαν την ευρεία γεωγραφική εξάπλωση των κοραλλιγενών σχηματισμών στις περισσότερες περιοχές της Μεσογείου, και κυρίως στις βόρειες ακτές της λεκάνης (89% των σημειακών αναφορών παρουσίας). Παράλληλα, η εξίσου εκτεταμένη κατανομή των πληθυσμών της *E. cavolini* στο Αιγαίο και σε άλλες περιοχές της Β Μεσογείου, υπογραμμίζει τη σημασία διερεύνησης του συγκεκριμένου είδους και των κοραλλιγενών φάσεων που αυτό δημιουργεί, ως βάση για συγκριτικές μελέτες σε τοπικό και Μεσογειακό επίπεδο.

Για την μελέτη της δομής και ποικιλότητας των κοραλλιγενών βιοκοινοτήτων στο Αιγαίο (Κεφάλαιο 2) έγινε καταγραφή των μακροβενθικών κοινοτήτων που αναπτύσσονται σε φάσεις επικράτησης της κίτρινης γοργονίας *E. cavolini*. Συνολικά, διερευνήθηκαν έξι σταθμοί εντός τριών αντιπροσωπευτικών γεωγραφικών περιοχών (Πήλιο, Χαλκιδική και Λέσβος) σε βάθη έως και 35 m. Για τη συλλογή ποσοτικών δεδομένων εφαρμόστηκε μη-καταστρεπτική φωτογραφική μέθοδος με αυτόνομη επιστημονική κατάδυση. Η ποσοτική ανάλυση των φωτογραφικών δειγμάτων έδειξε την παρουσία σημαντικού αριθμού ειδών (100 είδη / ομάδες ειδών), με τα ενασβεστωμένα ροδοφύκη και τους σπόγγους να αποτελούν τις κυρίαρχες ομάδες σε επιφανειακή κάλυψη. Παρόλο που τα επίπεδα βιοποικιλότητας δεν παρουσίασαν σημαντικές χωρικές διαφοροποιήσεις, εντοπίστηκαν σημαντικές διαφορές στη σύνθεση των βιοκοινοτήτων μεταξύ σταθμών που βρίσκονται στην ίδια γεωγραφική περιοχή. Τα αποτελέσματα αναδεικνείουν τη δομική πολυπλοκότητα των κοραλλιγενών βιοκοινοτήτων και το ρόλο των τοπικών αβιοτικών και ανθρωπογενών παραμέτρων στη διαμόρφωσή τους. Επίσης οι κοραλλιγενείς βιοκοινότητες του Αιγαίου φαίνεται πως διαφοροποιούνται από τις αντίστοιχες κοινότητες της ΒΔ Μεσογείου και της Αδριατικής, κυρίως λόγω της απουσίας άλλων ειδών γοργονιών και μαλακών κοραλλιών σε βάθη ρηχότερα των 50 m, της χαμηλής αφθονίας διακλαδισμένων βρυόζωων, και του αυξημένου αριθμού σκληρακτινίων.

Η διερεύνηση των δημογραφικών χαρακτηριστικών της κίτρινης γοργονίας *E. cavolini* (Κεφάλαιο 4) στηρίχτηκε στη συλλογή πρωτογενών δεδομένων βάσει επιτόπιας οπτικής μεθόδου καταγραφής σε εφτά πληθυσμούς του Αιγαίου (2 στο Πήλιο, 3 στη Χαλκιδική, και 2 στη Λέσβο). Τα δεδομένα αναλύθηκαν συνδιαστικά με επιπλέον στοιχεία από έξι πληθυσμούς της ΒΔ Μεσογείου και έξι πληθυσμούς της Αδριατικής, τα οποία συλλέχθηκαν από συνεργάτες επιστήμονες του εξωτερικού. Εστιάζοντας στο ανώτερο βαθυμετρικό εύρος εξάπλωσης του είδους (νερά ρηχότερα των 40 m), καταγράφηκε το ανώτερο βαθυμετρικό όριο των πληθυσμών ανά σταθμό δειγματοληψίας, η πυκνότητα, η κατανομή ύψους, και η έκταση τραυματισμού των αποικιών. Για την διερεύνηση των χωρικών προτύπων πραγματοποιήθηκαν συγκριτικές αναλύσεις σε τρία επίπεδα (γεωγραφική περιοχή, τοποθεσία, σταθμός δειγματοληψίας). Επίσης, αξιολογήθηκε ο τύπος και η έκταση τραυματισμού των αποικιών υπό το πρίσμα διαφορετικών ανθρωπογενών πιέσεων. Σύμφωνα με τα αποτελέσματα, η δομή και η δυναμική των πληθυσμών του είδους *E. cavolini* παρουσιάζουν σημαντικές διαφοροποιήσεις μεταξύ γεωγραφικών περιοχών, οι οποίες εκφράζονται ως διαφορές στην κατανομή ύψους και πυκνότητας. Η κλίμακα της μελέτης αναδεικνύει την αξία διεξαγωγής ερευνών σε Μεσογειακό επίπεδο για την

καλύτερη κατανόηση της οικολογίας και της δυνατότητας ανάκαμψης των πληθυσμών ενός είδους υπό διαφορετικές περιβαλλοντικές συνθήκες και ανθρωπογενείς πιέσεις.

Καθώς ελάχιστα είναι γνωστά σχετικά με τον κύκλο ζωής της κίτρινης γοργονίας, το τελευταίο Κεφάλαιο της Διατριβής (Κεφάλαιο 5) διερευνά το ρυθμό ανάπτυξης και τα αναπαραγωγικά χαρακτηριστικά του είδους *E. cavolini* σε έναν πληθυσμό του ΒΑ Αιγαίου (Κεφάλαιο 5). Η ανάπτυξη των γοργονιών ποσοτικοποιήθηκε εφαρμόζοντας μία νέα, μη-καταστρεπτική μέθοδο που βασίζεται στην επαναληπτική φωτογράφηση συγκεκριμένων αποικιών σε βάθος χρόνου, και στην ανάλυση των φωτογραφικών δειγμάτων με το λογισμικό photoQuad για την ποσοτικοποίηση επιλεγμένων μορφολογικών χαρακτηριστικών (ύψος, πλάτος, συνολική επιφάνεια αποικίας). Επιπλέον, η συλλογή βιολογικού υλικού επέτρεψε τη διερεύνηση των αναπαραγωγικών χαρακτηριστικών του είδους. Τα αποτελέσματα έδειξαν ότι η *E. cavolini* έχει αργή σωματική ανάπτυξη (1.4 cm σε ύψος ανά έτος). Είναι είδος γονοχωριστικό, βασίζεται κατά κύριο λόγο στην εγγενή, αμφιγονική αναπαραγωγή, και φτάνει σε αναπαραγωγική ωρίμανση όταν οι αποικίες έχουν ύψος περίπου 20 cm. Ο αναπαραγωγικός κύκλος παρουσιάζει σχεδόν ταυτόχρονη απελευθέρωση θηλυκών και αρσενικών γαμετών ή/και λαρβών, και φαίνεται να ολοκληρώνεται κατά τα τέλη άνοιξης με αρχές καλοκαιριού.

Summary

Coralligenous assemblages form one of the most typical hard substrate habitat types of the Mediterranean. They develop biogenic structures (coralligenous formations) through the multilayered accumulation of encrusting coralline algae (especially of the genus Corallinacea and Peyssoneliacea) and the calcareous remains of other sessile organisms, such as anthozoa, bryozoa, sponges and polychaetes, which grow under dim light conditions. They are characterized by increased structural complexity and species diversity, and serve as reservoirs of natural resources. However, they are particularly vulnerable to anthropogenic pressures, as the majority of the habitat-forming species are long-lived with slow growth and low recovery capacity. Despite their high ecological and economic value, there are still important knowledge gaps regarding the spatial distribution, community composition, and conservation status of coralligenous assemblages in different parts of the Mediterranean. Available information is particularly fragmented and mainly comes from studies conducted in the NW Mediterranean. The need for the systematic assessment and rigorous evaluation of coralligenous assemblages was for the first time highlighted through the adoption of the “Action Plan for the conservation of coralligenous and other calcareous bio-concretions in the Mediterranean Sea” in 2008 in the framework of the Barcelona Convention for the Mediterranean Biodiversity. The Action Plan acknowledged the value of coralligenous assemblages, identified the main pressures and threats, and underlined the necessity for the collection of reference data regarding their distribution, structure, diversity, and dynamics.

The general scope of the Thesis is the investigation of biodiversity patterns of coralligenous assemblages in the Aegean Sea, and the ecology of the yellow gorgonian *Eunicella cavolini*, a species whose populations form typical coralligenous facies. Specifically, the Thesis aims to: a) document the geographical distribution of coralligenous formations and *E. cavolini* populations across the Mediterranean, b) investigate spatial patterns in community composition and diversity of coralligenous assemblages found in different parts of the Aegean Sea, c) explore the demographic characteristics of *E. cavolini* populations in the Aegean and other parts of the Mediterranean, and d) study the growth rates and reproductive characteristics of *E. cavolini*. To achieve these research objectives, a number of inter-related studies were designed and conducted, using both descriptive and experimental methodological approaches. Three representative geographic localities of the Aegean Sea were investigated (Pelio, Chalkidiki and Lesvos) through scientific SCUBA diving at depths up to 45 m. Standardised protocols were used for the *in situ* assessment of coralligenous assemblages via photographic and visual methods, while new sampling tools and image analysis software were designed and developed for the quantification of calibrated image samples. Complementary laboratory analysis of biological samples enabled the identification of characteristic species and the investigation of *E. cavolini* reproductive characteristics. The findings regarding the Aegean Sea were selectively combined with data from other regions of the Mediterranean through shared publications and collaborative works with specialist scientists and European research Institutes.

The depiction of the geographic distribution of coralligenous assemblages (Chapter 1) and *E. cavolini* populations (Chapter 3) at a Mediterranean scale was achieved through a thorough review of available literature and other data sources, in combination with information provided by expert scientists and divers. The results indicate that

coralligenous formations have a widespread distribution across most parts of the Mediterranean, and particularly at the northern areas of the basin (89% of point data representing presence). At the same time, the similar and extensive geographic distribution of *E. cavolini* populations in the Aegean Sea and the northern Mediterranean coasts highlights the value of investigating this particular species, and the associated coralligenous facies, as a basis for comparative studies across the basin.

For the study of community structure and diversity of coralligenous assemblages in the Aegean Sea (Chapter 2), an assessment of the macrobenthic assemblages found within the *E. cavolini* coralligenous facies was carried out. Overall, six sites were investigated within three representative geographical localities (Pelio, Chalkidiki and Lesvos) at depths up to 35 m. Data were collected based on a standardised, non destructive, photographic method using scientific SCUBA diving. The quantitative analysis of photographic samples indicated that coralligenous assemblages of the Aegean Sea host a large number of conspicuous sessile species (100 species / groups of species), with encrusting coralline algae and sponges being the dominant groups in terms of area cover. Although biodiversity patterns showed no significant spatial differentiation, community composition was found to be statistically different at the level of sites found within the same geographic locality. These results highlight the structural complexity of coralligenous formations and the particular role of local abiotic and anthropogenic factors in the shaping of assemblages. Furthermore, despite the overall similarity to their NW Mediterranean and E Adriatic counterparts, coralligenous assemblages of the Aegean Sea presented several peculiarities, such as the lack of other gorgonian and soft coral species in waters shallower than 50 m depth, the low abundance of arborescent bryozoans, and the higher number of scleractinian species.

The demographic characteristics of *E. cavolini* (Chapter 4) were investigated based on data collected in situ through visual census in seven distinct populations of the Aegean Sea (2 in Pelio, 3 in Chalkidiki, and 2 in Lesvos). The Aegean records were then combined with additional data provided by fellow scientists from six populations of the NW Mediterranean and six populations of the E Adriatic Sea. Focusing on the upper bathymetric range of the species (i.e. waters shallower than 40 m), at each sampling station data collected regarded: the upper depth limit of each population, colony density, height, and extent of injuries. In order to investigate spatial patterns, a three level statistical analysis was carried out (i.e. based on geographic region, locality and site). According to the results on colony height and density, the structure and dynamics of *E. cavolini* populations showed several differences at the level of geographic region. Besides, disturbance levels, as a function of extent and type of injury were evaluated in relation to past or present anthropogenic pressures. The study highlights the value of basin scale studies in the better understanding of the ecology and recovery capacity of a species thriving across variable gradients of environmental conditions and anthropogenic pressures.

Up until now little is known about the life history traits of the yellow gorgonian. For this reason the last Chapter (Chapter 5) examines the growth rates and reproductive characteristics of an *E. cavolini* population thriving in a coralligenous assemblage at the NE Aegean Sea. Morphometric characteristics and growth rates of colonies were assessed based on an original non-destructive photographic method which enables the quantification of different colony features (height, width, and surface area) using the photoQuad software. The additional collection of biological material enabled the investigation of the reproductive characteristics of the species. Results showed that *E. cavolini* has a slow somatic growth (1.4 cm per year), and colonies reach sexual maturity at approximately 20 cm height. It is a dioecious, gonochoric species, which primarily depends on sexual reproduction for population growth and maintenance. The reproductive cycle culminates with the simultaneous release of female and male gametes and/or larvae, some time between the end of spring and the beginning of summer.

General Introduction

Coastal marine ecosystems are among the most productive and diverse systems globally, and play a crucial role in the provision of several goods and services to humans, such as food, coastal protection, leisure activities and tourism (Agardy et al. 2005; Barbier et al. 2011). Today, these ecosystems are being altered and restructured at an unprecedented rate, due to a wide range of human-induced pressures that have serious consequences on biodiversity and ecosystem functioning (Thrush & Dayton 2002; Micheli & Halpern 2005; Lotze et al. 2006; Jackson 2008).

In the Mediterranean Sea, historical overfishing, habitat loss, and pollution are reducing the complexity of underwater seascapes and food webs, while the introduction of invasive species induces changes in biodiversity patterns and community structure (Lotze et al. 2006; Airoldi & Beck 2007; Coll et al. 2010; Zenetos et al. 2012; Katsanevakis et al. 2014). These impacts are further exacerbated by the superimposed modifications that are brought about by global climate change, including seawater temperature rise, acidification, and changes in water circulation (Hughes et al. 2003; Harley et al. 2006; Lejeusne et al. 2010; Raitsos et al. 2010; Martin & Gatusso 2009; Cerrano et al. 2013). The effects of these disturbances are particularly deleterious for benthic sessile organisms that are unable to relocate, and especially for species with long generation times that have little potential to adapt in response to rapid changes (Lasker & Coffroth 1999; Solan et al. 2004). Furthermore, the lack of historical data preceding large-scale human impacts restricts the proper evaluation of present conditions (Sala et al. 2011), while conservation plans are effectively rendered inadequate due to poor knowledge regarding the current distribution of habitats and species, and the often arbitrary classification of habitat types (Fraschetti et al. 2008; Claudet & Fraschetti 2010).

In this context, it is critical to document the spatial distribution of habitats and species, and conduct systematic research on diversity patterns and population dynamics along environmental gradients (Thomas et al. 2004; Doney et al. 2012). Such information offers valuable reference data, upon which to develop scientifically sound conservation plans and mitigation strategies (Claudet & Fraschetti 2010; Levin et al. 2014).

1. Mediterranean coralligenous formations

1.1 Definition and structure

Mediterranean coralligenous formations (or coralline reefs) are biogenic structures that develop on hard substrates under dim light conditions, and represent one of the most important endemic marine habitats of this semi-enclosed sea (Ballesteros 2006). They develop at depths ranging approximately from 20 to 150 m, where the relatively stable conditions of light, temperature, current intensity and salinity, foster the extensive growth of encrusting coralline algae and other slow-growing sciaphilous organisms (Laborel 1987). Over time, the multi-layered accumulation of calcareous deposits is maintained and modulated by the dynamic interplay of the bio-construction and bio-erosion processes, caused by biotic activity and the natural weathering of the system (Cerrano et al. 2001). This results to the build up of complex biogenic structures (bioherms) that contain patchworks of microhabitats and host a rich diversity of species assemblages (**Fig 1**).

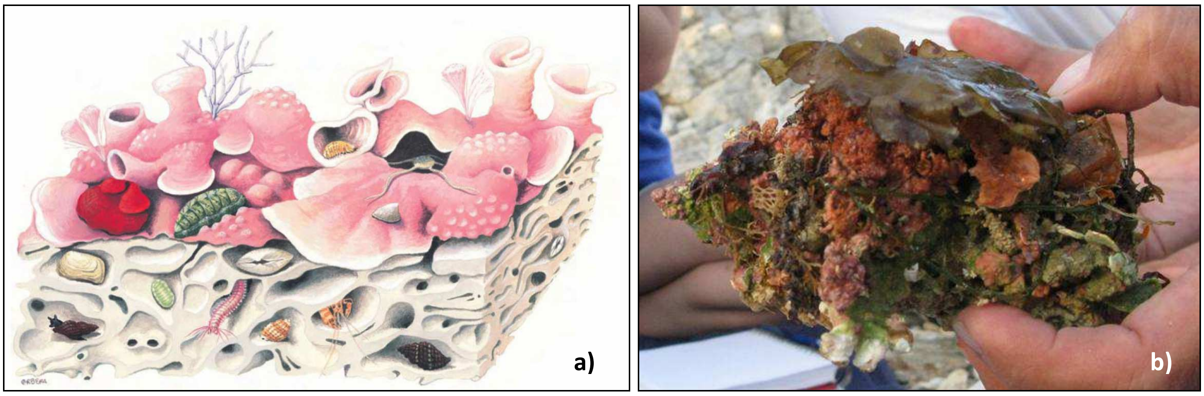

Fig 1. Basal layer of coralligenous assemblage. a) Diagrammatic section of a coralligenous formation, illustrating the increased small-scale complexity and the different microhabitats (adopted from Ballesteros 2006, drawing by J. Corbera). b) Photograph of a corresponding small block of coralligenous basal layer collected from a vertical wall in the NE Aegean.

Although coralligenous formations may occur as enclaves in other habitat types (e.g. cracks and crevices of shallow rocks or in *Posidonia oceanica* rhizomes), two main morphotypes have been described to date: a) *Rims* or *coralligenous of the littoral rock*, which develop on steep cliffs, isolated rocks, and at the entrances of submarine caves, and b) *Banks* or *platform coralligenous* which grow on concretionary detritic substrates or rocks of low inclination, that are usually surrounded by sedimentary substrates (Laborel 1961; Pérès & Picard 1964; Sarà 1969, **Fig 2**). Accumulation rates of biogenic material are generally low (0.006 – 0.83 mm yr^{-1}), while the thickness of coralligenous formations ranges from approx. 20 cm to >2 m in rims, and from 0.5 to 4 m in platforms (Sartoretto et al. 1996). Coralligenous formations are characterised by increased complexity both in physical structure and community composition, and encompass a broad range of species assemblages and ecological facies[1] that are collectively referred to as coralligenous assemblages (**Fig 3**).

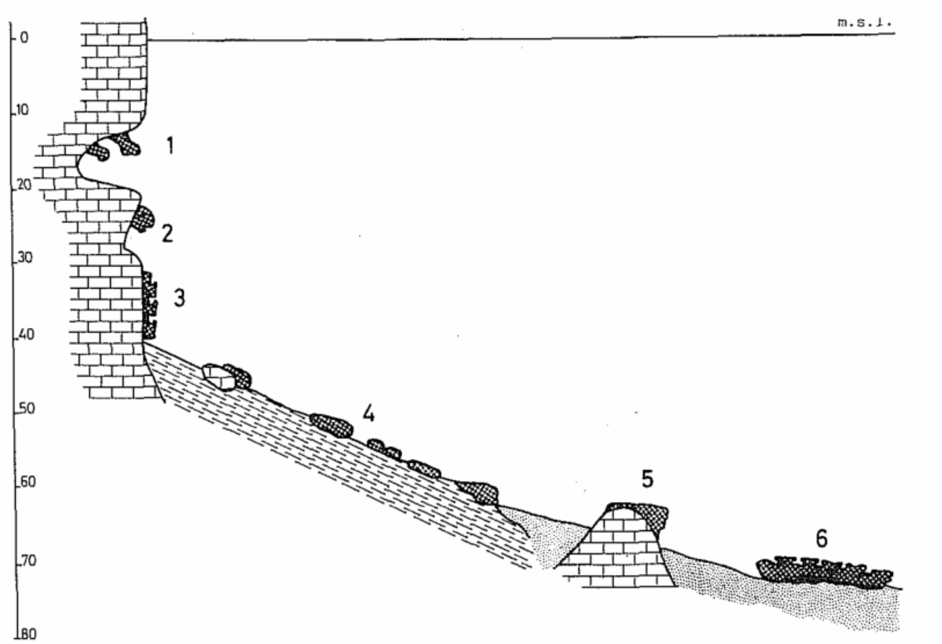

Fig 2. Different types of coralligenous formations: 1) at the entrance of a shallow cave, 2) at an overhang, 3) on a vertical wall, 4) on crumbling rocks from vertical walls, 5) over rock soles/blocks, 6) on concretionary (detritic) substrate. Types 1–5 belong to the morphotype *rims* or *coralligenous of the littoral rock*; type 6 is referred to as *platform* or *bank* coralligenous. The vertical axis indicates depth in meters, and the horizontal black line (m.s.l.) denotes mean sea level (diagram adopted from Ros et al. 1985, redrawn from Laborel 1961).

The term "coralligenous" (in French coralligène), which derives from the Greek words "korali" and "genesis" (meaning coral-producing), was first introduced by Marion (1883) who described the coarse gravel biogenic substrates off Marseille that were rich in red coral (*Corallium rubrum*, Linnaeus, 1758). However, the term soon lost its original meaning, as it was incorporated in bionomic studies that focused on the community composition of hard substrates; specifically, those that presented a lower layer of encrusting coralline algae and a large variety of conspicuous sessile animal species, regardless the presence of red coral (e.g. Feldmann 1937; Pérès & Picard 1964; True 1970; Boudouresque 1973, Hong 1980; Ros et al. 1985; but see Ballesteros 2006 for a full review).

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[1] Facies: aspect exhibited by a biocenosis when the local predominance of certain biotic and abiotic factors causes the prevalence of either one or a very small number of animal species (UNEP-MAP-RAC/SPA, 2006).

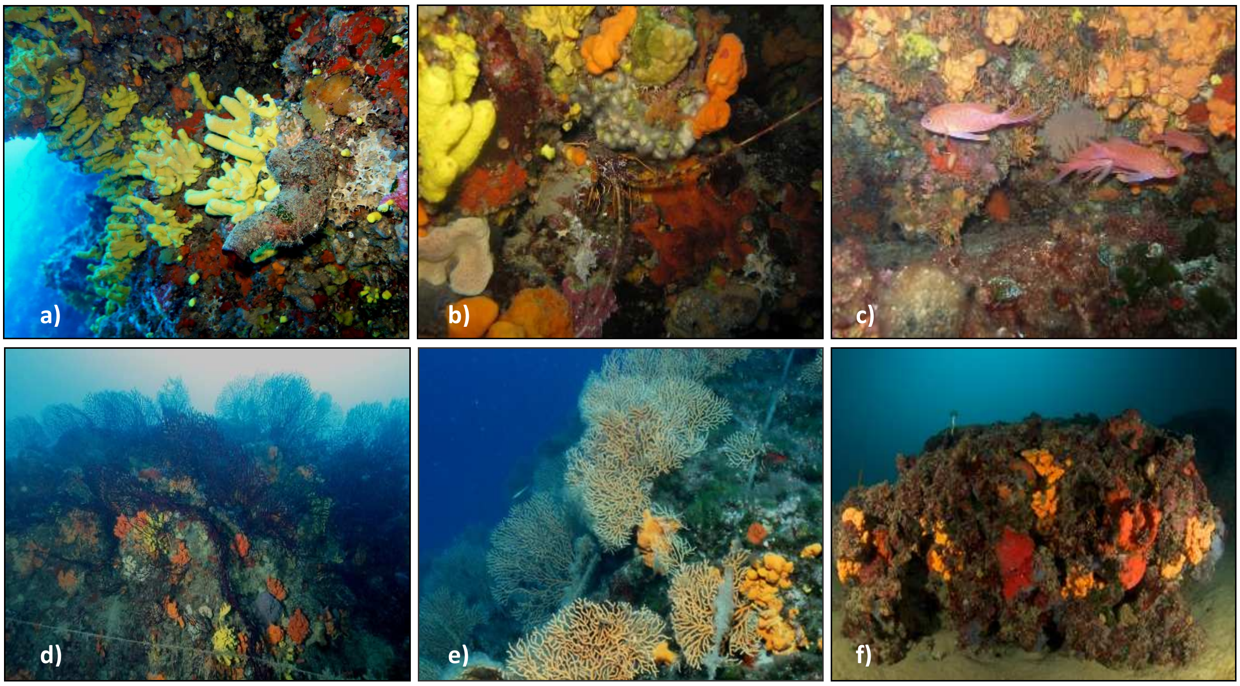

Fig 3. Coralligenous assemblages of the Aegean Sea: a) cave entrance, b) negatively inclined wall, c) overhang, d) cliff with *Paramuricea clavata* facies, e) wall with *Eunicella cavolini* facies, f) outcrop surrounded by sand.

Whereas encrusting coralline algae –primarily of the genus Corallinacea and Peyssonneliacea– are the main builders, animal species also play an important role in the creation and maintenance of coralligenous formations, either by contributing to the bio-construction (e.g. bryozoans, serpulid polychaetes, scleractinian corals) and bio-erosion processes (e.g. sponges and molluscs), or by providing secondary substrate for other species to settle (e.g. gorgonians and sponges), **Fig 4**. Other abundant taxa include several non-calcified algal species, as well as a large number of molluscs, annelids and crustaceans, which dwell in the cavities of coralligenous formations. Overall, coralligenous assemblages host more than 1.666 species (Ballesteros 2006). However, this figure is most likely an underestimate, considering the high structural variability and complexity of the formations, the low number of studies outside the NW Mediterranean, the presumably large number of cryptic species that have not been recorded to date, and the general discrepancies confounding the taxonomic status of several taxa, especially coralline algae (e.g. Ballesteros 2006; Kaleb et al. 2011; Bertollino et al. 2013; Rindi et al. 2014; Calcinai et al. 2015; Peña et al. 2015). Nevertheless, the Ballesteros (2006) estimate corresponds to approximately 10% of the known Mediterranean marine species, and renders coralligenous as one of the top marine biodiversity hotspots in the basin, alongside the *P. oceanica* meadows (Boudouresque 2004; Coll et al. 2010).

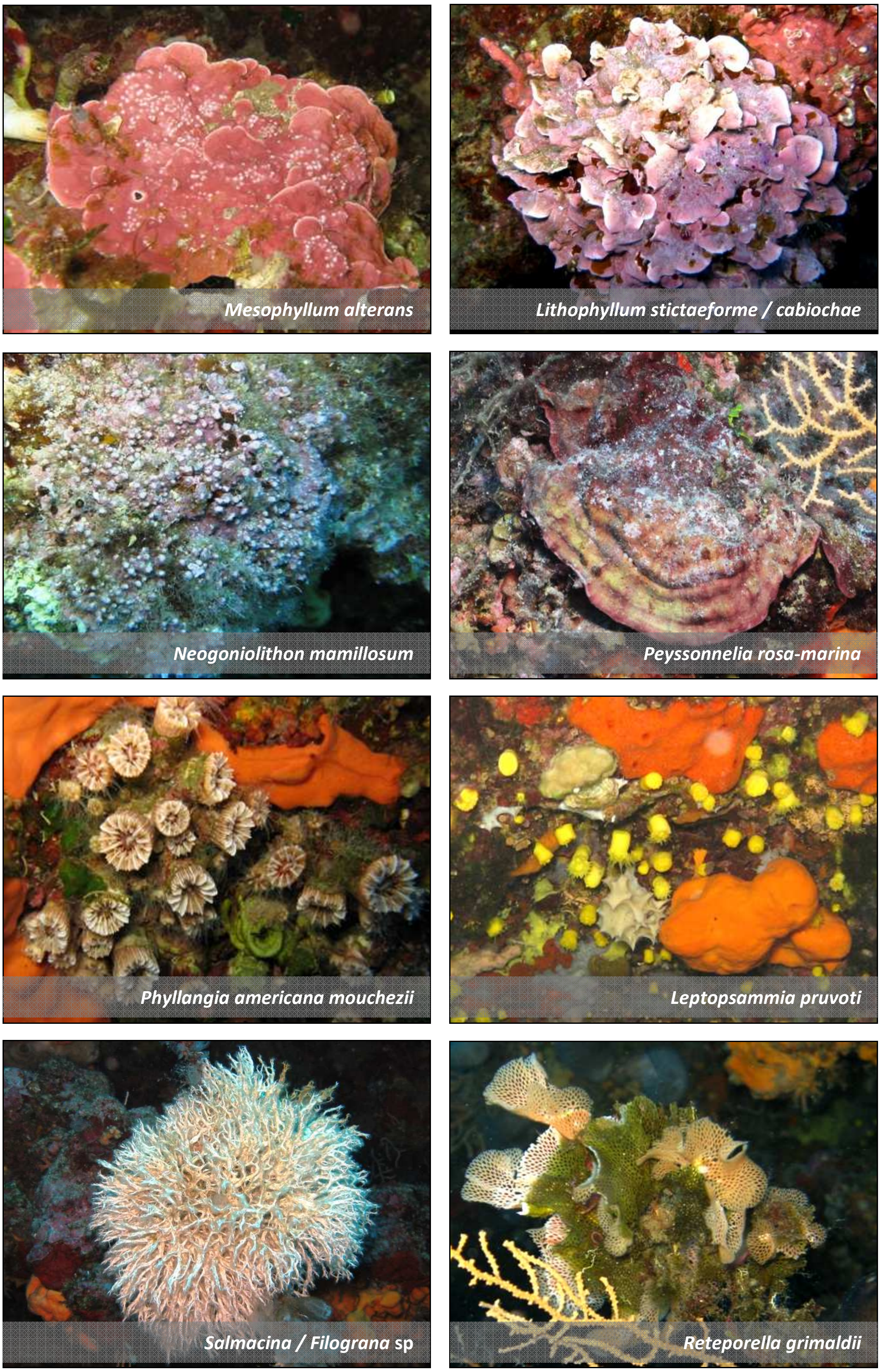

Fig 4. Common algal and animal bio-constructors of Mediterranean coralligenous bioherms.

Furthermore, coralligenous assemblages host several endemic, endangered and commercially important species, and create impressive seascapes that represent a focal attraction for diving tourism (e.g. Boudouresque 2004; Ballesteros 2006; Giaccone 2007). A key aspect of coralligenous assemblages however, is that the majority of habitat-forming species present slow growth, and thereby low resilience to imminent threats and disturbances (e.g. Sartoretto et al. 1996; Garrabou & Ballesteros 2000; Garrabou & Zabala 2001; Marschal et al. 2004; Teixido et al. 2011a).

1.2 Distribution and natural variability

Coralligenous assemblages occur across most parts of the Mediterranean Sea, with the exception of the southern and eastern coasts of the Levantine basin (see Chapter 1). While light intensity is the primary factor determining the bathymetric extent of coralligenous (Ballesteros 2006), a wide range of environmental parameters, such as temperature, productivity, turbidity, current intensity, and sedimentation rates, also affect community composition across different spatial scales (e.g. Morganti et al. 2001; Piazzi et al. 2004; Balata et al. 2005, 2006; Virgilio et al. 2006; Holon et al. 2014). For example, coralligenous formations in the cold and highly turbid waters off Marseille develop even at depths of 15 m or shallower, and present a high abundance of large suspension feeders, such as gorgonians. On the contrary, the upper depth limit of coralligenous reefs in the transparent oligotrophic waters of the Balearic Islands is displaced to waters deeper than 40 m, while the primary suspension feeders are sponges, bryozoans, and small hexacorals (Zabala & Ballesteros 1989). At a more local scale, coralligenous assemblages display a generalised pattern of zonation in response to light intensity, according to which algal species have a higher area cover in shallower or well-lit surfaces, while animal species predominate at deeper or darker areas (Ros et al. 1985; Cocito et al. 2002; Garrabou et al. 2002a; Virgilio et al. 2006). As previously mentioned however, coralligenous frameworks present high structural heterogeneity and support the coexistence of several microhabitats. For this reason, environmental factors and associated biotic interactions can change abruptly at the microscale level (e.g. due to small differences in substrate inclination), while smooth gradients are generally lacking. Spatial variability of community composition is thereby commonly reported to be higher at small scales (i.e. within site, Fredeghini et al. 2000; Cocito et al. 2002; Balata et al. 2006; Virgilio et al. 2006) rather than at larger geographical scales. In the latter, coralligenous assemblages are reported as relatively homogenous, at least with respect to their algal components (Piazzi et al. 2004; 2014). On the other hand, temporal variability is generally low, and is mainly related to differences in the seasonal abundance of soft algal species (Piazzi et al. 2004; Balata et al. 2006). This temporal stability is partially due to the fact that coralligenous assemblages develop in deep waters under relatively constant environmental conditions (Garrabou et al. 2002a; Virgillio et al. 2006), while the majority of constituent organisms have slow population dynamics (Teixido et al. 2011a).

2. Gorgonians

Gorgonians are important structural elements of the Mediterranean sublittoral seascape. Out of the approximately twenty species known to occur in the Mediterranean (Carpine & Grasshoff 1975; Vafidis et al. 1994), three species commonly develop distinct facies within the coralligenous assemblages (Ballesteros 2006; UNEP-MAP-RAC/SPA 2006); namely, *Eunicella cavolini* (Koch, 1887), *E. singularis* (Esper, 1971), and *Paramuricea clavata* (Risso, 1826), **Fig 5**. Although not amongst the primary bio-constructors of coralligenous formations, their three-dimensional tree-like colonies add to the complexity of the assemblages, and enhance diversity and biomass by providing additional surface for shelter and growth of other species (True 1970; Cerrano et al. 2010; Carvalho et al. 2014; Cúrdia et al. 2015). Gorgonians also play a key role as ecosystem engineers (*sensu* Jones et al. 1994), as they modulate the structure of the assemblages by modifying current flow, sedimentation rates, and shading levels (Ponti et al. 2014). Similar to other corals, Mediterranean gorgonians are long-lived species with slow growth, delayed maturity, low or infrequent recruitment success, and reduced post-settlement survival (e.g. Coma et al. 1998; Torrents et al. 2005; Linares et al. 2007).

Fig 5. Gorgonian species forming typical facies within coralligenous assemblages. a) *Eunicella cavolini*, b) *Eunicella singularis,* and c) *Paramuricea clavata*

The slow population dynamics, combined with the fragile structure of colonies, render gorgonian populations particularly susceptible to ongoing disturbances that threaten the integrity of gorgonian forests and coralligenous assemblages as a whole (e.g. Harmelin & Marinopoulos 1994; Bavestrello et al. 1997; Cerrano et al. 2000; Coma et al. 2004; Garrabou et al. 2009; Cebrian et al. 2012; Linares et al. 2012). Their ecological significance, their particular life-history and vulnerability traits, as well as the conspicuous size of colonies that favors *in situ* measurements, support the common use of gorgonians as model/indicator organisms to assess the effects of disturbances on coralligenous assemblages (Linares et al. 2005, 2007, 2010b; Deter et al. 2012; Gatti et al. 2012, 2015).

2.1 The yellow gorgonian *Eunicella cavolini* (Koch, 1887)

Distribution

Eunicella cavolini is one of the most abundant gorgonian species in the Mediterranean. It is widespread in the northern Mediterranean basin, and is also found in the Sea of Marmara (Weinberg 1980; Vafidis et al. 1994; Topçu & Öztürk 2015; Sini et al. 2014; Chapter 3). Within the Aegean Sea, *E. cavolini* is the most common gorgonian species, and frequently develops dense populations within coralligenous assemblages in waters shallower than 50 m (Gerovasileiou et al. 2009; Salomidi et al. 2009). The occurrence of *E. cavolini* over such a broad geographical scale provides a unique setup for comparative studies across the Mediterranean.

The bathymetric range of *E. cavolini* spans from approximately 10 to 220 m, while optimum colony densities are usually found deeper than 15 m (Russo 1985; Watremez 2012). Its bathymetric and geographic extent is affected by substrate type, light and current intensity, temperature, and availability of food resources (Weinberg 1980). *E. cavolini* is a hard substrate octocoral species that thrives not only on coralligenous outcrops, but also on other habitat types, such as shallow overhangs, marine caves, tunnels, rocky reefs or boulders, as well as at the deep slopes of seamounts (e.g. Carpine & Grasshoff 1975; Bianchi et al. 2010; Bo et al. 2011; Angiolillo et al. 2012). According to Weinberg (1980), the species is mainly found on surfaces with a mean relative irradiance of 6.8% (range: 0.1 to 44% of surface irradiance), and can withstand low sedimentation rates. With respect to temperature tolerance, shallow (<10 m) *E. cavolini* colonies have been reported to survive under high seawater temperatures (over

25°C, although heavily overgrown by algae; Velimirov 1975). Recent findings however contradict the Velimirov (1975) report. Evidence from laboratory studies and field observations during recent mass mortality events has shown that colonies can suffer a high percentage of tissue necrosis or even total mortality soon after exposure to seawater temperatures of 23°C (Cerrano et al. 2000; Garrabou et al. 2009; Gambi et al. 2010; Previati et al. 2010).

Morphological characteristics and life history traits

Although the number of studies that investigate the ecology and life history traits of Mediterranean gorgonian species has increased over the last decades, *E. cavolini* remains one of the least studied gorgonians, despite its high abundance. Practically, the reports of Velimirov (1973, 1975, 1976) and Weinbauer & Velimirov (1995a, b; 1996a, b) are the main sources of information on the ecological and morphological characteristics of this species.

According to the aforementioned studies, *E. cavolini* is an azooxanthellate, heterotrophic passive suspension feeder that is characterised by great morphological plasticity in response to the prevailing water currents. Its colonies can modulate their structural characteristics and growth form (fan shape, size, orientation, spicule morphology, branch thickness, number of polyps) according to the degree of exposure to water flow and current direction. This plasticity allows colonies to dynamically adjust their position and form, in order to reduce the drag from hydrodynamic forces, whilst maximizing feeding efficiency (Velimirov 1973; Velimirov 1976; Russo 1985; Weinbauer & Velimirov 1995a).

E. cavolini is a long-lived species with a maximum reported life span of 21 years (Weinbauer & Velimirov 1995b, 1996b). It has slow growth (between 0.85 and 1.14 cm yr^{-1}, see also Chapter 5), secondary production is between 0.3–7.4 g dry weight (dw) m^{-2} yr^{-1}, and production to biomass ratio is generally low and ranges from 0.24 to 0.32 yr^{-1} (Weinbauer & Velimirov 1995b). Maximum recorded standing stock biomass ranges from 304 g dw m^{-2} in Marseille (True 1970) to 584.6 g dw m^{-2} in Corsica (Weinbauer & Velimirov 1996b), and is comparable to values reported for several tropical gorgonian populations (Goldberg 1973; Opresko 1973).

Growth rates are more pronounced in small-sized colonies (Weinbauer & Velimirov 1995a) and are higher in cold rather than in warm months, possibly indicating that gorgonians enter a summer dormancy period (Velimirov 1975). This is in agreement with the energetic constraints hypothesis, according to which higher seawater temperature and low food availability during Mediterranean summers pose a metabolic stress on benthic suspension feeders (Coma et al. 2000; Coma & Ribes 2003; Coma et al. 2009). In response to these unfavorable environmental conditions, gorgonians enter a period of dormancy characterised by low rate of new tissue synthesis, low respiration rates, and contraction of polyps (indicative of reduced feeding activity). In further support of the latter, Rossi et al. (2006) reported a minimum of gorgonian lipid and carbohydrate levels in *P. clavata* colonies during summer-autumn, which coincides with low food concentration/quality.

Currently, very little is known about the reproductive characteristics of *E. cavolini* and the size or age of colonies reaching sexual maturity. Equally unknown are the embryonic development and early life stages of this species. Regarding recruitment and mortality dynamics, Weinbauer and Velimirov (1996a,b) reported variations among successive years within the same population, similar to other Mediterranean gorgonians (Linares et al. 2008; Gori et al. 2011). In the absence of human disturbances, natural mortality rates of gorgonian species are usually very low (2.7%, Coma et al. 2004), and *E. cavolini* has shown the ability to regenerate lost tissue (Bavestrello & Boero 1986). Although no quantitative estimates exist regarding the effects of direct anthropogenic disturbances on *E. cavolini*, mass mortality events have severely affected local populations in the NW Mediterranean, with mortalities sometimes reaching up to 90% of local populations (Cerrano et al. 2000; Garrabou et al. 2009; Gambi et al. 2010; Gambi et al. 2012).

3. Key threats and disturbances of coralligenous assemblages

Dwelling in the rapidly altered Mediterranean marine environment, coralligenous assemblages are invariably affected by the cumulative effects of multiple anthropogenic stressors, which pose a significant threat to the long-term functional integrity and resilience of these highly diverse habitats.

Disturbances that directly affect coralligenous assemblages include mechanical damage by destructive fishing practices (benthic trawling, static nets or traps; Chiappone et al. 2005; Bavestrello et al. 1997; Maldonado et al. 2013), unintentional damage caused by unregulated recreational activities such as SCUBA diving and boat anchoring (Garrabou et al. 1998; Coma et al. 2004; Linares et al. 2010a,b; Tsounis et al. 2012), harvesting or poaching of specimens for commercial use or souvenirs (Tsounis et al. 2007, 2010), sedimentation, pollution, marine debris (Hong 1983; Airoldi et al. 2003; Bo et al. 2011; Piazzi et al. 2012; Angiolillo et al. 2015), and the expansion of invasive species, especially *Caulerpa racemosa* and *Wormsleyla setacea* (Cebrian et al. 2012; Piazzi et al. 2007, 2012).

At a larger scale, mass mortality events linked to climate change are reportedly occurring in the Mediterranean with increasing frequency since the 1980s (Coma et al. 2009). Although the exact causes that trigger these events are unknown, existing information suggests a link between their occurrence with atypically high seawater temperatures, prolonged stratification of the water column, and thermocline deepening, especially during the late summer and early autumn months. These environmental conditions expose organisms to a protracted summer setting that induces extended physiological stress, due to high respiratory demand and low food availability, and reduces the organisms' resistance to proliferating pathogens such as fungi and protozoan ciliates (Cerrano et al. 2000). Informative insights into these phenomena were provided during the well-documented mass mortality events of 1999 and 2003; the former affected a large part of the Ligurian Sea, while the latter was detectable across more than 1000 km of the NW Mediterranean coastline (Cerrano et al. 2000; Garrabou et al. 2009). *In situ* monitoring efforts revealed abnormally high seawater temperatures down to 25 m or more, which were up to 3 to 4^{o}C above average. Approximately 30 species were affected belonging to four invertebrate phyla, namely Cnidaria, Porifera, Bryozoa, and Mollusca, while mortality of gorgonian populations ranged between 40 to 100% (Cerrano et al. 2000, 2005; Garrabou et al. 2009). Although not of the same magnitude in terms of spatial scale or number of affected species, numerous, more localised events are being reported regularly (Benssousan et al. 2010; Cebrian et al. 2011; Gambi et al. 2010, 2012; Huete-Stauffer et al. 2011; Stabili et al. 2012; di Camillo et al. 2012; di Camillo & Cerrano 2015). Their impacts appear to be long-lasting, and the monitoring of affected gorgonian populations has showed that delayed effects may be much stronger than the immediate ones (Linares et al. 2005), due to overgrowth of necrosed branches by opportunistic species and eventual detachment of colonies from substrate.

Overall, the aforementioned stressors lead to a structural, taxonomical, and functional homogenization of coralligenous assemblages that gradually shift communities to a less complex state that is dominated by opportunistic species with short life cycles (Thrush & Dayton 2002; Piazzi et al. 2012; Rossi 2013).

4. Sampling difficulties and current monitoring approaches

Operational difficulties related to the underwater sampling of coralligenous assemblages at the limits of decompression SCUBA diving have greatly hindered their systematic assessment through an integrated approach. The bulk of scientific information stems from studies that employ an assortment of quantitative or semi-quantitative methodological protocols, using different tools (e.g. scrapping, visual census or image sampling) and different sampling unit sizes (True 1970; Hong 1980, 1983; Ferdeghini et al. 2000; Cocito et al. 2002; Piazzi et al. 2004; Balata et al. 2005). In response to these well-known inconsistencies, the 2008 "*Action Plan for the conservation of the coralligenous and other calcareous bio-concretions in the Mediterranean Sea*" was adopted in the framework of the Barcelona Convention for the Mediterranean Biodiversity (UNEP-MAP-RAC/SPA 2008), to facilitate the emerging need for rigorous evaluation, monitoring, and conservation of coralligenous outcrops at a regional scale. Since then, important steps have been made to establish standard methodological protocols for the assessment of biodiversity patterns and health status of coralligenous (e.g. Kipson et al. 2011; Deter et al. 2012; Gatti et al. 2012, 2015; Casas et al. 2015). Still, the majority of these studies are restricted in the NW Mediterranean, while information from other parts of the basin, such as the eastern Ionian and Aegean seas, remains fragmented and limited to opportunistic or qualitative assessments (e.g. Gerovasileiou et al. 2009; Salomidi et al. 2009; Issaris et al. 2012).

5. Scope and structure of the Thesis

The general scope of this Thesis is the study of biodiversity in coralligenous assemblages of the Aegean Sea and the ecology of the yellow gorgonian *E. cavolini*. Addressing the need for quantitative baseline information regarding coralligenous assemblages in different parts of the Mediterranean, this research work aims to: a) document the geographical distribution of coralligenous assemblages and *E. cavolini* populations across the Mediterranean, b) investigate the spatial patterns in diversity and community structure of coralligenous assemblages thriving in different parts of the Aegean Sea, and c) explore the demographics and dynamics of *E. cavolini* populations in the Aegean and other parts of the Mediterranean. To meet these objectives, a multitude of inter-related studies were performed using both descriptive and experimental methodological approaches. Three representative geographic areas of the Aegean Sea were sampled by scientific SCUBA diving at depths up to 45 m. Standardized protocols were used to assess the coralligenous outcrops based on photographic and visual methods, and novel software tools were designed and implemented to extract quantitative information from the photographic samples. Laboratory analyses were realized using biological samples of selected specimens for taxonomical purposes and for the investigation of *E. cavolini* reproductive characteristics. The findings regarding the Aegean Sea were selectively combined with data from other regions of the Mediterranean through shared publications and collaborative works with European research Institutes.

Chapter 1 - *Distribution of coralligenous outcrops in the Mediterranean Sea*

Obtaining information about the present-day distribution of habitats and species is the fundamental block for understanding spatio-temporal patterns in biodiversity, and for the prediction of future shifts in response to climatic change and other human-related disturbances (Thomas et al. 2004; Doney et al. 2012). This is especially important for benthic communities of the Mediterranean Sea, a marine region where current temperature trends, species invasions, and habitat destruction are altering the characteristics of the environment at a rapid pace (Bianchi & Morri 2003; Bianchi 2007; Coll et al. 2010). As a first step into this Thesis, information regarding the presence of coralligenous assemblages and *E. cavolini* populations across the Mediterranean was compiled in order to produce descriptive distribution maps. Data were collected through an extensive review of available literature and other data sources, as well as through communications with international experts, local fishermen, and divers. The outcomes of these assessments are presented in Chapter 1 for coralligenous assemblages and Chapter 3 for *E. cavolini* populations, as they provide distinct, yet interrelated information.

Chapter 2 - *Community structure and diversity of coralligenous assemblages in the Aegean Sea*

Given the high ecological and economic importance of coralligenous assemblages, as well as the numerous disturbances threatening their integrity, there is an ever increasing need to assess current diversity patterns, evaluate conservation status, and provide baseline data that will enable future monitoring (UNEP-MAP-RAC/SPA 2008). Although evidence regarding the presence of coralligenous outcrops in the Aegean Sea is available since the late 1950s (Pérès & Picard 1958; Laborel 1960), to date, there are no dedicated studies regarding the diversity and structure of their assemblages, while conservation status is virtually unknown. Furthermore, due to the lack of information regarding their distribution in the region, coralligenous assemblages remain largely under-represented in existing conservation management schemes (e.g. Natura 2000; Fisheries Regulation for the Mediterranean - 1967/2006 EC). In this context, the aim of this Chapter is to assess the community composition and diversity of coralligenous outcrops thriving in different parts of the Aegean Sea, and to provide baseline data that will enable future comparisons and monitoring. Specifically, macrobenthic assemblages were investigated within one of the most typical coralligenous facies, dominated by the yellow gorgonian *E. cavolini*. Data were collected *in situ* using a standardised, non-destructive photographic method that enables the rapid acquisition of quadrat image samples through SCUBA diving in deep waters, satisfies minimum data requirements, and facilitates comparisons across different spatial scales (Kipson et al. 2011). The photoQuad software was developed and used to extract quantitative information from the benthic images (Trygonis & Sini 2012).

Chapter 3 - *Distribution of* Eunicella cavolini *(Koch, 1887) across the Mediterranean Sea*

Multiple studies have highlighted the importance of gorgonian forests in the structuring of hard substrate communities and coralligenous outcrops (e.g. Gili & Coma 1998; Linares et al. 2008; Cerrano et al. 2010; Gorri et al. 2011; Rossi et al. 2013). However, there is a notable lack of unified maps that document the spatial distribution of gorgonian species. Focusing on the yellow gorgonian *E. cavolini*, this Chapter summarizes the status of scientific information regarding this gorgonian species, and provides a descriptive map depicting the current knowledge on its spatial distribution across the Mediterranean. Information provided in this section is complementary to that presented in Chapter 1.

Chapter 4 - *The yellow gorgonian* Eunicella cavolini*: demography and disturbance levels across the Mediterranean Sea*

Although *E. cavolini* is a key representative of coralligenous assemblages and is widespread across the Mediterranean (Chapter 3), very little is known about its population characteristics and conservation status in different parts of the basin. In this Chapter, the demographic characteristics of *E. cavolini* were investigated based on data collected *in situ* from populations located in different parts of the Aegean Sea, alongside additional data that were provided by fellow scientists in the NW Mediterranean and Adriatic Sea. This collaborative work enabled a comprehensive analysis of *E. cavolini* populations' structure and disturbance levels across a large part of the species' distribution range, and facilitated a better understanding of the observed patterns across contrasting environmental gradients.

Chapter 5 - *Growth and reproductive characteristics of* Eunicella cavolini *in the NE Aegean Sea*

Both from an ecological as well as from a conservational standpoint, defining somatic growth rates and reproductive characteristics is key for understanding basic life history processes which entail population dynamics and resilience to disturbances (Gotelli 1991; Garrabou & Harmelin 2002; Linares et al. 2007). Aiming to contribute to a better understanding of *E. cavolini* life history parameters, and improve knowledge regarding population dynamics of hard substrate gorgonian species in the Aegean Sea, this last Chapter examines the growth rates and reproductive characteristics of an *E. cavolini* population thriving in a coralligenous assemblage at the NE Aegean Sea. Morphometric characteristics and growth rates of gorgonian colonies were assessed based on an original non-destructive photographic method, which enables the quantification of different morphometric parameters, such as colony height, width, and rectangular area, as well as the more complex metric of colony surface area. Furthermore, the complementary study of reproductive characteristics provides some first insights regarding size of colonies at first maturity and approximate time of spawning.

Κεφάλαιο 1

Γεωγραφική εξάπλωση των κοραλλιγενών σχηματισμών στη Μεσόγειο

Περίληψη

Στόχος της εργασίας είναι η συγκέντρωση της υπάρχουσας πληροφορίας σχετικά με την παρουσία κοραλλιγενών σχηματισμών σε διαφορετικές περιοχές της Μεσογείου, ώστε να χαρτογραφηθεί η γεωγραφική τους εξάπλωση. Η συλλογή της σχετικής πληροφορίας έγινε μέσω λεπτομερούς ανασκόπησης της επιστημονικής βιβλιογραφίας, διερεύνησης διαδικτυακών πηγών και βάσεων δεδομένων, επικοινωνίας με ειδικούς επιστήμονες, καταδυτικά κέντρα και δύτες, καθώς και μέσω επιτόπιων παρατηρήσεων σε κοραλλιγενείς βιοκοινότητες του Αιγαίου. Τα χωρικά δεδομένα ψηφιοποιήθηκαν και μετατράπηκαν σε γεω-αναφερμένα σημεία για την παραγωγή ενός χάρτη κατανομής. Σύμφωνα με τα αποτελέσματα, οι κοραλλιγενείς σχηματισμοί παρουσιάζουν ευρεία γεωγραφική και βαθυμετρική εξάπλωση, και αναπτύσσονται στις περισσότερες περιοχές της Μεσογείου, σε βάθη από 10 έως 140 m. Το μεγαλύτερο ποσοστό των σημειακών δεδομένων (89%) που συγκεντρώθηκαν αφορούν στην παρουσία των κοραλλιγενών σχηματισμών σε βόρειες περιοχές της Μεσογειακής λεκάνης, ενώ οι περιοχές της ΝΑ Μεσογειακής λεκάνης και οι ακτές της Δ Αδριατικής παρουσίασαν σημαντική έλλειψη αναφορών. Τα πρότυπα χωρικής κατανομής που αποτυπώθηκαν στο χάρτη δύναται να συνδεθούν με συγκεκριμένα γεωμορφολογικά και ωκεανογραφικά χαρακτηριστικά των επιμέρους περιοχών, όπως η ύπαρξη κατάλληλου υποστρώματος, τα επίπεδα παραγωγικότητας, και η θερμοκρασία νερού. Εξίσου σημαντικός παράγοντας φαίνεται να είναι η ανομοιόμορφα κατανεμημένη δειγματοληπτική προσπάθεια διερεύνησης αυτών των σχηματισμών σε διαφορετικές περιοχές. Ο τελικός χάρτης αποτελεί ένα χρήσιμο εργαλείο που μπορεί να αποτελέσει βάση για το σχεδιασμό ερευνητικών αποστολών, την αποτίμηση των χωρικών προτύπων βιοποικιλότητας, τη μοντελοποίηση της κατανομής οικοτόπων και πιέσεων, καθώς και σε πρωτοβουλίες προστασίας και διατήρησης.

Chapter 1

Distribution of coralligenous formations in the Mediterranean Sea

Part of this work was published in Giakoumi et al. (2013) | doi: 10.1371/journal.pone.0076449

Abstract

This work compiles existing information regarding the distribution of coralligenous outcrops in order to map their geographic extent across the Mediterranean. Spatial data were obtained through a comprehensive review of the scientific literature, several web sources and online databases, direct communications with expert scientists, diving centers, recreational divers, and *in situ* field observations. The collected information was digitized and transformed into geo-referenced data points to compose a distribution map. The results show that coralligenous outcrops develop in most parts of the Mediterranean Sea and over a relatively wide bathymetric range (from less than 10 to 140 m). Information documenting their presence was more pronounced at the coasts of the N Mediterranean (89% of data points), while very few, to no reports, were found from the SE Mediterranean basin and the coasts of the W Adriatic Sea. The observed distribution patterns can be linked to the specific hydro-morphological features that characterise distinct parts of the basin, such as substrate availability, productivity levels, and seawater temperature. Differences in scientific sampling effort were also prominent. The resulting map provides a valuable tool to assist the sampling design of future studies, and facilitate large-scale biodiversity estimates, modelling of habitats and threats, and conservation initiatives.

1. Introduction

Coralligenous formations provide key marine habitats, which, along with the *Posidonia oceanica* meadows, play a major role in the maintenance of marine biodiversity in the Mediterranean Sea (Boudouresque 2004). However, scientific knowledge regarding these biogenic formations is poor compared to the extensively-studied *P. oceanica* habitats, mainly due to the greater bathymetric extent of coralligenous formations and the operational limitations posed by sampling through SCUBA diving in deep waters (Ballesteros 2006).

In 2009, Agnesi et al. (on behalf of UNEP-MAP-RAC/SPA) carried out a detailed analysis of available cartographic data in order to compile high resolution maps depicting the distribution of coralligenous and other calcareous bio-constructions in different parts of the Mediterranean. Their analysis was based on scientific literature, feedback from international experts, and contacts with the managers' network of Marine Protected Areas in the Mediterranean (MedPAN). This work revealed that cartographic information was limited in number and distribution, being exclusively restricted to the W Mediterranean (31 sites). Moreover, the Agnesi et al. (2009) study identified important knowledge gaps in the Adriatic, Ionian, and Levantine (with only 6, 6, and 1 mapped areas, respectively), whereas no cartographic information was found for the Aegean Sea. Fourty-three percent of the mapped sites occurred within marine protected areas (14 sites) and Natura 2000 sites (6). Using this census as a starting point, and focusing on data-deficient areas, the current work compiles additional information from a variety of data sources in order to provide an updated depiction of the distribution of coralligenous outcrops.

2. Materials and Methods

Multiple data sources were reviewed and scrutinized. These included peer-reviewed and grey literature, online databases, national catalogues, scientific and naturalist fora, unpublished data provided by scientific officers and researchers located in several Mediterranean countries, and communications with diving centers (see Appendix A for a complete list of data sources). Spatial information was extracted or provided in the form of raw geographic coordinates, navigation software placemarks, pre-compiled maps, and shapefile layers. The largest part of the dataset regarding the coasts of E Adriatic was collated and provided by Petra Rodich (State Institute for Nature Conservation, Croatia) in the form of 5×5 km grid shapefiles, whereas for the greatest part of the Turkish coastline a map was constructed and provided by Melih Ertan Çinar and Ergun Taskin (Ege University and Celal Bayar University, respectively). Within the Aegean, additional information was obtained through direct communications with local recreational divers, as well as *in situ* field observations. When and where possible, depth range and characteristic species were also recorded. The information was digitized, and subsequently transformed into geo-referenced point data that were combined into a GIS platform to produce a distribution map. The proportion of point data corresponding to presence of coralligenous formations within eight distinct ecoregions of the Mediterranean Sea (as defined Notarbartolo di Sciara & Agardy – UNEP-MAP-RAC/SPA 2010, after Spalding et al. 2007, **Fig 1**) was used to describe the relative frequency of occurrence of this biotope throughout the basin.

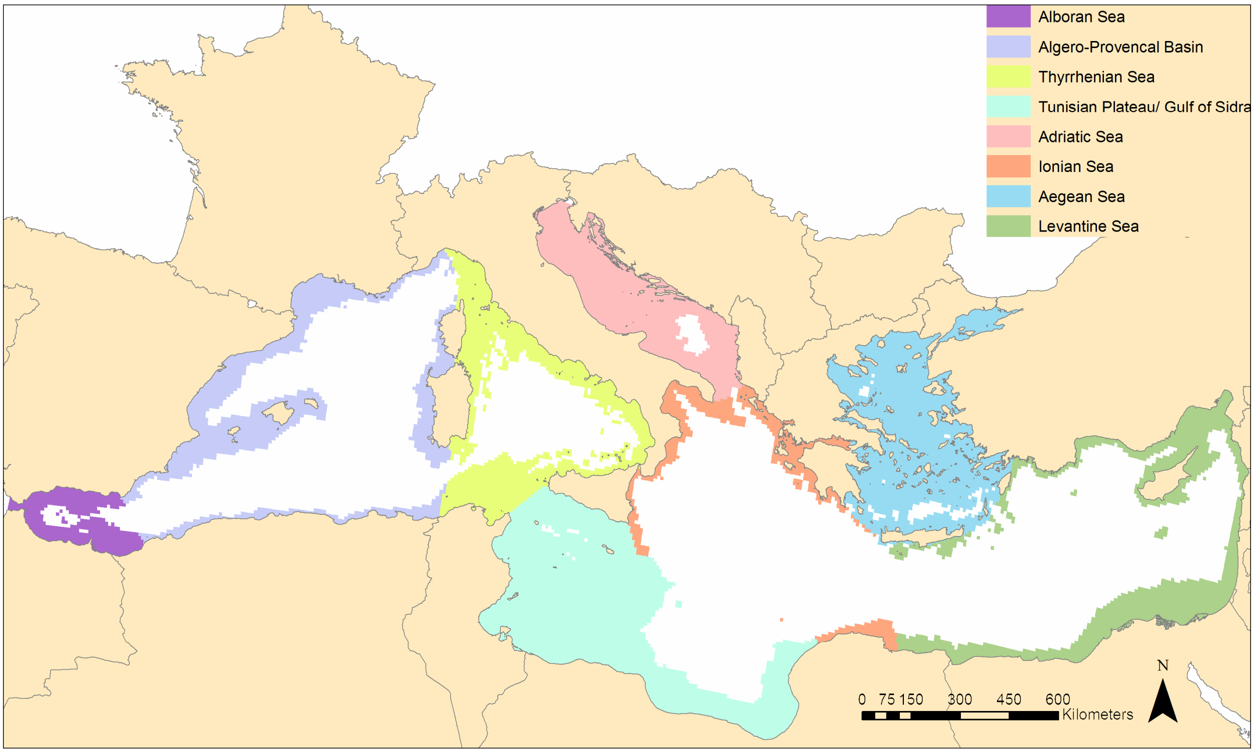

Fig 1. Map of the Mediterranean divided into eight ecoregions, *sensu* Notarbartolo di Sciara and Agardy (UNEP-MAP-RAC/SPA 2010), excluding areas deeper than 1000 m (Giakoumi et al. 2013).

3. Results

The presence of coralligenous formation across the Mediterranean Sea is depicted in **Fig 2**. A total of 1269 data points corresponding to coralligenous formations were recorded in 16 Mediterranean countries; namely Albania, Algeria, Croatia, Cyprus, France, Greece, Italy, Israel, Lebanon, Libya, Malta, Monaco, Morocco, Spain, Tunisia, and Turkey. The greatest amount of information was recovered from the northern regions of the Mediterranean Sea (89% of data points). Less information was available from the coasts of Albania, Lebanon, Israel, and Libya, while no data regarding presence/absence were found for Egypt or Syria. The relative frequency of occurrence of data points was higher in the Adriatic Sea (27.7%) and particularly in the NE coasts (21%), followed by the Algero-Provencal Basin (24.8%), the Aegean (17.6%), and the Tyrrhenian Sea (13%). The proportion of data points was lower in the Ionian Sea (6.5%), the Levantine (5.3%), the Tunisian plateau (2.8%), and the Alboran Sea (2.3%). Overall, depth range of coralligenous records was between 7–140 m, with the majority of data points corresponding to the 20–40 m bin (**Fig 3**).

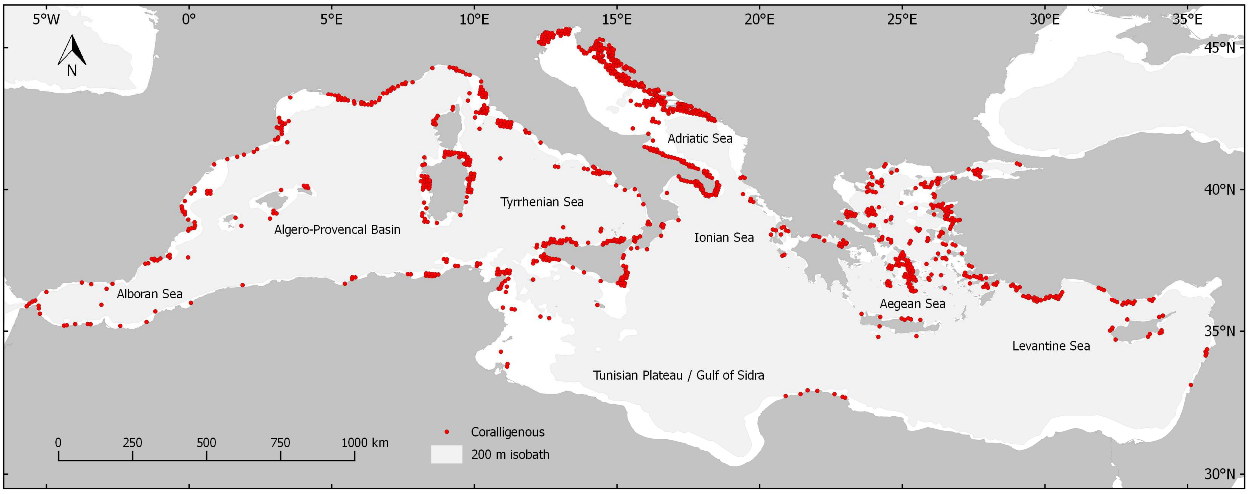

Fig 2. Map of the Mediterranean depicting the presence of coralligenous formations across eight marine ecoregions.

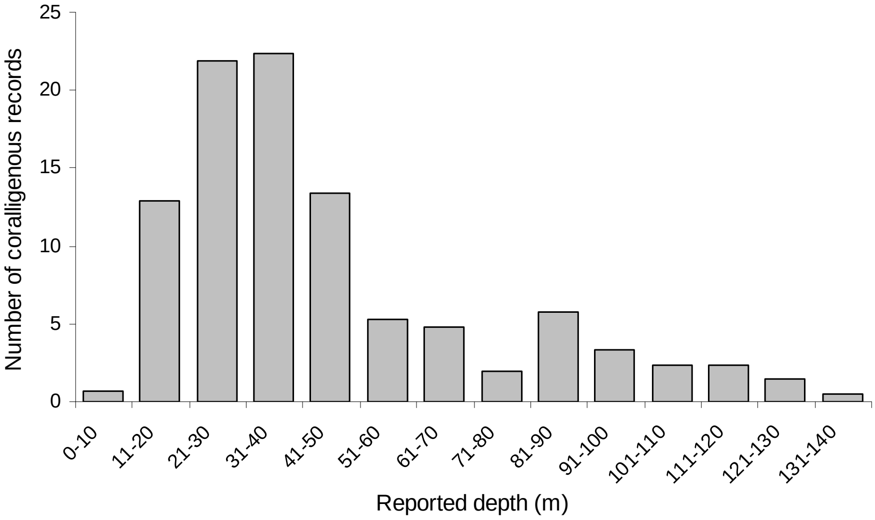

Fig 3. Reported depth of coralligenous assemblages according to the review of available information.

4. Discussion

Elaborating on under-explored areas of the Mediterranean, this review enabled the production of one of the most comprehensive distribution maps of coralligenous to date, and revealed that these hard substrate benthic habitat are widespread in the basin. The practical importance of this mapping effort is highlighted in Giakoumi et al. (2013), where the presented data are combined with respective information on other key Mediterranean habitats (*Posidonia* *oceanica* and marine caves) to propose spatial conservation priorities across the basin following an ecoregion-based systematic planning approach[1].

Our findings suggest that the presence of coralligenous outcrops is particularly pronounced at the northern parts of the basin (89% of data points), whereas they appear to be rare or absent from the W Adriatic, the SE Ionian, and the SE coasts of the eastern Mediterranean. While the observed distribution patterns partially reflect differences in scientific effort and data availability, they can also be linked to the specific geomorphological and oceanographic profiles that characterise distinct regions and which may impede or promote the development of coralligenous accordingly. Specifically, compared to other Mediterranean sub-regions, the SE Mediterranean basin is characterised by a higher mean annual seawater surface temperature, higher salinity and lower nutrient levels (Zenetos et al. 2002; Coll et al. 2010; Würtz et al. 2010), all of which represent limiting factors for the development of coralligenous (Ballesteros 2006). Besides, the greatest extent of the southern and eastern coastline is comprised of accretion coasts (73%), hence there is little availability of hard substrates for coralligenous assemblages to develop (Steward & Morhange 2009). Similarly, the predominance of alluvial coastal substrates in the W Adriatic, as opposed to the island-dominated E Adriatic (Duplančić Leder et al. 2004), may explain the highly contrasting distribution of coralligenous formations in this ecoregion. Moreover, the insular character of both the E Adriatic and the Aegean Sea has resulted to a more scattered distribution of coralligenous formations around the numerous islands and islets, as opposed to the NW Mediterranean, where data are much more uniformly distributed along the coastline. Note however, that point data can only account for corelligenous presence, and they disregard information on the actual habitat cover and bathymetric extent. Therefore, using point data solely, no direct quantitative comparisons can be made across regions. Based on a similar mapping approach that incorporated various point/line/polygon data, Martin et al. (2014) estimated that coralligenous and maërl beds cover approximately 30% of the Mediterranean coastline. Although our results are comparable, the Martin et al. (2014) estimate does not account for a considerable amount of information regarding coralligenous along the Turkish coasts, and it refers to a mixture of habitats by pooling coralligenous and maërl beds together.

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[1] Shapefiles are available at http://www.plosone.org/annotation/listThread.action?root=76571

Unavoidably, using heterogenous data sources of variable resolution to map this highly complex and discontinuous habitat is a challenging task. The main problems encountered during data compilation were related to: a) the inaccurate definition of coralligenous that is often confused with other bio-concretional habitats such as maërl beds, b) the parsing of peer-reviewed or gray literature articles that do not report coordinates or only present qualitative maps, c) the insufficient reporting of habitat spatial extent, including depth range, d) the unreported coralligenous typology (e.g. bank, rocky wall, rocky outcrop), and e) the poor information regarding the type of assemblages and the associated dominant species or ecological facies. The aforementioned parameters are vital for evaluating the spatial cover of different coralligenous types, and mapping efforts such as the one presented herein highlight the importance of reporting adequate metadata about the study areas and target species.

The combined, integrated use of different observation tools and sampling methods, such as SCUBA diving, ROVs, and underwater acoustics, can improve our ability to adequately map coralligenous and assess the associated threats or disturbances (e.g. Holon et al. 2015). Archiving this information into data depositories of standardised format is equally important (UNEP-MAP-RAC/SPA 2008, 2015). Still, low-resolution maps such as the one presented herein provide a valuable background for large-scale estimates of diversity, predictive habitat models, assessment of individual or cumulative threats, and conservation planning (e.g. Coll et al. 2010, 2011; Giakoumi et al. 2013; Micheli et al. 2013, 2015; Katsanevakis et al. 2014).

Acknowledgements

This work would not have been possible without the input of numerous observers that provided critical data. Special thanks to Sylvaine Giakoumi, Vasilis Gerovasileiou and Stelios Katsanevakis for our collaborative work and discussions. This work has been co-financed by the EU Social Fund and Greek national funds through the NSRF 2007-2013 Research Funding Program: Heracleitus II, Investing in knowledge society.

Κεφάλαιο 2

Δομή και ποικιλότητα των κοραλλιγενών βιοκοινοτήτων στο Αιγαίο

Περίληψη

Οι κοραλλιγενείς βιοκοινότητες συγκροτούν έναν από τους πλέον σημαντικούς τύπους οικοτόπου σκληρού υποστρώματος της Μεσογείου. Δημιουργούν βιογενείς σχηματισμούς που παρουσιάζουν αυξημένη δομική πολυπλοκότητα και βιοποικιλότητα, και παρέχουν πληθώρα φυσικών αγαθών. Αποτελούν καταφύγιο για μεγάλο αριθμό μακρόβιων ειδών, τα περισσότερα εκ των οποίων παίζουν σημαντικό ρόλο στη δημιουργία και διατήρηση του βιογενούς ανάγλυφου. Ωστόσο, είναι ιδιαίτερα ευπαθείς σε επικείμενες ανθρωπογενείς πιέσεις και απειλές. Λόγω της ιδιαίτερης σημασίας τους, οι κοραλλιγενείς βιοκοινότητες έχουν διερευνηθεί εκτεταμένα σε διάφορες περιοχές της ΒΔ Μεσογείου. Όμως, η υπάρχουσα επιστημονική πληροφορία σχετικά με τη σύνθεση και την οικολογία τους στις υπόλοιπες περιοχές της Μεσογειακής λεκάνης παραμένει ιδιαίτερα περιορισμένη και αποσπασματική. Στόχος της παρούσας μελέτης είναι η ποσοτική διερεύνηση της δομής και ποικιλότητας των κοραλλιγενών βιοκοινοτήτων στο Αιγαίο, ως ένα από τα λιγότερο μελετημένα θαλάσσια βενθικά οικοσυστήματα της περιοχής. Δεδομένης της δομικής ποικιλομορφίας των κοραλλιγενών βιοκοινοτήτων, η παρούσα μελέτη επικεντρώνεται στην οικολογική φάση επικράτησης της κίτρινης γοργονίας *Eunicella cavolini*, μία από τις πιο χαρακτηριστικές φάσεις της ευρύτερης κοραλλιγενούς βιοκοινότητας. Με αυτόν τον τρόπο, η παρούσα μελέτη παρέχει τη δυνατότητα μελλοντικών συγκρίσεων τόσο σε τοπικό, όσο και σε Μεσογειακό επίπεδο. Συνολικά, διερευνήθηκαν έξι σταθμοί σε τρεις αντιπροσωπευτικές περιοχές του Αιγαίου. Για τη συστηματική αποτύπωση των βιοκοινοτήτων εφαρμόστηκε ταχεία, μη-καταστρεπτική, φωτογραφική μέθοδος, σε βάθη από 18 έως και 35 m. Η συγκεκριμένη μέθοδος αφορά στη συλλογή φωτογραφικών δειγμάτων (25×25 cm) κατά μήκος τριών επαναληπτικών διατομών, για την κάλυψη ελάχιστης συνολικής επιφάνειας 1.5 m^2 ανά σταθμό. Για την ποσοτική ανάλυση των φωτογραφικών δειγμάτων και την εκτίμηση του ποσοστού κάλυψης των διαφορετικών ειδών χρησιμοποιήθηκε το λογισμικό photoQuad. Σύμφωνα με τα αποτελέσματα, οι κοραλλιγενείς βιοκοινότητες του Αιγαίου συνιστούν έναν οικότοπο αυξημένης βιοποικιλότητας, και παρουσιάζουν

συγκεκριμένες ομοιότητες –αλλά και ιδιαιτερότητες– σε σχέση με αυτές τις ΒΔ Μεσογείου. Συγκεκριμένα, η ανάλυση των φωτογραφικών δειγμάτων επέτρεψε την ταυτοποίηση 100 ειδών/ομάδες ειδών από 10 ταξινομικές ομάδες. Ο αριθμός ειδών ανά σταθμό δειγματοληψίας ήταν 43 ± 4 (μέσος ± τυπική απόκλιση), με τα ενασβεστωμένα ροδοφύκη και τους σπόγγους να αποτελούν τις κυρίαρχες ομάδες σε επιφανειακή κάλυψη. Παρόλο που οι τιμές βιοποικιλότητας δε είχαν στατιστικές διαφορές στα διαφορετικά χωρικά επίπεδα μελέτης, η σύνθεση των βιοκοινοτήτων διέφερε σημαντικά μεταξύ σταθμών που βρίσκονται στην ίδια γεωγραφική περιοχή. Οι χωρικές διαφοροποιήσεις που παρατηρήθηκαν αποδίδονται κυρίως στις κατά τόπους διαφορετικές αβιοτικές συνθήκες και στην επίδραση ανθρωπογενών πιέσεων. Η παρούσα μελέτη αποτελεί την πρώτη συστηματική καταγραφή των κοραλλιγενών βιοκοινοτήτων στην ΒΑ Μεσόγειο, και επισημαίνει την ανάγκη συστηματικής διερεύνησης και παρακολούθησής τους στο Αιγαίο και στις γειτονικές θαλάσσιες περιοχές.

Chapter 2

Community structure and diversity of coralligenous assemblages in the Aegean Sea

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Manuscript to be submitted for publication

Abstract

Mediterranean coralligenous assemblages are important benthic habitats of high ecological and economic value. They are characterised by high structural complexity and species diversity, and provide a wide range of natural resources.They host a large number of long-lived, slow-growing benthic species, most of which play a pivotal role in the development and maintenance of these biogenic formations, but are particularly vulnerable to ongoing disturbances and threats. Although coralligenous assemblages have been extensively studied in the NW Mediterranean, information regarding their species composition and ecology in other parts of the basin remains limited and fragmented. The scope of this study is to quantitatively assess the community structure and diversity of the under-explored coralligenous outcrops of the Aegean Sea. Given the great variety of species assemblages that compose coralligenous outcrops, the study focuses on assemblages that are dominated by the yellow gorgonian *Eunicella cavolini*, a typical coralligenous facies across the Mediterranean, in order to facilitate future comparisons both at a regional and at a basin scale level. Based on a hierarchical sampling design, six sites were investigated within three representative geographical localities of the Aegean Sea. A standardised, rapid, non-destructive sampling method was applied at depths ranging from 18 to 35 m. Within each site, a total area of 1.5 m^2 was sampled using photoquadrats (25x25 cm) over three 0.5 m^2 randomly placed transects. Number and area cover of conspicuous macrobenthic species were assessed using the image segmentation tool provided by the photoQuad software. Results suggest that coralligenous assemblages dominated by *E. cavolini* in the Aegean Sea constitute a highly diverse habitat that presents several similarities and peculiarities to its western Mediterranean counterparts. Analysis of photoquadrad samples resulted to the identification of 100 species/categories of species belonging to 10 taxonomic groups. Mean number of species per site was 43 ± 4, while encrusting coralline algae and sponges were the dominant groups in terms of area cover. Although biodiversity values were relatively similar along different spatial scales, community structure presented significant differences at the level of sites found within the same locality. Distinct patterns were mainly linked to the specific environmental conditions and/or disturbance levels that characterise individual sites. This study represents the first systematic assessment of coralligenous assemblages in the NE Mediterranean, and highlights the need for further exploration and monitoring of this highly valued marine habitat throughout the Aegean and the neighbouring seas.

1. Introduction

Coralligenous communities growing on hard substrates under dim light conditions represent one of the most complex and diverse benthic marine habitats of the Mediterranean Sea. They encompass a wide range of species assemblages, which form biogenic structures through the multi-layered accumulation of encrusting coralline algae and the calcareous remains of animal species (Sarà 1969; Sartoretto et al. 1996). These biogenic outcrops are acknowledged to be of high ecological and economic importance, as they host more than 10% of the known Mediterranean species, including a large number of endemic, vulnerable and protected organisms (Boudouresque 2004; Ballesteros 2006; Coll et al. 2010). They serve as reservoirs of natural resources that provide important fisheries grounds, aesthetic seascapes which act as poles of attraction for diving tourism, and a wide range of raw materials (e.g. Ballesteros 2006; Lloret 2010; Salomidi et al. 2012). Among the most typical taxonomic groups that characterise coralligenous assemblages are encrusting coralline rhodophytes (especially of the families Corallinacea and Peyssonneliacea), sponges, cnidarians, and bryozoans. The majority of the species involved in the structuring of these assemblages are perennial, long-lived organisms, which are particularly vulnerable to natural and human-induced disturbances (Garrabou & Ballesteros 2000; Linares et al. 2007; Teixidó et al. 2011a). Mechanical damage (mainly caused by destructive fishing practices), sedimentation, increased nutrient loads, mass mortality events related to positive thermal anomalies of the water column, and invasive species are amongst the main disturbances that severely affect coralligenous assemblages, both at the individual, as well as at the community structure level (e.g. Bavestrello et al. 1997; Garrabou et al. 1998; Cebrian et al. 2012; Teixidó et al. 2013; Piazzi et al. 2007, 2012; Maldonado et al. 2013).

The importance of coralligenous assemblages as a priority habitat of the Mediterranean was for the first time directly addressed through the adoption of the "*Action Plan for the conservation of the coralligenous and other calcareous bio-concretions in the Mediterranean Sea*" (UNEP-MAP-RAC/SPA 2008). The action plan solidified the significance of coralligenous among the scientific community, identified main threats, and underpinned the need to gain further information regarding the distribution, composition, dynamics, and conservation status of coralligenous assemblages throughout the Mediterranean. During the same year, the Marine Strategy Framework Directive (MSFD, 2008/56/EC) introduced the notion of "seafloor integrity" as one of the eleven indicators to evaluate the Good Environmental Status of the marine environment. This novel ecosystem approach further substantiated the need to assess and systematically monitor biogenic structures, such as coralligenous assemblages (Rice et al. 2012; Borja et al. 2013).

The presence of coralligenous outcrops in the Aegean Sea was first documented in the late 1950s (Pérès & Picard 1958; Laborel 1960). In these early expeditions, scientists reported the extensive development of coralligenous assemblages in the region, both as outcrops of the littoral rock at the lower infralittoral and circallitoral zones, as well as biogenic banks surrounded by sand at depths up to 130 m (also known as *coralligène de plateau*). Since then, information regarding coralligenous assemblages in the Aegean Sea remains particularly scarce and fragmented. Available data primarily originate from broader biodiversity studies on specific taxonomic groups and hard substrate communities (e.g. Vafidis et al. 1994; Antoniadou et al. 2005; Antoniadou & Chintiroglou 2005; Voultsiadou 2005; Kefalas & Castritsi-Catharios 2007), and from geographically-scattered species inventories of variable resolution (Gerovasileiou et al. 2009; Salomidi et al. 2009; Topaloglu et al. 2010). Recent mapping efforts have revealed the presence of numerous coralligenous outcrops in most parts of the Aegean Sea (Georgiadis et al. 2009; Giakoumi et al., 2013; Martin et al., 2014, Chapter 1). Still, the structure, diversity and ecology of their assemblages rest largely unexplored, while conservation status is effectively unknown. As a result, they are entirely neglected by existing conservation management schemes (e.g. NATURA 2000; Mediterranean Fisheries Regulation - 1967/2006 EC). This underlines the need for dedicated scientific studies that will systematically assess and monitor coralligenous outcrops in order to enable the development of meaningful conservation plans at the local and regional scale. Such an approach is vital for the Aegean Sea, which is exposed to severe alterations caused by destructive fishing practices, sea surface temperature rise, and introduction of invasive species (Raitsos et al. 2010; Coll et al. 2011; Tsikliras et al. 2015; Katsanevakis et al. 2015).

In this context, the key objective of the present study is to assess the community structure and species diversity of coralligenous assemblages dominated by the yellow gorgonian *Eunicella cavolini* (Koch 1887) in three representative geographic localities of the Aegean Sea. *E. cavolini* is a long-lived gorgonian with a widespread distribution across several parts of the

Mediterranean Sea, and it is known to form one of the most typical coralligenous facies (UNEP-MAP-RAC/SPA 2007). Furthermore, it is the most common gorgonian in the Aegean Sea, found in waters shallower than 50 m (Salomidi et al. 2009; Sini et al. 2015, Chapter 4). Focusing on this particular coralligenous facies, we used a standardised, non destructive method, aiming to: a) describe community structure and diversity in waters shallower than 40 m, b) assess community patterns across different spatial scales, c) identify potential disturbances or threats, and d) provide reference data to enable future comparisons.

2. Materials and Methods

2.1 Sampling design

The community structure and diversity of six coralligenous assemblages dominated by the yellow gorgonian *E. cavolini* were investigated within three representative geographic localities of the Aegean Sea. Specifically, two sites where investigated in the locality of Pelio (Ag. Vasso and Lefteris), two in Chalkidiki (Nemessis and Spilia), and two in Lesvos island (Palios and Kalloni), at depths ranging from 18 to 35 m (**Fig 1**, **Table 1**). Most sites were sampled during the summer months of 2011, except from Kalloni site that was sampled in May 2013.

Fig 1. Map of the Aegean Sea depicting sampling localities (in bold font) and sites (bullets annotated with regular font).

Table 1. Characteristics of the sites investigated in three distinct localities of the Aegean Sea for the assessment of coralligenous assemblages dominated by the yellow gorgonian *Eunicella cavolini*. Density values of *E. cavolini* were obtained from Chapter 4 (Sini et al. 2015).

Locality	**Site**	**Depth range (m)***	**Sampled depth (m)**	**Latitude**	**Longitude**	**Habitat**	**Inclination**	**Mean density of *E. cavolini* (m^{-2})**
Pelio	Ag.Vasso	30–50+	30–35	39°05'08"N	23°07'48"E	Rocky outcrops	Sub vertical	7.84
	Lefteris	20–30	25–30	39°08'31"N	23°20'39"E	Reef wall	Vertical	10.36
Chalkidiki	Nemessis	30–50+	30–35	39°56'46"N	23°59'10"E	Wall	Sub-vertical	11.35
	Spilia	32–50+	32–35	39°56'38"N	23°57'31"E	Reef wall	Sub-vertical	13.29
Lesvos	Palios	30–44	30–35	39°19'42"N	26°26'10"E	Reef wall	Sub-vertical	6.00
	Kalloni	10–27	18–25	39°04'56"N	26°05'25"E	Rocky outcrops	Sub-vertical	23.52

* The "+" symbol indicates that assemblages expanded to depths greater than the maximum depth reported herein.

Within each site, assemblages were quantitatively assessed with a standardised photographic method which involves the acquisition of benthic images using a quadrat frame (25×25 cm = 625 cm^2) along specific transects. Each transect consisted of eight contiguous images, hereafter referred to as the "transect-sample". The first image of each transect-sample was taken from a haphazardly chosen position within the coralligenous assemblage, whereas the remaining seven images were obtained in a contiguous manner (**Fig 2**). A total of three transect-samples were collected per site, summing up to a total sampled surface area of 1.5 m^2 per site. This is in accordance with the minimum sample requirements proposed by Kipson et al. (2011) based on the assessment of coralligenous assemblages dominated by the purple gorgonian *Paramuricea clavata* in three distinct geographic regions of the NW Mediterranean.

Photographs where obtained using a Canon G9 powershot camera (12.1 MP resolution) with equivalent underwater housing, which was mounted on a custom-made quadrat frame in order to maintain standard distance and position of the camera from the sampled surface (**Fig 2a**). A photographic method was chosen as it provides a fast and non-destructive way to sample relatively large surface areas, whilst creating a permanent record that enables direct visual comparisons and monitoring (Bianchi et al. 2004; Deter et al. 2012). These characteristics are of particular importance when studying vulnerable or difficult to approach benthic habitats, such as the Mediterranean coralligenous. Furthermore, in order to overcome the limitations involved in the identification of organisms through image samples alone (Bianchi et al. 2004), photoquadrat sampling was combined with *in situ* field observations and collection of voucher specimens used for further processing and identification in the laboratory (**Fig 2b**).

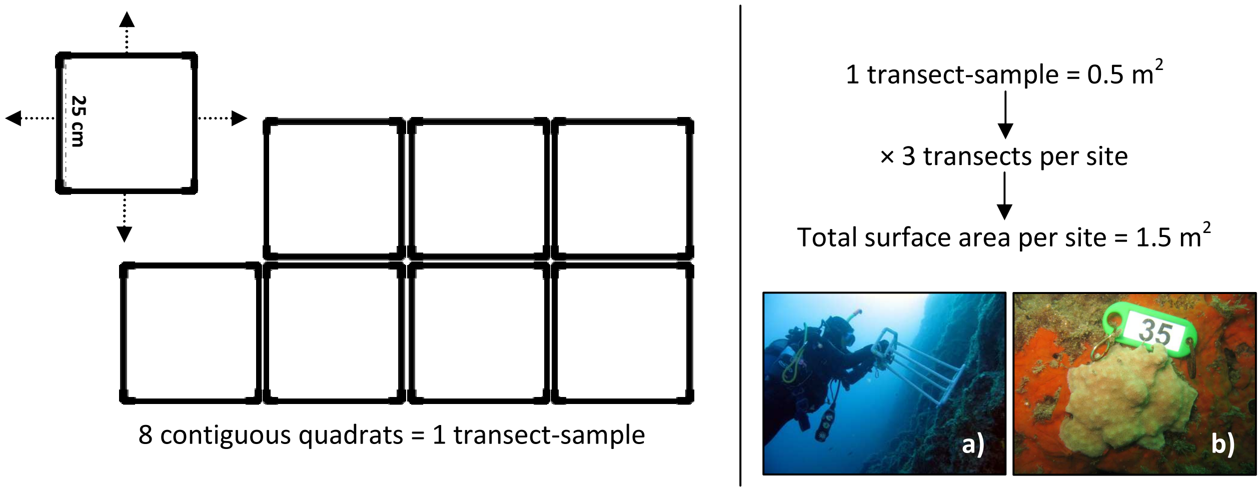

Fig 2. Schematic representation of the sampling protocol adopted for the study of coralligenous assemblages through the acquisition of benthic images using a quadrat frame. The first image of each transect-sample was taken from a haphazardly chosen position within the coralligenous assemblage, while the remaining seven images were obtained in a contiguous manner, following any possible direction (black dotted arrows) in order to avoid potential discontinuities of the assemblage. Inset images illustrate: a) *in situ* use of quadrat with mounted camera, b) shot of labeled voucher specimen before collection.

2.2 Processing of photographic samples

Photographic quadrat samples were pre-processed and analysed using the custom-made image analysis software photoQuad (Trygonis & Sini 2012). The software is specifically built to accommodate the analysis of benthic photographic quadrat samples, and provides interactive tools for image enhancement and calibration, quadrat boundary detection, feature annotation and measurement, as well as a suit of quadrat analysis methods. These are functional in a layer-based environment that simplifies the laborious processing of quadrat samples and facilitates the automatic quantification of selected image features. Key to the photoQuad software is a user-defined species library that allows the manual association of objects and annotations to particular species or other custom categories.

The analysis of photographic samples was realized using the image segmentation method (Teixidó et al. 2011b; Trygonis & Sini 2012). Image segmentation refers to the automatic partitioning of the source photograph into distinct segments (patches) that share similar colour properties. Individual segments may then be interactively selected by the user and grouped into regions of interest (ROIs) in order to be assigned to specific species, or any other custom category enlisted in the species library. In the present study, the library was constructed retrospectively, using all species or groups of species that were identified by the thorough examination of image samples, the analysis of voucher specimens, and *in situ* field observations. Each image was calibrated to metric units, and the quadrat boundary was traced to define the sampled surface area. Segmented images were analysed as described above, and specific ROIs were manually assigned to species and substrate categories (**Fig 3**). The actual surface area (cm^2) of species and substrate categories, as well as their relative proportion to the total quadrat area (% cover), were automatically calculated and exported as a plain text comma-separated (csv) file.

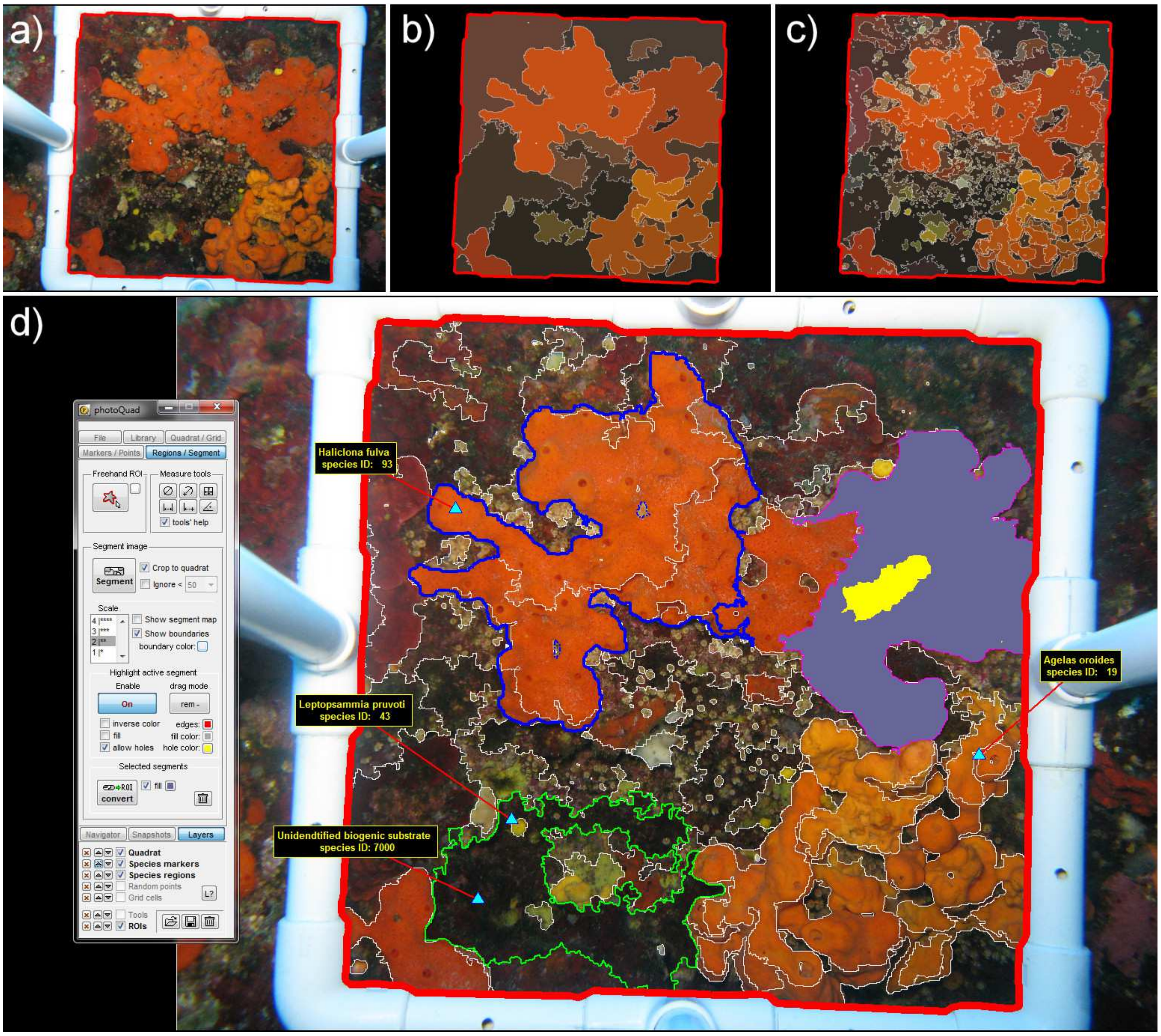

Fig 3. Snapshots of the photoQuad software depicting: a) photograph of a quadrat sample in which the sampled surface area is defined by the quadrat boundary (red line); b-c) segmentation maps of the quadrat sample at different segmentation levels; d) segmented quadrat sample featuring selected regions that were manually assigned to specific species and substrate categories (blue and green lines) according to the user-defined species library. Annotations display species or substrate category names of identified features. Purple patch represents a selected area which has not yet been assigned to some category. The yellow patch indicates an internal hole. photoQuad's user interface shows the segmentation panel and layer adjustment tools.

2.3 Data treatment and statistical analysis

Information extracted from the analysed photoquadrat samples corresponded to four substrate categories. These included: 1) *UBS*: unidentified biogenic substrate, 2) *Holes*: including small cracks and crevices, 3) *Sediment*: image regions of sediment patches, and 4) *Species cover*: all benthic organisms identified to the lowest taxonomic level possible. Also included in this latter category were visually similar taxa that could not be identified through photographs and which were grouped into higher taxonomic levels (e.g. genus of Bugula, family of Serpulidae, order of Scleractinia, class of Hydrozoa, phylum of Bryozoa), or taxonomic categories with distinctive morphological features (e.g. turf, mucilagenous algae, encrusting calcareous algae, small encrusting sponges). All taxonomic names used were cross-checked using the World Register of Marine Species (WoRMS Editorial Board 2015).

The mean number and area cover of the main taxonomic groups recorded per site were initially described in a graphical manner. The most common species/groups of species characterising the studied coralligenous assemblages were determined using presence/absence data and a SIMPER analysis (Clark & Gorley 2006) on untransformed total species cover among the three localities. Further on, spatial patters of biodiversity and community structure were assessed considering two main spatial scales: a) level of geographic localities (located hundreds of km apart), and b) level of sites within localities (located few km apart). For the biodiversity assessment only organisms identified up to genus level were used. The total number of species (S) and Shannon's index of biodiversity (H') were estimated per transect-sample, and were then compared among localities and sites using permutational univariate analysis of variance (PERANOVA) based on Euclidean distances (Anderson 2001). The relative contribution of individual species to the total species cover per site was assessed through the construction of a pseudo-colour map.

For the investigation of community composition a multivariate analysis was realized based on square root transformed data of species cover per transect-sample, and a Bray-Curtis resemblance matrix. Cover data were square root transformed in order to down-weight the effect of dominant species in community patterns (Clark & Gorley 2006). A non-metric multidimentional scaling (MDS) ordination was constructed to graphically depict spatial patterns. Moreover, a Spearman's rank order correlation analysis was carried out, the results of which were superimposed on the MDS graph, in order to identify the main groups of taxa responsible for the observed patterns at a correlation level of >0.6 (indicative of strong correlation). Community structure was compared among localities and sites through a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). Both PERANOVA and PERMANOVA tests were set up according to a two-way hierarchical design using geographic locality (3 levels) as a fixed factor, and sites nested within locality (6 levels) as a random factor. Additional pair-wise comparisons were performed for groups of data only when the main tests indicated significant differences. In all cases, statistical significance was determined based on 9999 permutations. Finally, SIMPER analysis was employed to detect the species/groups of species contribution to the estimated Bray-Curtis dissimilarity between sites with statistically different community structure. Statistical analyses were carried out using SPSS 17 and PRIMER v6 software with PERMANOVA+ add-on package (Clark & Gorley 2006; Anderson et al. 2008).

3. Results

3.1 Structural components

Community structure and diversity of coralligenous assemblages was assessed based on the analysis of 144 benthic images. A description of the main substrate categories observed in the investigated sites is presented in **Table 2**. Mean *Species cover* had the greatest percentage cover of the sampled surface area (93.7% ± 4, mean ± SD), ranging from 88% at the site of Lefteris (Pelio locality) to 99% at the site of Spilia (Chalkidiki locality). The lower mean *Species cover* at Lefteris site was related to the pronounced proportion of the substrate category *Holes* in the specific site (approximately 11% of total sampled surface area), indicating increased substrate rugosity. Furthermore, *Sediment* cover was generally low in all sites (i.e. less than 5%), while *UBS* was mostly observed in Kalloni site (10%).

Table 2. Mean ± standard deviation of area cover (%) of the main substrate categories recorded in the photographic transect-samples per site. Total area sampled per site is 1.5 m^2.

	Site					
Substrate category (%)	**Ag. Vasso**	**Lefteris**	**Nemessis**	**Spilia**	**Palios**	**Kalloni**
Species cover	95.3 ±1.5	87.8 ± 3.6	97.1 ± 1.9	98.8 ± 0.7	93.5 ± 3.7	89.2 ± 9.4
UBS	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 2.6	0.2 ± 0.1	0.2 ± 0.4	9.7 ± 8.6
Holes	1.4 ± 0.4	11.1 ± 3.4	0.1 ± 0.1	0.5 ± 0.5	2.9 ± 2.8	0.1 ± 0.1
Sediment	3.3 ± 1.5	1.2 ± 0.3	1.3 ± 1.0	0.6 ± 0.5	3.5 ± 1.3	0.3 ± 0.3

With regards to *Species cover*, the combined investigation of photoquadrats and voucher specimens led to the identification of 100 macrobenthic taxa that belonged to 10 major taxonomic groups, namely Porifera (41 taxa), Rhodophyta (12), Cnidaria (11), Bryozoa (11), Chlorophyta (7), Tunicata (6), Annelida (5), Mollusca (4), Ochrophyta (2) and Foraminifera (1), see **Table 3** for a full list. Of the total number of taxa recorded, 89 sessile organisms were identified to the species or genus level, whereas the remaining organisms were grouped into higher taxonomic levels, or taxonomic categories with distinctive morphological features (hereafter referred to as "groups of species"). Mean number of species/groups of species of the most common taxonomic categories per site are illustrated in **Fig 4**. Porifera presented the highest number of species in the majority of sites (14.3 ± 4), followed by Rhodophyta (7.3 ± 3). Aditionally, the sites of Nemessis and Spilia (Chalkidiki locality) had an increased number of Chlorophyta (5.5 ± 0.5) and Bryozoa (6.5 ± 1.4), while the sites of Lefteris and Ag. Vasso (Pelio locality) had the highest number of Cnidaria (7.3 ± 1.5), which were primarily represented by scleractinian corals.

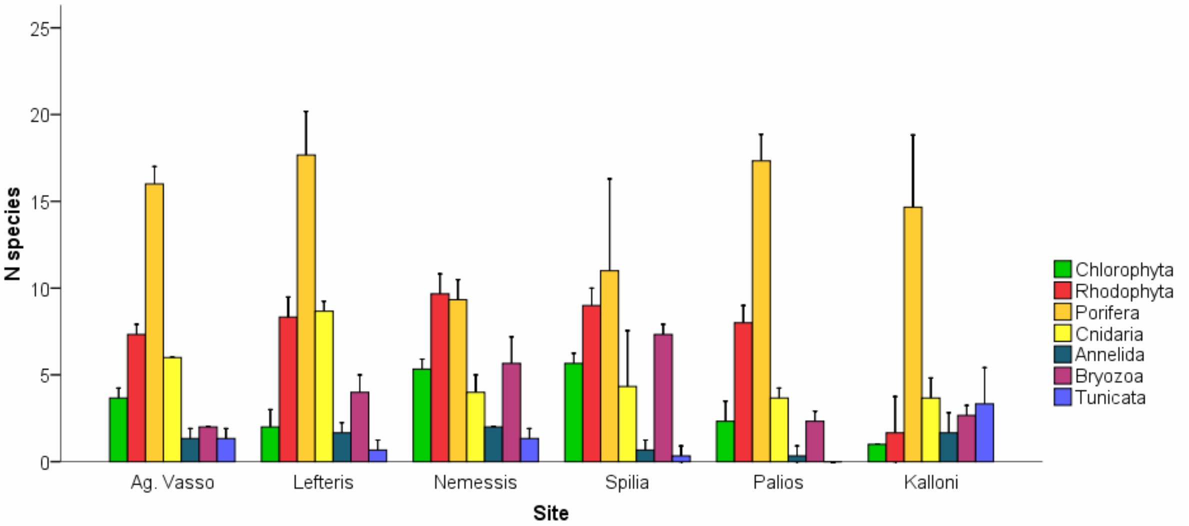

Fig 4. Number of species or species categories of the most common taxonomic groups encountered per site. Bar height expresses the mean, error bars depict standard deviation.

In terms of species cover (%), macroalgae were the dominant group in the majority of sites (**Fig 5**). Specifically, Rhodophyta had the highest mean cover (40% ± 12 of total *Species cover*), being mainly represented by the encrusting coralline algae *Neogoniolithon mamillosum*, *Lithophyllum stictaeforme/cabiochiae*, and *Mesophyllum alternans*, as well as several *Peyssonnelia* species. Mean cover of Chlorophyta (20% ± 7) was generally much lower than Rhodophyta, and was mainly characterised by turf-forming species (e.g. *Pseudochlorodesmis furcellata*, *Cladophora pellucida*).

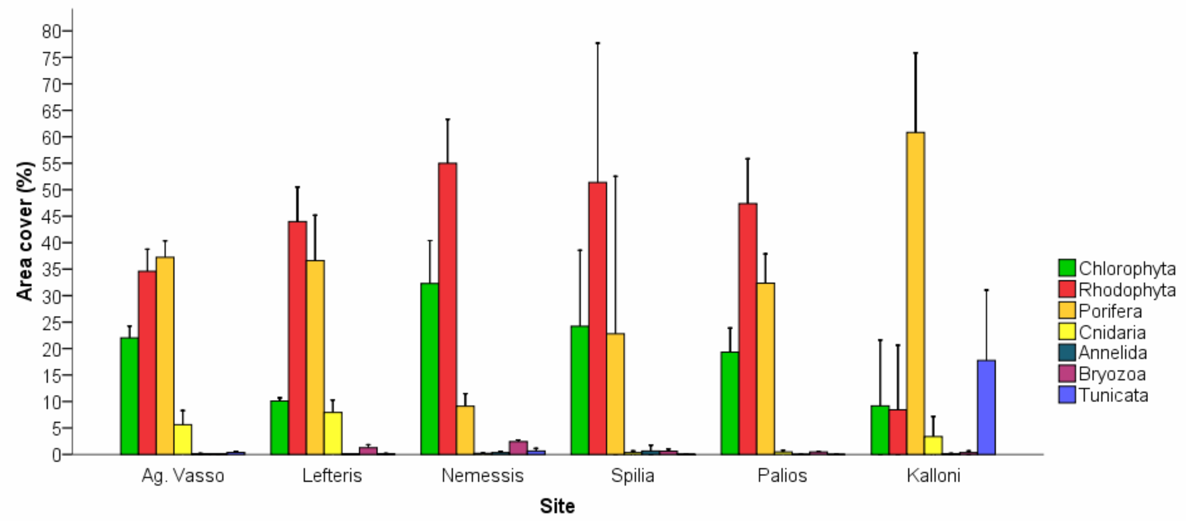

Fig 5. Area cover of the main taxonomic categories encountered per site. Percentages were calculated against total *Species cover* (i.e. excluding *UBS*, *Holes* and *Sediment* presented in **Table 2**). Bar height expresses the mean, error bars depict standard deviation.

Porifera was the second most important taxonomic group in terms of cover (31.6% ± 14.3), whereas it was the dominant group in two sites, namely Ag. Vasso and Kalloni. The species displaying the highest relative cover were the massive sponges *Agelas oroides*, *Petrosia ficiformis*, *Sarcotragus foetidus*, and *Chondrosia reniformis*, as well as the encrusting species *Crambe crambe*, *Spirastrella cunctatrix*, *Phorbas tenacior*, and *Haliclona fulva*.

The remaining groups presented a particularly low surface area cover, whilst specifically pronounced in certain sites. Cnidaria cover (3% ± 3, excluding *E. cavolini*) was more prominent in the sites of Ag. Vasso, Lefteris and Kalloni. The species that accounted for most of the Cnidaria cover was the zoantharian *Parazoanthus axinellae*, which was primarily recorded as an epibiont on other species (particularly sponges). Bryozoa cover (0.8% ± 0.6) presented a slight increase at the sites of Lefteris and Nemessis, while the most common taxa in all localities were *Adeonella* spp., *Rhynchozoon neapolitanum*, and *Schizomavella* spp. Finally, area cover of Tunicata (2.5% ± 3.9) was exceptionally high at the site of Kalloni, reaching a within-site relative mean cover of 18%, mainly due to the encrusting species of ascidians *Cystodytes dellechiajei* and *Didemnum* spp., and the increased presence of *Clavelina dellavallei*.

Overall, 40 taxa corresponded to species/groups of species that were present across all geographic localities. Among them, 26 taxa had a large contribution to the overall similarity of assemblages across different localites, as suggested by the SIMPER analysis (**Table 3**). These included 4 algal biocontructors (i.e. *L. stictaeforme/cabiochiae*, *N. mamilosum*, *M. alterans*, and *P. rosa-marina*), 6 animal bioconstructors (*R. neapolitanum*, *Schizomevella* spp. *Adeonella* spp., *Salmacina/Filograna*, *Leptopsammia pruvoti*, *Caryophyllia inornata*), 2 bio-eroders (*Cliona viridis* and *C. schmidtii*), and several species of structural importance, such as the massive sponge species *A. oroides*, *S. foetidus*, and the encrusting species *Crambe crambe*, *Spirastrella cunctatrix*, and *Haliclona fulva*.

Table 3. Main species/groups of species encountered in coralligenous assemblages of the Aegean Sea. Upper-case superscripts indicate sites; A: Ag. Vasso, L: Lefteris, N: Nemessis, S: Spilia, P: Palios, K: Kalloni. Asterisk (*) and dark grey background denote species with >1% contribution to the overall species cover recorded, based on SIMPER analysis. Double asterisk (**) and/or light grey background indicate species/groups of species that were present in all geographic localities.

Taxa
Ochrophyta
Dictyota implexa (Desfontaines) J.V.Lamouroux, 1809 $^{\text{N}}$
Mucilagenous algae indet $^{\text{NSK}}$
Chlorophyta
Codium effusum (Rafinesque) Delle Chiaje $^{\text{N}}$
Cladophora pellucida (Hudson) Kützing $^{\text{ALNS}}$
Flabellia petiolata (Turra) Nizamuddin $^{\text{ANSP */**}}$
Halimeda tuna (J.Ellis & Solander) J.V.Lamouroux $^{\text{NSP}}$
Pseudochlorodesmis furcellata (Zanardini) Børgesen $^{\text{NS}}$
Valonia macrophysa Kützing $^{\text{ALNS}}$
Turf indent $^{\text{ALNSPK */**}}$
Rhodophyta
Acrodiscus vidovichii (Meneghini) Zanardini $^{\text{NSP}}$
Amphiroa rigida J.V.Lamouroux $^{\text{N}}$
Lithophyllum stictaeforme/cabiochiae cf. $^{\text{ALNSP */**}}$
Mesophyllum alternans (Foslie) Cabioch & M.L.Mendoza $^{\text{ALNSPK */**}}$
Neogoniolithon mamillosum (Hauck) Setchell & L.R.Mason $^{\text{ALNSP */**}}$
Peyssonnelia rosa-marina Boudouresque & Denizot $^{\text{ALNSP */**}}$
Peyssonnelia rubra / bornetii cf. $^{\text{ALNSPK */**}}$
Peyssonnelia squamaria (S.G.Gmelin) Decaisne $^{\text{ALNSPK */**}}$
Peyssonnelia indet $^{\text{ALNSP */**}}$
Sphaerococcus coronopifolius Stackhouse $^{\text{NS}}$
Soft red algae indet $^{\text{ALNSP */**}}$
Encrusting calcareous algae indet $^{\text{ALNSPK */**}}$
Foraminifera
Miniacina miniacea (Pallas, 1766) $^{\text{LN}}$
Porifera
Acanthella acuta Schmidt, 1862 $^{\text{APK}}$
Agelas oroides (Schmidt, 1864) $^{\text{ALNSP */**}}$
Aplysilla sulfurea Schulze, 1878 $^{\text{ALSPK **}}$
Axinella cannabina (Esper, 1794) $^{\text{K}}$
Axinella damicornis (Esper, 1794) $^{\text{ALNSPK */ **}}$
Axinella verrucosa (Esper, 1794) $^{\text{ALPK}}$
Axinella indet $^{\text{ALNSP **}}$
Cacospongia mollior (Schmidt, 1862) $^{\text{P}}$
Chondrosia reniformis Nardo, 1847 $^{\text{LSK */**}}$
Clathrina clathrus (Schmidt, 1864) $^{\text{LK}}$
Cliona celata Grant, 1826 $^{\text{P}}$
Cliona schmidti (Ridley, 1881) $^{\text{LNP **}}$
Cliona viridis (Schmidt, 1862) $^{\text{ALNSK */**}}$
Cliona indet $^{\text{LNS}}$
Crambe crambe (Schmidt, 1862) $^{\text{ALNSPK */**}}$
Dendroxea lenis (Topsent, 1892) $^{\text{ALP}}$
Dictyonella incisa (Schmidt, 1880) $^{\text{ASPK */**}}$
Dictyonella indet $^{\text{SK}}$
Dysidea fragilis (Montagu, 1814) $^{\text{ALP}}$
Fasciospongia cavernosa (Schmidt, 1862) $^{\text{K}}$
Haliclona (Halichoclona) fulva (Topsent, 1893) $^{\text{ALSPK */**}}$
Haliclona (Soestella) mucosa (Griessinger, 1971) $^{\text{ALNP **}}$
Haliclona sp.1 $^{\text{K}}$
Haliclona sp.2 $^{\text{S}}$
Hemimycale columella (Bowerbank, 1874) $^{\text{P}}$
Hexadella racovitzai Topsent, 1896 $^{\text{ALNS}}$
Ircinia oros (Schmidt, 1864) $^{\text{ASPK */**}}$
Ircinia paucifilamentosa Vacelet, 1961 $^{\text{S}}$
Ircinia variabilis (Schmidt, 1862) $^{\text{AS}}$
Oscarella imperialis Muricy, Boury-Esnault, Bézac & Vacelet, 1996 $^{\text{L}}$
Petrosia (Petrosia) ficiformis (Poiret, 1789) $^{\text{LNPK**}}$
Phorbas tenacior (Topsent, 1925) $^{\text{ALPK}}$
Plakina sp. $^{\text{L}}$
Pleraplysilla spinifera (Schulze, 1879) $^{\text{P}}$
Sarcotragus foetidus Schmidt, 1862, $^{\text{ASPK */**}}$
Sarcotragus spinosulus Schmidt, 1862 $^{\text{LPK}}$
Spirastrella cunctatrix Schmidt, $^{\text{ALNSPK */**}}$
Suberitidae $^{\text{K}}$
Tethya aurantium (Pallas, 1766) $^{\text{P}}$
Yellow encrusting Porifera $^{\text{ALNSPK */**}}$
Small encrusting Porifera $^{\text{ALNSPK */**}}$
Cnidaria
Hydrozoa spp. $^{\text{NS}}$
Caryophyllia (Caryophyllia) inornata (Duncan, 1878) $^{\text{ALNSPK **}}$
Eunicella cavolini (Koch, 1887) $^{\text{ALNSPK **}}$
Hoplangia durotrix Gosse, 1860 $^{\text{LS}}$
Leptopsammia pruvoti Lacaze-Duthiers, 1897 $^{\text{ALNSP **}}$
Madracis pharensis (Heller, 1868) $^{\text{ALP}}$
Paracyathus pulchellus (Philippi, 1842) $^{\text{LS}}$
Parazoanthus axinellae (Schmidt, 1862) $^{\text{ALNSPK */**}}$
Phyllangia americana mouchezii (Lacaze-Duthiers, 1897) $^{\text{L}}$
Polycyathus muellerae (Abel, 1959) $^{\text{ALK}}$
Scleractinia indet $^{\text{ALNSK **}}$
Annelida
Eupolymnia nebulosa (Montagu, 1818) $^{\text{K}}$
Myxicola infundibulum (Montagu, 1808) $^{\text{AL}}$
Filograna implexa / Salmacina dysteri $^{\text{LNSK **}}$
Serpula vermicularis Linnaeus, 1767 $^{\text{LPK}}$
Serpulidae $^{\text{ALNPK **}}$
Bryozoa
Adeonella spp. $^{\text{LNSK**}}$
Beania magellanica (Busk, 1852) $^{\text{NS}}$
Bugula spp. $^{\text{LN}}$
Cellaria sp. $^{\text{NS}}$
Hornera frondiculata (Lamarck, 1816) $^{\text{NS}}$
Reteporella grimaldii (Jullien, 1903) $^{\text{ALS}}$
Rhynchozoon neapolitanum Gautier, 1962 $^{\text{ALNSPK */**}}$
Schizomavella spp. (Hassall, 1842) $^{\text{ALNSPK */**}}$
Schizoretepora sp. $^{\text{S}}$
Smittina cervicornis (Pallas, 1766) $^{\text{S}}$
Bryozoa indet $^{\text{ANSP **}}$
Tunicata
Aplidium elegans (Giard, 1872) $^{\text{AL}}$
Clavelina dellavallei (Zirpolo, 1825) $^{\text{NSK}}$
Cystodytes dellechiajei (Della Valle, 1877) $^{\text{K}}$
Didemnum sp1 $^{\text{K}}$
Didemnum sp2 $^{\text{K}}$
Halocynthia papillosa (Linnaeus, 1767) $^{\text{ALNK **}}$
Mollusca
Lithophaga lithophaga (Linnaeus, 1758) $^{\text{P}}$
Rocellaria dubia (Pennant, 1777) $^{\text{N}}$
Thylacodes arenarius (Linnaeus, 1758) $^{\text{P}}$
Bivalvia indet $^{\text{N}}$

3.2 Biodiversity patterns

To investigate biodiversity patterns, only organisms identified to a low taxonomic level were used, i.e. 89 taxa identified to species or genus level. Mean number of species per transect-sample was 29.7 ± 5, while total number of species per locality ranged between 55 and 60 species (**Fig 6**). Biodiversity indices showed that biodiversity patterns were relatively similar among different sites (**Fig 7**). Although number of species (S) presented some variability across sites (38–49 species), Shannon's diversity index (accounting both for number of species and relative cover) was more stable with values ranging between 2.2 and 2.6.

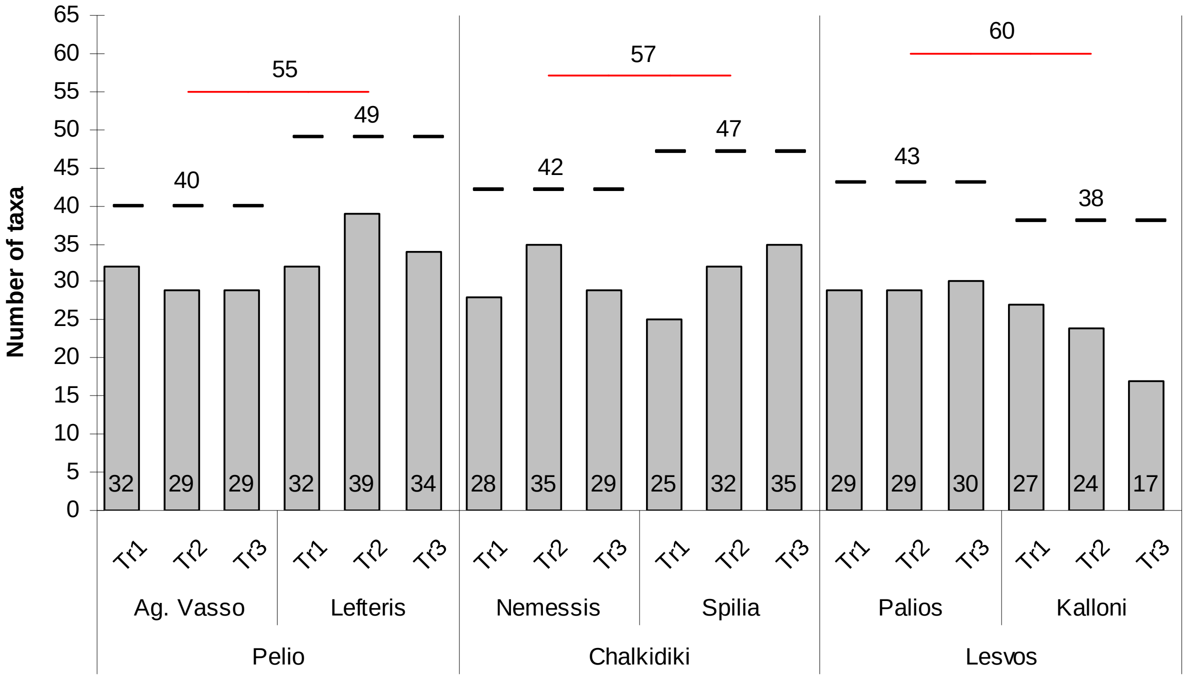

Fig 6. Total number of taxa identified at the level of species/genus per transect-sample (grey bars and values within), site (black dashed lines and associated standing values), and geographic locality (continuous red lines and associated standing values). The prefix "Tr" indicates transect-sample number.

According to the PERANOVA results biodiversity indices displayed no significant differences among localities, or between sites found within the same locality (**Table 4**). The relative contribution of different species per site is presented in **Fig 8**.

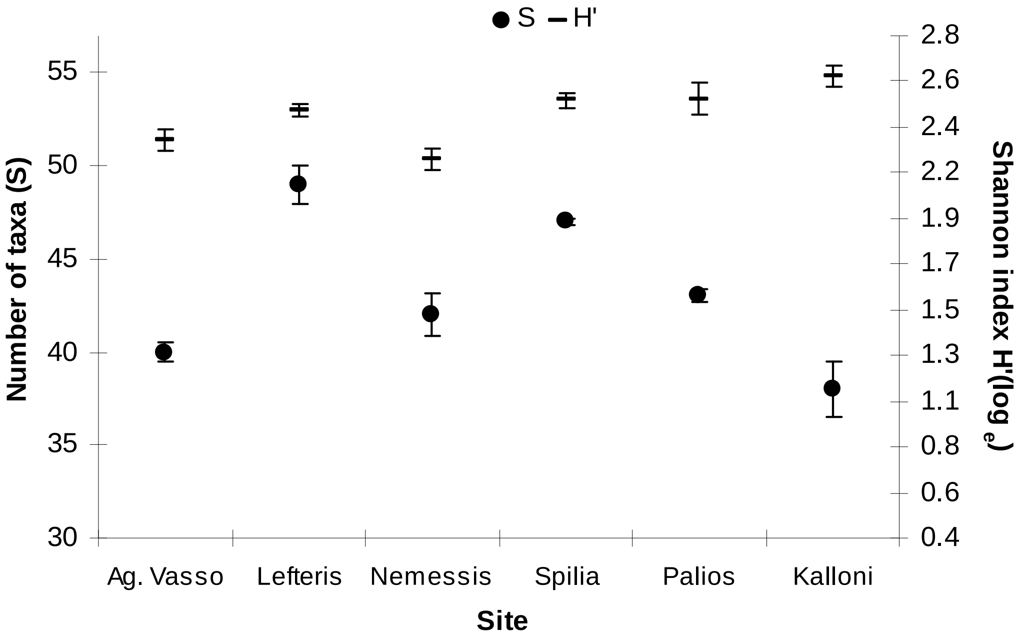

Fig 7. Diversity indices per site. S: total number of taxa identified to the species or genus level, $H'(\log_e)$: Shannon's index of biodiversity. Whisker span indicates standard error of the mean.

Table 4. PERANOVA analysis on biodiversity indices describing coralligenous assemblages dominated by *E. cavolini* across localities (fixed factor), and between sites (random factor) nested within the same locality.

Species Number - S						**Shannon - $H'(\log_e)$**					
PERANOVA						PERANOVA					
Source	**df**	**SS**	**MS**	**Pseudo-F**	**p**	**Source**	**df**	**SS**	**MS**	**Pseudo-F**	**p**
Locality	2	152.33	76.17	2.5	0.2	Locality	2	0.3	0.15	8.8	0.06
Site(Locality)	3	92.83	30.94	2.03	0.16	Site(Locality)	3	0.05	0.02	0.5	0.7
Res	12	183.33	15.28			Res	12	0.4	0.03		
Total	17	428.5				Total	17	0.7			

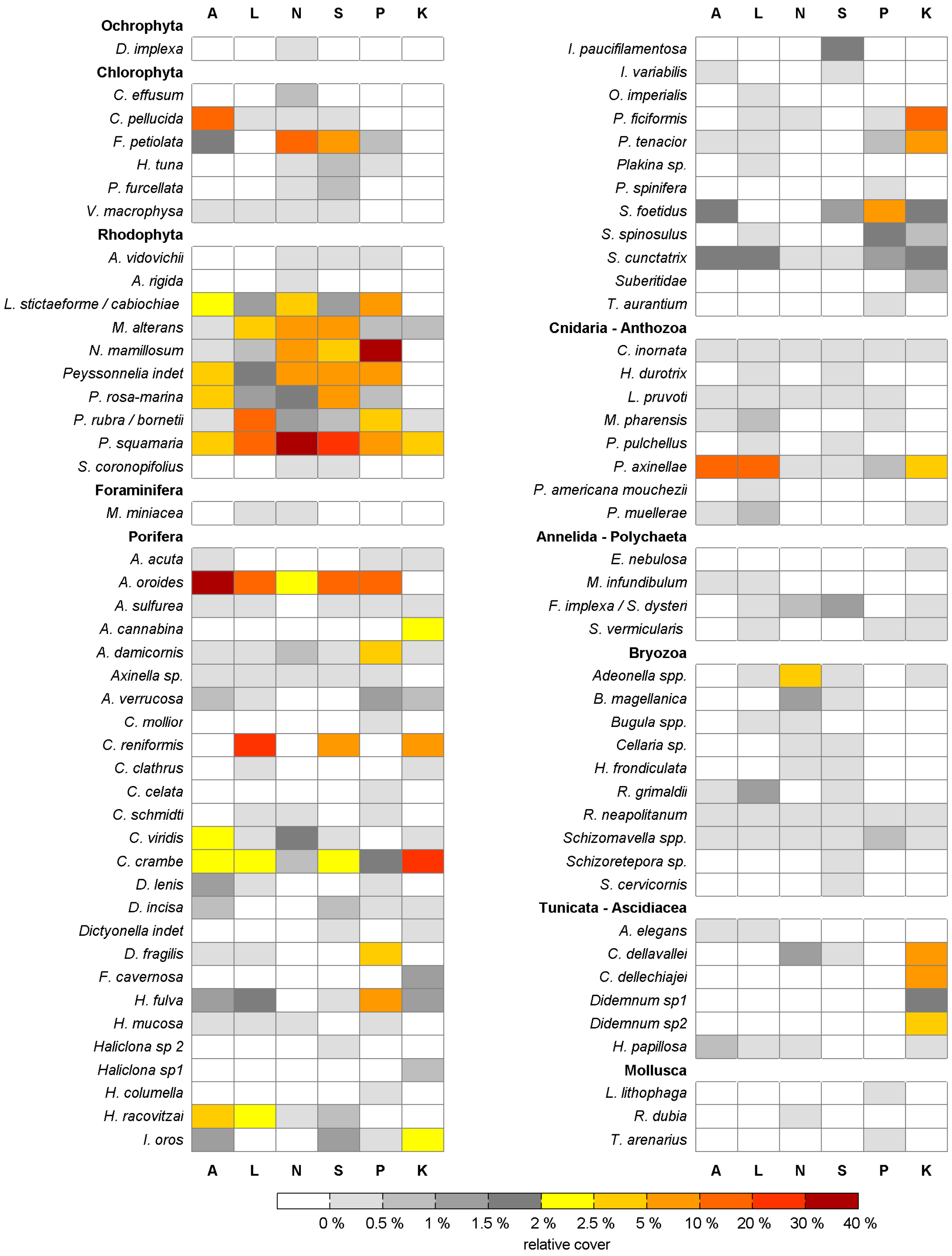

Fig 8. Contribution of different taxa identified at the level of species/genus to the relative species area cover per site. Upper-case letters indicate sites; **A**: Ag. Vasso, **L**: Lefteris, **N**: Nemessis, **S**: Spilia, **P**: Palios, **K**: Kalloni.

3.3 Community structure at different spatial scales

The ordination (i.e. non-metric multidimentional scaling – MDS) of the examined localities and sites according to the structural similarity of their coralligenous assemblages, revealed that most geographic localities formed a single main cluster (**Fig 9a**). Specifically, the localities of Chalkidiki, Pelio, Lesvos (with the only exception of Kalloni site), were grouped together at a similarity level of 50%. Furthermore, individual sites formed distinct smaller clusters at a similarity level of 65%. The only exceptions were the sites of Chalkidiki where the majority of transect-samples did not show further differentiation at the similarity level of 65%, as well as the site of Kalloni (locality of Lesvos), which was positioned at a distance from the primary clustering of sites. To determine the main species responsible for the observed spatial patterns, a Spearman rank order correlation of the main taxa associated to specific sites was projected on the MDS graph using correlation values higher than 0.6 (**Fig 9b**).

Along the notional 1st axis of the MDS graph (i.e. x-axis), the separation of Kalloni from the rest of the sites appears to be due to a predominance of the encrusting species *C. crambe*, *S. cuntantrix*, *P. tenacior*, *C. dellechiajei*, and *P. axinellae*, and the presence of several scleractinian species, whereas sites located at the other extreme of the axis are more strongly associated with *Lithophyllum* sp., *N. mamillosum*, *Peyssonelia indet*, and unidentified Encrusting calcareous algae. Correlation values along the 2nd MDS axis (i.e. y-axis) revealed that sites located at the upper part of the graph (i.e. sites of the Chalkidiki locality) were more strongly correlated to the presence of several species of Chlorophyta (specifically, turf, *H. tuna*, *F. petiolata*, and *Codium effusum*), Rhodophyta (*Sphaerococcus coronopifolius* and *Acrodiscus vidovichii*), and Bryozoa (*Adeonella* spp., *B. mangellanica*, *Bryozoa indet*). On the other hand, sites positioned at the lower parts of the graph, i.e. Palios, Ag. Vasso and Lefteris, displayed a high correlation with several massive and encrusting sponge species (*A. oroides*, *Dendroxea lenis*, *H. mucosa*, Small encrusting Porifera), the scelractinian *L. pruvoti*, and several unidentified Soft red algal species.

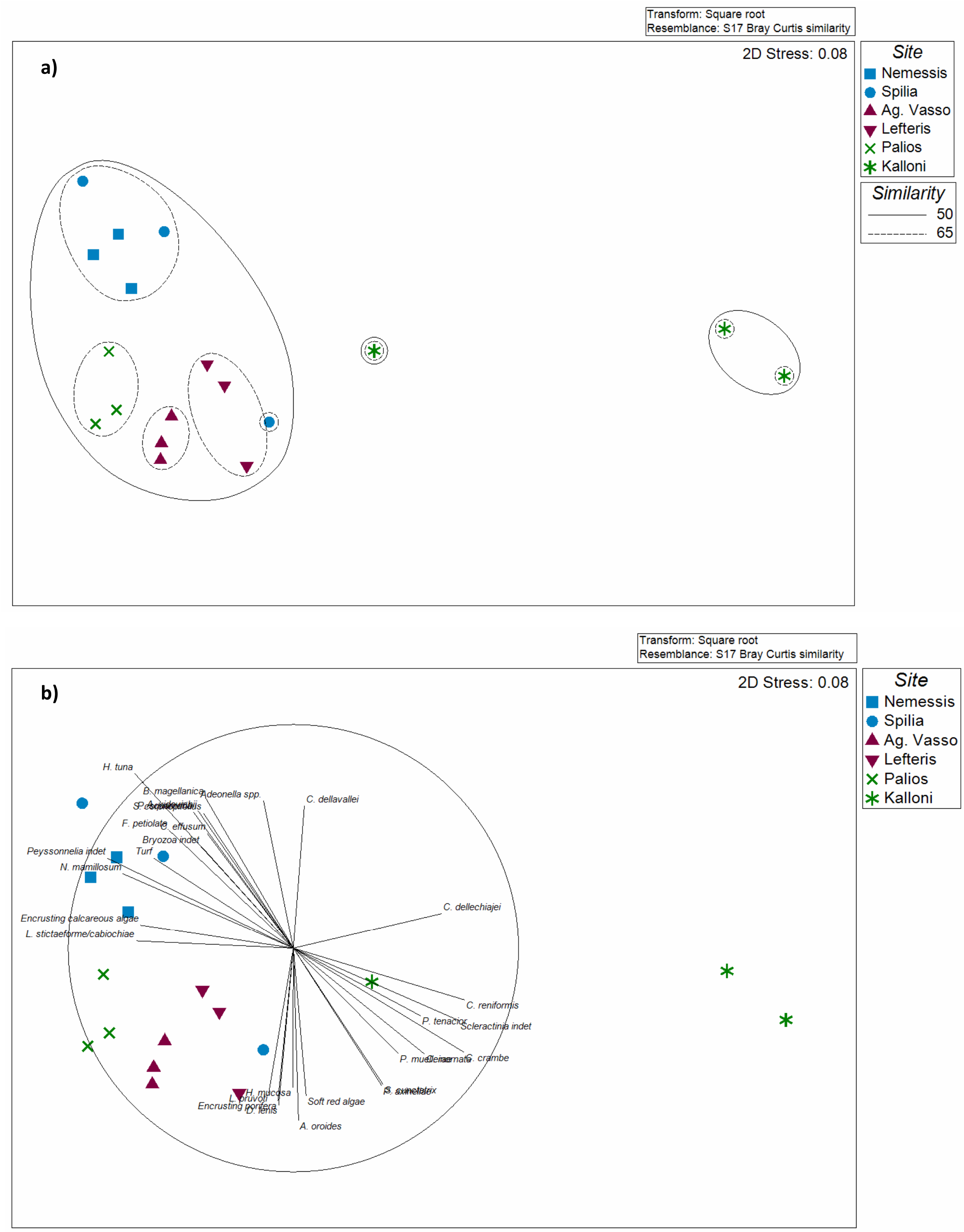

Fig 9. Multidimensional scaling analysis (MDS) of community structure in coralligenous assemblages dominated by *E. cavolini*. Symbols indicate the three photographic transect-samples taken per site (i.e. corresponding to eight images per transect-sample); colours denote geographic locality. a) Clustering lines show groups of assemblages at a similarity level of 50% (continuous line) or 65% (dashed line). b) Spearman rank order correlation projection on the main MDS graph, showing the species/groups of species responsible for the clustering patterns at a correlation level >0.6.

The two-way PERMANOVA analysis confirmed that variability in community composition was higher between sites found within the same geographic locality, rather than between localities (**Table 5**). The pair-wise comparisons detected significant differences only between the sites of Ag. Vasso and Lefteris (Pelio locality), and Palios and Kalloni (Lesvos locality).

According to the SIMPER analysis (**Table 6a**), average dissimilarity of the former group of sites was 40% and was mainly due to a greater relative cover of Chlorophyta (i.e. Turf, and *C. pellucida*) and the sponge *A. oroides* at the site of Ag. Vasso, whereas Lefteris site had a higher cover of different Peyssonelia species, *M. alterans*, the massive sponge *C. reniformis*, and the erect bryozoan *R. grimaldii*.

Table 5. PERMANOVA analysis on community composition of coralligenous assemblages dominated by *E. cavolini* across localities (fixed factor), and between sites (random factor) nested within the same locality. Pair-wise comparisons were undertaken only when the main test indicated significant differences.

Community structure								
	PERMANOVA					Pair-wise comparisons		
Source	**df**	**SS**	**MS**	**Pseudo-F**	**p**	**Sites within locality**	**t**	**p**
Locality	2	8338.6	4169.3	1.45	0.24	Ag. Vasso - Lefteris	2.5	0.01*
Site(Locality)	3	8645.1	2881.7	4.74	0.0001*	Nemessis - Spilia	1.2	0.27
Res	12	7287.2	607.27			Palios - Kalloni	2.6	0.02*
Total	17	24271						

* indicates statistical significance.

Between the two sites in the locality of Lesvos, the SIMPER results validated the patterns revealed by the MDS and the associated Spearman rank order correlation, as the two sites displayed a large average dissimilarity (70%, **Table 6b**). In accordance with the correlation analysis, Kalloni was characterised by a greater cover of encrusting forms of sponge, tunicate and anthozoan species (e.g. *C. crambe*, *P. tenacior*, *C. dellechiajei*, *Didemnum* sp2, *P. axinellae*), and the massive sponge species *P. ficiformis* and *C. reniformis*. On the contrary, Palios had a higher cover of turf and encrusting coralline algae (e.g. *N. mamillosum*, *L. stictaeforme/cabiochiae*, Encrusting calcareous algae, *Peyssonnelia indet*), while the most abundant sponge species were *A. oroides* and *H. fulva*.

Table 6. SIMPER analysis of dissimilarity for the two groups of sites that had statistical differences in community structure according to the PERMANOVA results; a) Ag. Vasso and Lefteris, b) Palios and Kalloni. Only species with a contribution >2% to the observed dissimilarity are shown.

a)

Locality	**Pelio**					
Sites	**Ag. Vasso**	**Lefteris**				
Taxa/groups	**Av. Abund.**		**Av. Diss.**	**Diss./SD**	**Contrib.%**	**Cum.%**
C. reniformis	0	9.27	4.18	3.84	10.65	10.65
P. rubra / bornetii	0.47	7	2.94	6.3	7.5	18.15
P. squamaria	3.61	9.05	2.45	4.08	6.23	24.39
C. pellucida	5.24	0.96	1.92	2.34	4.89	29.28
A. oroides	10.76	6.96	1.72	3.7	4.38	33.66
Mesophyllum sp.	1	4.17	1.43	2.9	3.64	37.3
Turf	11.33	8.18	1.42	6.58	3.62	40.92
Soft red algae	4.97	2.58	1.36	1.48	3.48	44.4
Encrusting calcareous algae	13.61	10.69	1.32	1.93	3.37	47.77
Small encrusting porifera	10.32	7.82	1.13	5.54	2.87	50.64
F. petiolata	2.28	0	1.03	5.93	2.62	53.25
P. rosa-marina	2.77	2.03	0.95	1.33	2.41	55.67
H. fulva	1.25	1.96	0.89	1.19	2.26	57.92
R. grimaldii	0.11	1.88	0.83	1.39	2.12	60.04
S. foetidus	1.77	0	0.81	1.1	2.06	62.1
C. viridis	1.89	0.11	0.8	0.92	2.03	64.13
Average dissimilarity = 39.24						

b)

Locality	**Lesvos**					
Sites	**Palios**	**Kalloni**				
Taxa/groups	**Av. Abund.**		**Av. Diss.**	**Diss./SD**	**Contrib.%**	**Cum.%**
N. mamillosum	9.77	0	4.66	3.13	6.66	6.66
C. crambe	2.23	10.23	3.81	3.17	5.44	12.1
P. ficiformis	0.45	7.84	3.5	12.54	5	17.1
Encrusting calcareous algae	12.16	4.95	3.42	1.47	4.89	21.99
Turf	11.83	6.4	3.12	1.53	4.46	26.45
C. reniformis	0	6.55	3.12	3.89	4.46	30.91
Mucilagenous algae	0	6.39	3	1.33	4.29	35.2
A. oroides	5.95	0	2.82	17.34	4.03	39.23
L. stictaeforme/cabiochiae	5.63	0	2.66	4.26	3.8	43.03
C. dellechiajei	0	5.21	2.46	4.9	3.51	46.54
Small encrusting porifera	10.33	5.45	2.42	1.48	3.46	50
C. dellavallei	0	5.05	2.4	1.16	3.43	53.43
P. tenacior	0.92	6.02	2.39	1.59	3.41	56.84
Peyssonnelia indet	4.97	0	2.37	5.13	3.38	60.22
Didemnum sp2	0	3.77	1.78	1.28	2.55	62.76
P. squamaria	4.23	2.23	1.73	1.63	2.46	65.23
S. foetidus	3.57	2.12	1.58	1.24	2.26	67.48
H. fulva	4.88	1.63	1.57	1.82	2.24	69.73
P. axinellae	1.45	3.49	1.44	1.17	2.06	71.79
Average dissimilarity = 70.03						

4. Discussion

This study represents the first quantitative assessment of the shallow coralligenous assemblages of the Aegean Sea, and directly addresses the need for baseline data regarding their diversity and conservation status (UNEP-MAP-RAC/SPA 2008, 2015). By focusing on assemblages that are dominated by the yellow gorgonian *Eunicella cavolini*, this work contributes to the better understanding of one of the most characteristic coralligenous facies across the Meditteranean, and provides the basis for future comparisons both at a local and at a basin-scale level.

4.1 Community structure and composition

Results show that coralligenous assemblages of the Aegean Sea found in waters shallower than 40 m encompass an important number of conspicuous sessile organisms (see also Appendix B). The majority of these species have also been reported from coralligenous communities in other parts of the NW Mediterranean (e.g. Cocito et al. 2002; Kipson et al. 2011; UNEP-MAP-RAC/SPA 2011; Deter et al. 2012; Gatti et al. 2012; Teixidó et al. 2013; Piazzi et al. 2014), the Adriatic (Ponti et al. 2011), and in previous studies of hard substrate sciaphillous assemblages in the Aegean Sea over the same depth range (Antoniadou et al. 2006).

The main algal bio-constructors of coralligenous assemblages in the investigated sites were the calcareous species *N. mamilosum*, *L. stictaeforme/cabiochiae*, *M. alterans*, and *P. rosa-marina*, but their relative contribution to the area cover varied among different sites. These four species have been identified as the main algal builders in most regions of the Mediterranean (Feldmann 1937; Hong 1983; Piazzi et al. 2010; Teixidó et al. 2013), and differences in their relative contribution to the coralligenous built-ups have been related to depth, light, temperature, and hydrodynamism (Sartoretto et al. 1996; Garrabou & Ballesteros 2000; Ballesteros 2006).

In terms of animal species, most sites of the Aegean Sea were characterised by an extensive cover of sponges, which presented different forms and functional roles in the structuring of the frameworks. These included: a) several encrusting or errant species (e.g. *C. crambe*, *D. fragilis*, *H. fulva*) that expand over large surface areas and play a structural role by binding different substrate components together (i.e. Fagerstrom 1991; Cocito 2004); b) massive (e.g. *A. oroides*, *I. oros*, *S. foetidus*) or erect sponges (e.g. of the genus Axinella), which, alongside the gorgonian *E. cavolini*, contribute to the three-dimensional complexity of the assemblages and provide additional microhabitats for numerous macro- or micro-dwelling species (e.g. Koukouras et al. 1985; Carvalho et al. 2014; Cúrdia et al. 2015); and c) species of the genus Cliona, which together with sea urchins and the molluscs *Rocellaria dubia* and *Lithophaga lithophaga* represent the main bio-eroders of the coralligenous assemblages throughout the Mediterranean (Cerrano et al. 2001; Ballesteros 2006). On the contrary, the area cover of other animal species was low and only locally pronounced in few sites. Specifically, although bryozoans represent an important component of coralligenous assemblages in other parts of the Mediterranean (e.g. Ferdeghini et al. 2000, 2001; Kipson et al. 2011; Piazzi et al. 2014), the number of conspicuous, arborescent bryozoan species was relatively low in the investigated sites, and their total cover was less than 1%. Furthermore, although many scleractinian species were recorded, there was an overall lack of other large anthozoans (apart from *E. cavolini*), such as alcyonarians or other gorgonians. These observations are in line with previous reports regarding other regions of the Aegean Sea, which suggest that due to the higher water temperatures and more oligotrophic conditions, large anthozoans are usually confined in deeper waters (Pérès & Picard 1958; Laborel 1960; Salomidi et al. 2009); see also Chapter 4 (Sini et al. 2015).

4.2 Biodiversity patterns

In terms of biodiversity, variability in the number of species among sites was generally low (range: 38 to 49), and despite differences in the relative contribution of different species to the overall species cover per site, no statistical differences were observed at the level of sites or localities. Given the wide range of approaches that have been applied for the study of coralligenous assemblages to date, our results on biodiversity patterns can only be directly compared to the studies of Kipson et al. (2011) and Kipson (2013), who examiend coralligenous assemblages dominated by the purple gorgonian *P. clavata* in the NW Mediterranean and E Adriatic Sea, respectively. Application of a common sampling protocol indicated that the total number of species recorded in different sites of the Aegean Sea is comparable to that reported from NW Mediterranean sites (range: 44–58, depths: 17–24 m), but is lower to several sites of the E Adriatic Sea (range: 47–79, depths: 30–40 m).

With regards to the sampling design, a key parameter is the minimum sampling area used, which should be large enough to allow the adequate representation of patchily-distributed or less abundant species, concurrently accounting for time limitations imposed by the underwater scenario (Bianchi et al. 2004). Kipson et al. (2011) conducted a systematic biodiversity assessment of *P. clavata* coralligenous facies over wider surface areas (i.e. up to 4 m^2 per site), and concluded that the minimum sampling area of 1.5 m^2 per site, also used in the current study, accounts for more than 80% of the total number of within site conspicuous species. In comparison to the only other available work on *E. cavolini* assemblages, the number of conspicuous sessile animal species (approx. 27) collected by True (1970) by means of scraping 7500 cm^2 in Marseille was lower than any given site of the Aegean, although this destructive method provided a better account of the small and cryptic species.

4.3 Spatial patterns in community structure

Community structure of coralligenous assemblages in the Aegean Sea presented distinct patterns at different spatial scales. However, statistical differences were only detected at the level of sites situated within the same geographic locality. This suggests that despite localised differences, overall coralligenous assemblages found in different geographic regions of the Aegean Sea share some level of similarity in their species composition. This is in line with previous studies which report a generalized homogeneity in community structure at large geographic scales (Piazzi et al. 2004; 2014). Coralligenous assemblages are intrinsically variable, and identifying the scale at which variability is predominantly expressed is a focal issue in their study in order to meaningfully assess spatial patterns, e.g. in response to stressors. As commonly documented, abiotic conditions and associated biotic interactions for limited resources (space, light and food) result to the patchy distribution of organisms and increased variability within the same assemblage (Garrabou et al. 2002a; Piazzi et al. 2004, 2014). It is thereby not surprising that a number of previous studies have reported higher small-scale variability linked to physical habitat features (depth, orientation, substrate inclination and sedimentation), see for example Ferdeghini et al. (2000), Cocito et al. (2002), Balata et al. (2005), Virgilio et al. (2006), Ponti et al. (2011), Bedini et al. (2014), Piazzi et al. (2014). A common characteristic of these studies however was the much smaller sampling unit employed (400–600 cm^2), when compared to the 5000 cm^2 used in the current study. As pointed out by

Kipson et al. (2011), a small sampling unit tends to amplify stochastic variability of coralligenous species composition at small scales, which obscures and hinders the adequate assessment of variability beyond the scale of replicate samples. Truly, the analyses of Ferdeghini et al. (2000), Ponti et al. (2011) and Piazzi et al. (2014) identified the scale of replicate samples (individual quadrat throws) as the one with the highest variability. Our overall results suggest that the large sampling unit employed in the present study helped to overcome this limitation, whilst enabling detection of differences between sites in the same locality (**Table 5**).

At the wider level of geographic localities, coralligenous assemblages presented a certain degree of variability, as indicated by the clustering of most sites at a similarity level of 50% (**Fig 9**). Although not statistically significant, this variability was mainly due to the extended cover of the chlorophytes *Flabelia petiolata* and *Halimeda tuna*, which characterised the coralligenous assemblages of Chalkidiki, in contrast to the sites of other localities, where chlorophyte cover was lower and mainly restricted to turf-forming species. An extensive cover of *F. petiolata* and *H. tuna* has also been reported for coralligenous assemblages of the NW Mediterranean, where they appear in association with other encrusting calcareous algal species mainly in well-lit areas of relatively deep waters (i.e. zone of 30 m; Cocito et al. 2002; Piazzi & Balata 2011), as well as in shallow water banks (Ballesteros 2006).

On the other hand, at the level of sites belonging to the same geographic locality, significant differences were observed between the two sites of Pelio (i.e. Ag. Vasso and Lefteris), and the two sites of Lesvos (i.e. Palios and Kalloni), while no differences were detected between sites in Chalkidiki. As in previous reports, these differences can be related to variations in environmental factors, disturbance levels, and the associated species interactions. Regarding the differences observed within Pelio locality, Lefteris reef is a northward-facing vertical wall, characterised by increased substrate rugosity, whereas Ag. Vasso site is composed of numerous small rocky outcrops of small inclination and southeast orientation. As a consequence of these somewhat different physiognomic profiles, Lefteris reef is more sciaphilous than Ag. Vasso, despite the former being located in shallower waters. For this reason, the coralligenous assemblage at Lefteris has a lower cover of Chlorophytes than that of Ag. Vasso, and supports a very diverse animal community, particularly sponges and anthozoans. This observation is in line with previous studies which have indicated that coralligenous assemblages of vertical walls are mainly composed of sponges and scelractinians (Ros et al. 1985; Cocito et al. 2002).

Furthermore, within the locality of Lesvos, the site of Kalloni was found to differ significantly to the site of Palios. Overall, community composition at Palios reef was more similar to the coralligenous assemblages found in the localites of Pelio and Chalkidiki, and was characterised by a high cover of encrusting coralline algae (particularly *N. mamilosum* and *L. stictaeforme*) along with a high diversity of sponge species. On the contrary, coralligenous assemblages of Kalloni displayed high dissimilarity to all other investigated assemblages, as the cover of encrusting coralline algae was particularly reduced and replaced by a high cover of encrusting sponge and tunicate species. The specific site is situated in a narrow channel that connects a large enclosed bay with the open sea, and is characterised by increased turbidity, enhanced levels of naturally-induced sedimentation, and high current velocities generated by tidal and wind forces (Millet & Lamy 2002). The significant divergence of Kalloni from the rest of the investigated sites is likely due to the extreme environmental factors predominating in the specific area, which promote the growth of coralligenous assemblages and gorgonian populations in much shallower waters (15 m) than those of the rest of the Aegean (Sini et al. 2015, Chapter 4). Although further investigation of the abiotic factors is essential to better understand the observed community patterns, it is possible that the increased cover of animal species in Kalloni is due to a competitive advantage of animal versus coralline algal species under the reduced light conditions induced by the high turbidity and sedimentation levels (Irvin & Connell 2002; Balata et al. 2005). Besides, the relatively high within site variability in Kalloni (as illustrated by the MDS in **Fig 9**) may partly be explained in relation to *E. cavolini* colony density, which was on average much higher than the rest of the sites (**Table 2**). It is hypothesized that, in patches where the increased density of *E. cavolini* colonies formed a thick canopy, a further reduction in light levels and accessibility to food resources, restricted the growth of the understorey to only encrusting forms of animal species (especially sponges and tunicates). On the other hand, in patches of lower gorgonian density, a slight increase of light and substrate availability enabled the growth of algae and other massive or erect sponge species (e.g. encrusting coralline algae, *Peyssonelia* spp., *Axinella cannabina* and *S. fetidus*).

4.4 Potential threats and disturbances

Apart from the prevalent effects of natural disturbances, Kalloni site was also more exposed to human-induced disturbances. Considering its shallow depth range, stressors include direct mechanical damage caused by fishing gear (especially long-lines, traps and nets) that were scattered over most parts of the site, recurrent periods of nutrient loads which have previously been recorded in the wider area (SoHelME 2005; Spatharis et al. 2007, 2009), and potential thermal anomalies of the water column. During the course of this study, assessment of gorgonian populations at Kalloni indicated the occurrence of a mass mortality episode (**Fig 10**). Specifically, *E. cavolini* colonies showed extensive tissue loss and overgrowth by other organisms (Sini et al. 2015, Chapter 4), while in shallower, more photophilous parts of the site (<15 m) a dense population of the white gorgonian *E. singularis* almost disappeared within approximately two years. Although necrosis of other benthic organisms was not systematically measured in the photoquadrat samples, several sponge species had visible signs of partial damage or were overgrown by turf and filamentous mucilaginous algae. Given the lack of regular monitoring, neither the causes that triggered this outbreak, nor the time of initiation and duration of the stressor/s involved can be directly addressed through the present study. However, it is possible that the distinctive composition of the coralligenous assemblages in Kalloni site may be a result of a large disturbance which has led to a shift in community structure and caused the prevalence of encrusting animal forms. A similar observation of a shift from erect to encrusting forms was also observed by di Camillo & Cerrano (2015), following two consecutive mass mortality outbreaks in the NW Adriatic.

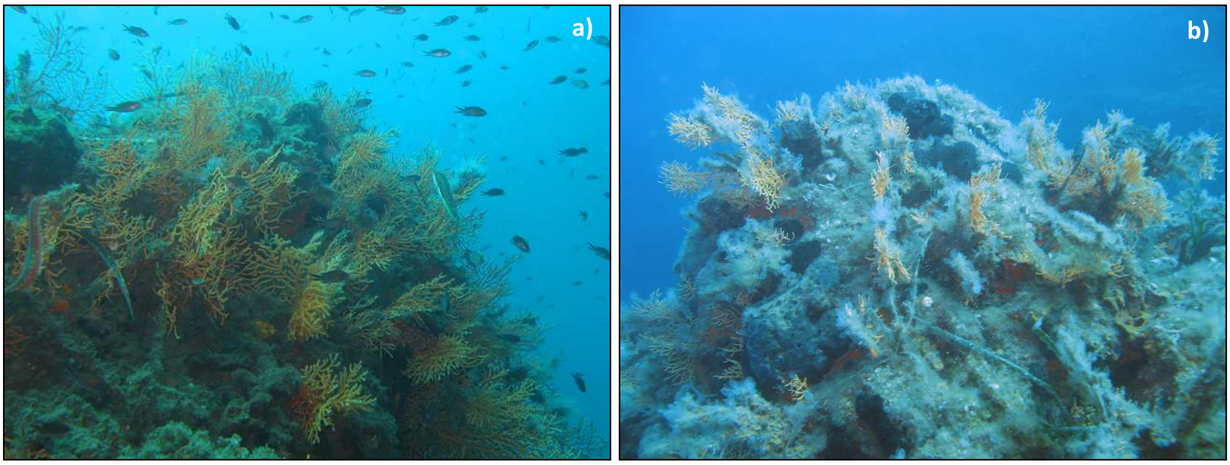

Fig 10. Coralligenous assemblage dominated by *E. cavolini* in Kalloni site; depth is 15 m. Image a) was taken in June 2010, while image b) in May 2013. Note the degraded state of the colonies in 2013, characterised by turf and ascidian overgrowth, alongside fishing gear leftovers.

In the remaining sites, the common presence of ghost nets and fishing lines in all investigated areas highlights the widespread occurrence of this potential threat, the effects of which are not easy to detect and quantify through one-off studies. Furthermore, the invasive species *Womersleyella setacea* was observed at both sites of Chalkidiki, while *Caulerpa cylindracea* was recorded in Palios site (Lesvos locality). The presence of these two species has previously been reported at a similar depth range from nearby sites to our respective investigated areas (Antoniadou et al. 2007; Gerovasileiou et al. 2009). In the current study, neither of them was present in the photographic samples, although visual observations during the surveys confirmed their pronounced cover at the shallower parts of the investigated sites. Moreover, filamentous mucilagineous algal aggregates were seen to periodically flourish in several sites and to fully cover gorgonian colonies. Although no apparent ecological damage was detected, their potentially harmful effects on benthic organisms (mainly caused through starvation or suffocation) may be exacerbated under conditions that enhance their prolonged persistence (Schiaparelli et al. 2007; Giuliani et al. 2005).

Overall, this study provides important reference data that serve as a basis for future assessment of coralligenous assemblages in the Aegean Sea, and for comparisons with other Mediterranean regions. It further highlights the necessity to implement systematic monitoring that will improve our understanding regarding current trends, reinforce the evaluation of conservation status in different parts of the Aegean Sea, and help mitigate and manage potential disturbances or threats.

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Κεφάλαιο 3

Γεωγραφική κατανομή της *Eunicella cavolini* (Koch, 1887) στη Μεσόγειο

Περίληψη

Η εργασία αφορά στη διερεύνηση και χαρτογράφηση της γεωγραφικής εξάπλωσης της κίτρινης γοργονίας *Eunicella cavolini* (Οκτωκοράλλια, Ανθόζωα) στη Μεσόγειο, συγκεντρώνοντας αναφορές παρουσίας/απουσίας και ετερογενή χωρικά δεδομένα από επιστημονικές μελέτες, γκρίζα βιβλιογραφία, και αυτόνομους παρατηρητές. Επιπλέον, μέσω εκτενούς ανασκόπησης των σχετικών επιστημονικών συγγραμμάτων, αποτιμήθηκε η υπάρχουσα γνώση σχετικά με την οικολογία και βιολογία του είδους. Τα αποτελέσματα συνηγορούν στο ότι το συγκεκριμένο είδος γοργονίας παρουσιάζει ευρεία εξάπλωση (από τη Θάλασσα του Αλμποράν έως τη Θάλασσα του Μαρμαρά), αλλά η παρουσία του είναι πιο συχνή κατά μήκος των Ιταλικών και Γαλλικών ακτών, καθώς και στην Α Αδριατική και στο Αιγαίο. Πληθυσμοί του είδους έχουν κυρίως καταγραφεί σε βάθη από <10–40 m, αν και συχνά εντοπίζονται σε βαθύτερα νερά έως και 220 m. Παρόλο που η κίτρινη γοργονία θεωρείται ως ένα από τα πιο σημαντικά είδη των υποθαλάσσιων περιοχών σκληρού υποστρώματος της Μεσογείου (συμπεριλαμβανόμενων των κοραλλιγενών σχηματισμών), η διερεύνηση της δυναμικής των πληθυσμών του είδους, της οικολογίας του, και της κατάστασης διατήρησης είναι ελλιπής, και κυρίως περιορίζεται σε μελέτες που έχουν λάβει χώρα στις ΒΔ και κεντρικές περιοχές της Μεσογειακές λεκάνης.

Chapter 3

Distribution of *Eunicella cavolini* (Koch, 1887) across the Mediterranean

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Abstract

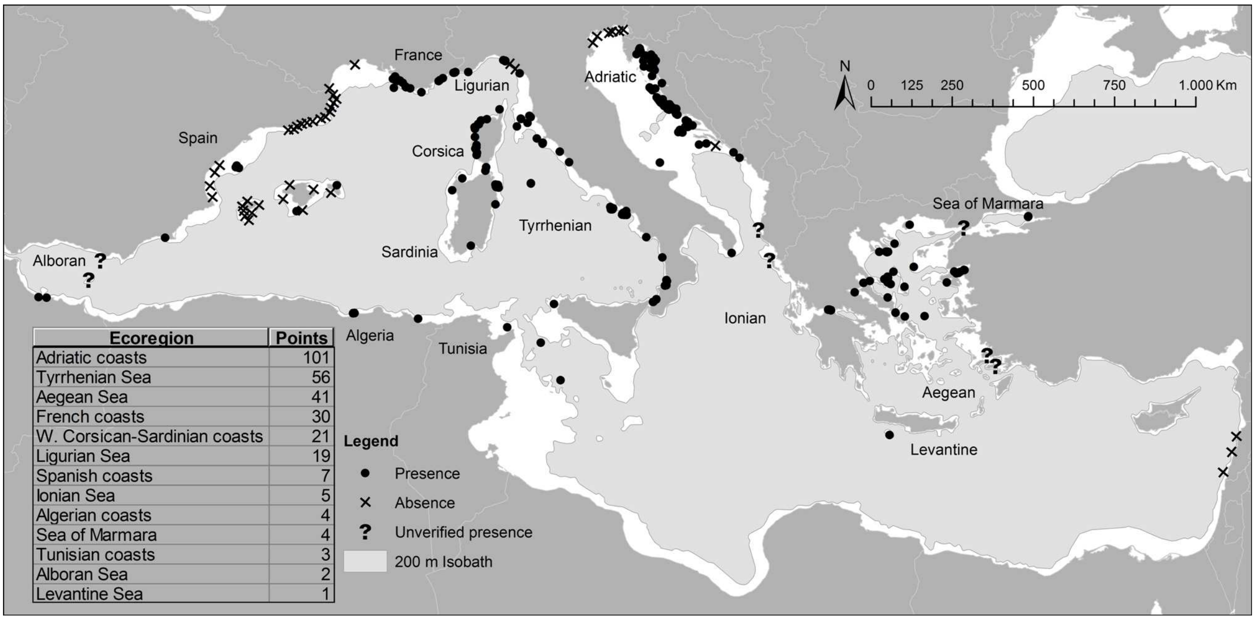
The distribution of *Eunicella cavolini* (Octocorallia, Anthozoa) was mapped based on scientific data and observers' information, in order to depict its geographical range across the Mediterranean. Moreover, an overview of scientific literature was realized to assess the current state of knowledge regarding its populations. Results show that *E. cavolini* displays an extensive distribution, from the Alboran to the Sea of Marmara, but is more common at the Italian, French, E Adriatic and N Aegean coasts. Populations were mainly recorded at depths of <10-40 m, but also in deeper waters up to 220 m. Although *E. cavolini* is regarded as one of the most common structural species of Mediterranean hard substrates, including coralligenous outcrops, scientific information regarding its population dynamics, ecology, and conservation status is very limited and restricted to certain regions of the northwestern and central Mediterranean.

1. Introduction

Coralligenous communities develop over a wide range of benthic habitats and encompass several assemblages. Mapping of constituent facies and acquisition of basic ecological information are key objectives to their conservation. *Eunicella cavolini* is one of the most common octocoral species in the W Mediterranean (Weinberg 1980), while benthic assemblages dominated by this gorgonian have been acknowledged as one of the most typical coralligenous facies (UNEP-MAP-RAC/SPA 2007). This work compiles information regarding the presence of *E. cavolini* populations across the Mediterranean, and provides new data from under-explored areas.

2. Materials and Methods

Information on presence/absence and depth distribution of *E. cavolini* was defined based on a thorough review of scientific documents, grey literature, diving guides, communications with divers, and *in situ* scientific research (see Appendix A for list data sources). Point data were combined in a GIS platform to visualize the geographical information, while scientific literature was categorized according to geographical region and research topic.



Ecoregion	Points
Adriatic coasts	101
Tyrrhenian Sea	56
Aegean Sea	41
French coasts	30
W. Corsican-Sardinian coasts	21
Ligurian Sea	19
Spanish coasts	7
Ionian Sea	5
Algerian coasts	4
Sea of Marmara	4
Tunisian coasts	3
Alboran Sea	2
Levantine Sea	1

Fig 1. Distribution of *E. cavolini* in the Mediterranean.

3. Results

E. cavolini populations are represented by a total of 294 points, located in 13 biogeographic areas (**Fig 1**). Its bathymetric range was from 5 to 220 m (mean 29, S.D. 25.6 m). Although primarily recorded within the coralligenous, it was found over several habitat types (e.g. boulders, overhangs, caves, maërl, and sea mounts). Most populations were located at W Italy and France (43%), E Adriatic (34%), and N Aegean seas (14%). In the remaining areas only a few scattered populations were recorded, being generally absent along most parts of the Spanish coasts, while there is a notable lack of information in the Ionian, W Adriatic, and the southern or eastern parts of the Mediterranean basin. Furthermore, a total of 84 scientific documents reported information on *E. cavolini*, out of which only 67.5% are included in the science citation index, while 71% concern the NW Mediterranean coasts. The majority of these documents elaborate on general species inventories/habitat mapping (40 studies), human impacts/mass mortality events (14), and taxonomy/genetics of gorgonians (7). Much fewer studies provide specific information on *E. cavolini* physiology/biochemistry (9), ecology (8), age/growth (6), or population characteristics (5).

4. Discussion and conclusions

E. cavolini populations display a patchy, yet relatively clustered distribution along the northern rocky coasts of the Mediterranean basin. Known to thrive on hard substrates (Weinberg 1980), the lack of information in the W Adriatic and W Ionian coasts could partly be due to the predominance of aluvial coastal substrates in these regions. Additionally, oligotrophic conditions, higher water temperatures, and low research effort may justify the reduced presence in southern and eastern Mediterranean coasts. However, its notable absence along the well-studied rocky coasts of Spain is peculiar, especially in localities known to support dense populations of other gorgonians, e.g. *E. singularis* and *Paramuricea clavata*. Although knowledge on octocoral species has increased considerably over the last years, information regarding the ecology, demographics and conservation status of *E. cavolini* is essentially lacking, and should be reinforced to allow future monitoring of this widespread, long-lived gorgonian.

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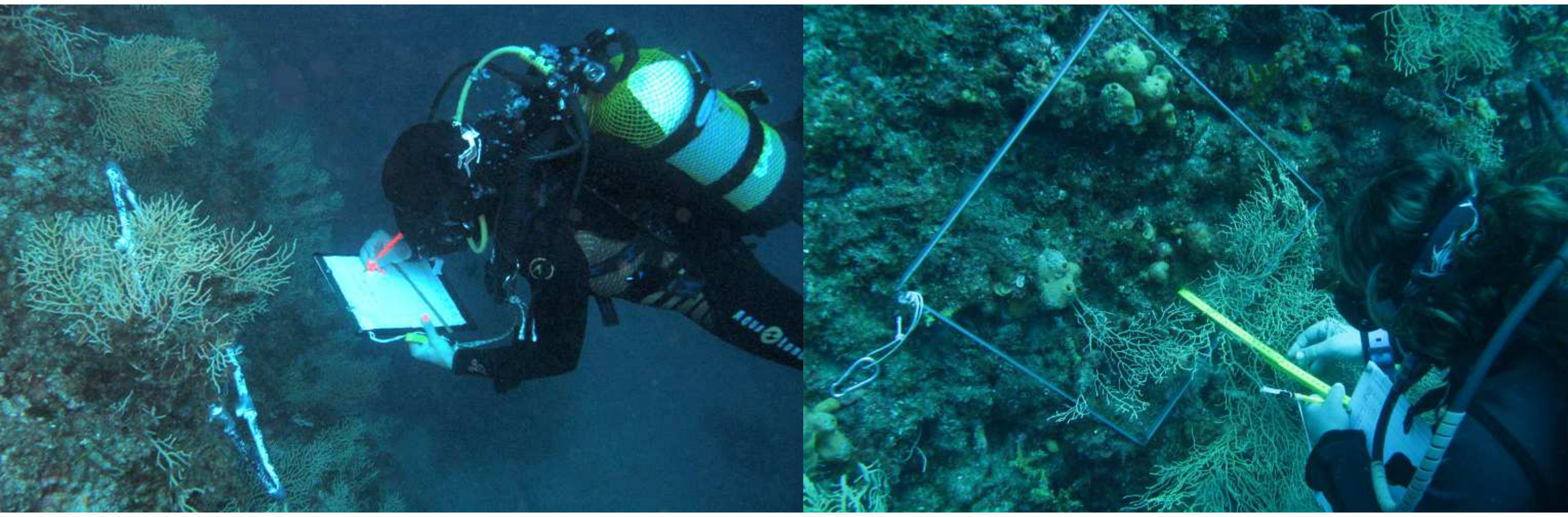
Κεφάλαιο 4



Η κίτρινη γοργονία *Eunicella cavolini*: δημογραφικά χαρακτηριστικά και κατάσταση διατήρησης στη Μεσόγειο

Περίληψη

Η *Eunicella cavolini* (Koch, 1887) είναι ένα από τα πιο κοινά είδη γοργονιών της Μεσογείου. Ωστόσο, η επιστημονική πληροφορία σχετικά με την κατανομή και τα οικολογικά χαρακτηριστικά του είδους στις διαφορετικές περιοχές της Μεσογείου είναι ιδιαίτερα περιορισμένη, ενώ ελάχιστα είναι γνωστά για τη δυναμική και την κατάσταση διατήρησης των πληθυσμών στις περιοχές εξάπλωσης. Στην παρούσα μελέτη διερευνήθηκαν 19 πληθυσμοί της *E. cavolini* σε τρεις αντιπροσωπευτικές γεωγραφικές περιοχές: στη ΒΔ Μεσόγειο, την κεντροανατολική (ΚΑ) Αδριατική, και το Β Αιγαίο. Εστιάζοντας στην ανώτερη βαθυμετρική ζώνη εξάπλωσης του είδους (<40 m), συγκεντρώθηκαν επιτόπια δεδομένα σχετικά με το ανώτερο βαθυμετρικό όριο των πληθυσμών, την πυκνότητα, το ύψος, και το βαθμό τραυματισμού των αποικιών. Για τη διερεύνηση των χωρικών προτύπων των ανωτέρω δημογραφικών χαρακτηριστικών ακολουθήθηκε ένα δομημένο σχέδιο δειγματοληψίας με τρία επίπεδα χωρικής ανάλυσης: α) επίπεδο γεωγραφικής περιοχής (αναφέρεται σε περιοχές που απέχουν μεταξύ τους χιλιάδες χιλιόμετρα), β) επίπεδο τοποθεσιών εντός της κάθε γεωγραφικής περιοχής (τοποθεσίες που απέχουν από δεκάδες έως εκατοντάδες χιλιόμετρα μεταξύ τους), και γ) επίπεδο σταθμών εντός της κάθε τοποθεσίας (σταθμοί που απέχουν από μερικές εκατοντάδες μέτρα έως λίγα χιλιόμετρα).

Στη ΒΔ Μεσόγειο και τη ΚΑ Αδριατική, το ανώτερο βαθυμετρικό όριο των πληθυσμών ήταν ≤15 m, ενώ στο Β Αιγαίο οι περισσότεροι πληθυσμοί βρίσκονταν σε νερά βαθύτερα των 30 m. Η πυκνότητα των πληθυσμών υπολογίστηκε μεταξύ 4.46–62 αποικίες ανά m^2, το μέσο ύψος των οποίων ήταν 15.6 cm (± 8.9 τυπική απόκλιση) με μέγιστο καταγεγραμμένο ύψος 62 cm. Στη ΒΔ Μεσόγειου, οι πληθυσμοί παρουσίασαν

την υψηλότερη πυκνότητα, και χαρακτηρίζονταν από αυξημένο αριθμό μικρών αποικιών (<20 cm σε ύψος), χαμηλό ποσοστό μεγάλων αποικιών (>30 cm), και περιοδικό ρυθμό επιτυχούς εγκατάστασης νεαρών γοργονιών. Στη ΚΑ Αδριατική, οι πληθυσμοί παρουσίασαν ενδιάμεσες τιμές πυκνότητας, καλά δομημένους πληθυσμούς με επαρκή εκπροσώπηση όλων των κλάσεων ύψους, και σταθερό ρυθμό εγκατάστασης νεαρών αποικιών. Στο Β Αιγαίο, οι περισσότεροι πληθυσμοί είχαν χαμηλή πυκνότητα, υψηλό ποσοστό μεγάλων αποικιών, αλλά μικρό αριθμό νεαρών αποικιών, γεγονός που υποδεικνύει περιορισμένη επιτυχία εγκατάστασης και επιβίωσης των νεαρών σταδίων. Εντοπίστηκαν ενδείξεις διαφοροποίησης της έκτασης και του τύπου τραυματισμού των γοργονιών ανά γεωγραφική περιοχή, σταθμό δειγματοληψίας, και έτος δειγματοληψίας, οι οποίες πιθανότατα οφείλονται στο διαφορετικό βαθμό έκθεσης των επιμέρους πληθυσμών σε ανθρωπογενείς πιέσεις. Η παρούσα μελέτη αποτελεί την πιο εκτεταμένη γεωγραφικά δημογραφική καταγραφή γοργονιών στη Μεσόγειο έως σήμερα. Τα πρωτογενή δεδομένα που συλλέχθηκαν, καθώς και τα συγκριτικά αποτελέσματα μεταξύ περιοχών, αποτελούν τη βάση για μελλοντικές μελέτες καταγραφής και παρακολούθησης του είδους, τόσο σε τοπικό, όσο και σε Μεσογειακό επίπεδο.

Chapter 4

The yellow gorgonian *Eunicella cavolini*: Demography and disturbance levels across the Mediterranean Sea

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Abstract

The yellow octocoral *Eunicella cavolini* is one of the most common gorgonians thriving in Mediterranean hard-bottom communities. However, information regarding its distribution and ecology in several parts of the Mediterranean is lacking, while population trends and conservation status remain largely unknown. We investigated 19 populations of *E. cavolini* over three representative geographic regions: the NW Mediterranean, CE Adriatic, and N Aegean. Focusing on the upper bathymetric range of the species (<40 m), data were collected on the populations' upper depth limit, density, colony height, and extent of injury. A three-level hierarchical sampling design was applied to assess the existence of spatial patterns, using: a) regions (located thousands of km apart), b) localities within regions (tens to hundreds of km apart), and c) sites within localities (hundreds of m to a few km apart). In the NW Mediterranean and CE Adriatic, the upper distribution limit was at depths ≤15 m, whereas in the N Aegean most populations were found deeper than 30 m. Population density ranged between 4.46–62 colonies per m^2, while mean colony height was 15.6 ± 8.9 SD cm with a maximum of 62 cm. The NW Mediterranean sites were characterized by dense populations dominated by small colonies (<20 cm), periodic recruitment, and low proportion of large gorgonians (>30 cm). The CE Adriatic displayed intermediate densities, with well-structured populations, and continuous recruitment. In the N Aegean, most populations presented low densities, high proportion of large colonies, but low number of small colonies, signifying limited recruitment. Disturbance levels, as a function of extent and type of injury, are discussed in relation to past or present human-induced threats. This work represents geographically the most wide ranging demographic study of a Mediterranean octocoral to date. The quantitative information obtained provides a basis for future monitoring at a Mediterranean scale.

1. Introduction

Demographic studies provide valuable information regarding the ecology of long-lived benthic octocorals (e.g. Bak & Meesters 1998; Harmelin & Garrabou 2005; Linares et al. 2008; Gori et al. 2011). The size structure of a population reflects how key life history parameters, such as growth, reproduction and mortality, have been shaped through its interaction with the surrounding environment and the local stressors (Grigg 1977; Gilmour 2004; Tsounis et al. 2006; Alvarado-Chácon & Acosta 2009). Similarly, knowledge on the distribution and population dynamics of a species over large spatial scales enables a more comprehensive understanding of its ability to persist under variable environmental conditions (Bak & Meesters 1999). Such information may further reveal relationships between populations and their environment, enabling the evaluation of habitat stability and suitability, and the monitoring of ecosystem change over time (Grigg 1975; Weinbauer & Velimirov 1996a).

Gorgonian octocorals represent one of the most important benthic taxonomic groups in the Mediterranean (Pérès & Picard 1964). Given the colonies' three dimensional growth, gorgonian populations greatly modulate benthic habitats and enhance the overall structural complexity, biomass, and species diversity (True 1970; Ballesteros 2006). Furthermore, they act as ecosystem engineers (*sensu* Jones et al. 1994) by modifying current flow, sedimentation rates and shading levels (Gili & Coma 1998; Cerano et al. 2010; Ponti et al. 2014). As several other coral species, Mediterranean gorgonians are long-lived, with slow growth, delayed maturity, low or infrequent recruitment success and reduced post-settlement survival (Coma et al. 1998; Garrabou & Harmelin 2002; Torrents et al. 2005; Linares et al. 2007). The slow population dynamics of gorgonians render them susceptible to a wide range of direct or indirect anthropogenic stressors. Mechanical damage (mainly caused by fishing and unregulated recreational diving), pollution and mucilagenous algal aggregates represent localized types of disturbance (Mistri & Ceccherelli 1996; Bavestrello et al. 1997; Coma et al. 2004), whereas biological invasions (Cebrian et al. 2012) and mass mortality outbreaks, related to climate induced temperature anomalies, constitute basin-scale threats (Cerrano et al. 2000; Garrabou et al. 2009).

The yellow octocoral *Eunicella cavolini* (Koch, 1887) is one of the most common gorgonian species of the Mediterranean hard-bottom communities, and forms distinct facies within the emblematic coralligenous assemblages (Weinberg 1980; Ballesteros 2006). Its distribution range is wide, although patchy in terms of abundance, and it is known to occur from the W Mediterranean and Tunisian coasts to the Aegean Sea, and the Sea of Marmara (Topçu & Öztürk 2013; Sini et al. 2014). Still, information regarding its distribution and ecological characteristics in different parts of the Mediterranean is lacking, while population trends and conservation status remain largely unknown. The limited number of studies on the ecology of this species are restricted in space and time (Velimirov 1973, 1975, 1976; Weinberg 1980; Russo 1985; Bavestrello & Boero 1986; Weinbauer & Velimirov 1995a, 1995b, 1996a; 1996b), while more recent information comes primarily from research regarding the effects of mass mortality events (MMEs) on gorgonian species (Cerrano et al. 2000; Garrabou et al. 2009; Cigliano & Gambi 2007; Gambi et al. 2010). These studies commonly underline the limitations posed by the absence of pre-disturbance data as critical baselines for the rigorous evaluation of gorgonian populations under stress (Linares et al. 2005; Coma et al. 2006).

Given the rapid alteration of the marine environment due to direct and indirect human induced pressures (Halpern et al. 2008; Lejeusne et al. 2010), assessment of ongoing threats and effective management decisions must be based on a thorough understanding of the natural spatial and temporal variability exhibited by species and their populations living in different geographic areas. In response to these requirements, *E. cavolini* populations were studied in three distinct biogeographical regions of the Mediterranean, namely the NW Mediterranean, the CE Adriatic and the N Aegean seas. Aiming to provide comparable, quantitative reference data for future monitoring and assessment of future impacts or threats, we focused on the upper depth distribution range of the species (<40 m), where populations are exposed to greater variability of environmental conditions (Garrabou et al. 2002; Ballesteros 2006) and higher level of human induced disturbances (Coli et al. 2010; Micheli et al. 2013). This study is the first to assess the population structure and disturbance levels of *E. cavolini* populations across most parts of its known distribution in the Mediterranean, and geographically represents the widest ranging demographic study of an octocoral in the basin.

2. Materials and Methods

2.1 Field survey

A three-level hierarchical sampling design was applied to assess the spatial patterns of *E. cavolini* populations, including: a) regions (located thousands of km apart), b) localities within regions (tens to hundreds of km apart), and c) sites within localities (hundreds of m to a few km apart). Three regions of the Mediterranean Sea were considered: the NW Mediterranean, CE Adriatic and N Aegean. Within each region, 2 to 3 localities were chosen, and within each locality 1 to 3 random sites were investigated. A total of 19 sites with well-developed *E. cavolini* populations were studied within 2 localities of the NW Mediterranean (Marseille, Scandola), 3 localities of the CE Adriatic (Kornati, Pag, Rogoznica), and 3 localities of the N Aegean (Pelio, Chalkidiki, Lesvos, **Fig 1**, **Table 1**). *In situ* underwater demographic surveys were conducted within the upper distribution depth range of the species (<40 m). Data for each population were collected once, during the period 2005–2013. Field surveys in the locality of Scandola were conducted under the authorization of the Scientific Comittee of Réserve Marine de Scandola – Parc Regional de Corse. In the case of Kornati National Park a special permission was issued by the Croatian Ministry of Culture – Department for Nature Protection. For the remaining sites, no specific permits were required at the time of field work for the sampling protocols described herein. Locations were not privately owned and the study did not involve endangered or protected species. Our study was based exclusively on non-destructive methods, and no plant or animal material was collected.

2.2 Assessment of demographic characteristics and disturbance levels

For the assessment of the main population characteristics we followed the methodology proposed by Linares et al. (2008). Colonies' density, height, proportion of injured surface and type of injury were chosen as the main population descriptors, and measurements were taken using 50×50 cm haphazardly placed quadrats within the *E. cavolini* populations.

Density was determined based on the number of colonies present within 50×50 cm quadrats, averaged and recalculated for 1 m^2 surface. For each colony found, maximum height was measured as the distance from the colony base to the tip of the furthest apical branch. At each site, the aforementioned parameters were assessed over an area of more than 3 m^2 and for more than 45 colonies, thus satisfying previously determined minimum sample size criteria (Linares et al. 2008).

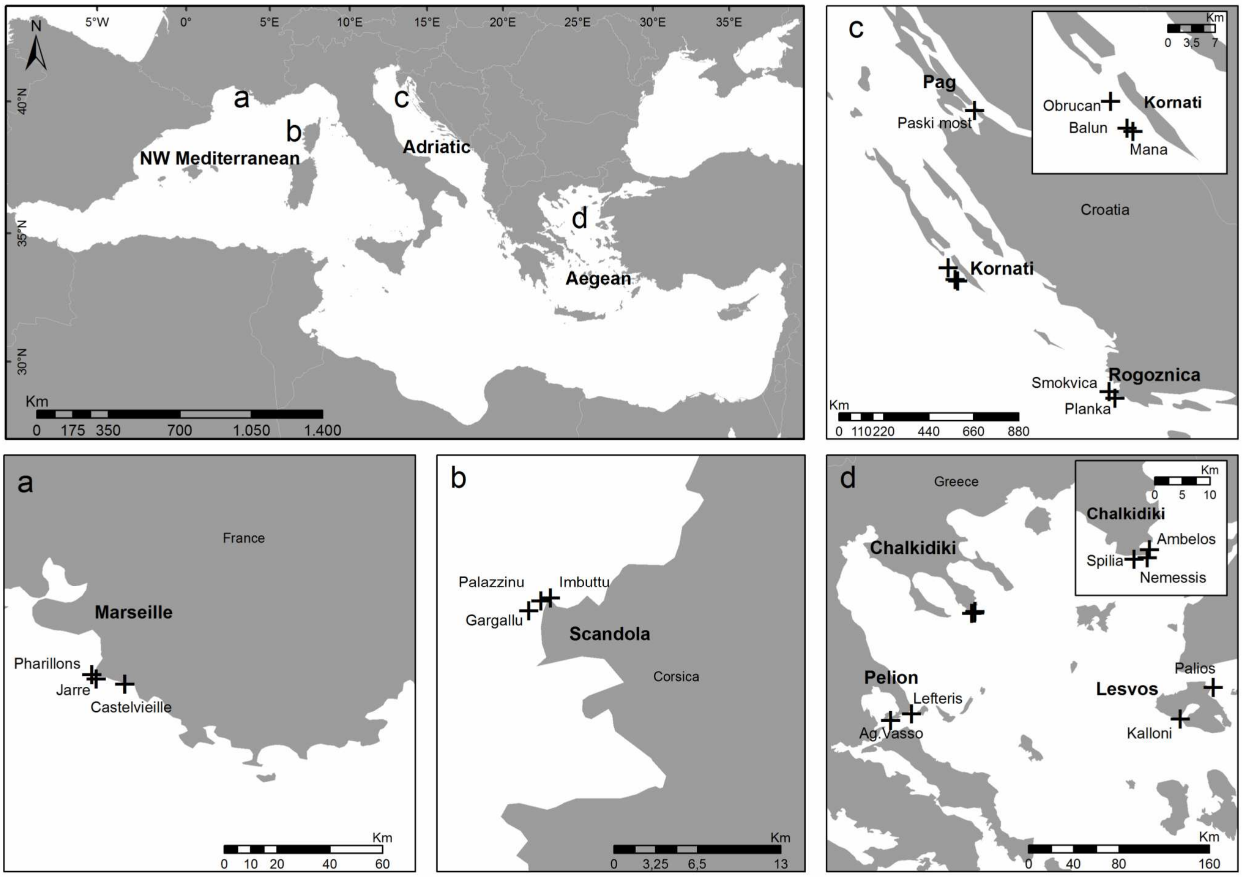

Fig 1. Map of the Mediterranean showing the investigated regions of the NW Mediterranean, CE Adriatic and N Aegean. Inset figures a – d present localities (in bold). Crosses mark the study sites of the yellow gorgonian *Eunicella cavolini*.

Three descriptors were used to assess the impact of potential disturbances: extent of injury per colony, type of injury, and proportion of healthy colonies. The combined investigation of the type and extent of injury may provide insights regarding past disturbance events, and allow for an estimation of the approximate time of their occurrence (Coma et al. 2004; Linares et al. 2005). Extent of injury was estimated as the proportion of the colony's total surface that appeared devoid of coenenchyma tissue (i.e. denuded axis) and/or that was overgrown by other organisms. Based on the presence/absence of different epibionts, and the time it takes for their development, three types of injury were identified; Type A: denuded colony axis, indicating a new injury up to 1 month; Type B: colony overgrowth by pioneer species, such as filamentous algae and hydrozoans, representing injuries of approximately 1–12 months old;

Type C: colony overgrowth mostly by bryozoans, sponges and algae, reflecting an old injury of approximately ≥12 months (Linares et al. 2005). Overall, out of the 3188 colonies measured, injury data were collected for 3045 colonies and where used to calculate mean extent of injury and percentage of healthy or affected colonies. Colonies with less than 10% of injured surface were considered as healthy, colonies with injuries ≥10% of total surface where classified as affected, whereas 100% of injury corresponded to death (Linares et al. 2008; Garrabou et al. 2009). Type of injury was quantitatively described only for colonies with ≥10% of injured surface (i.e. affected colonies); their proportion was calculated against the total number of colonies for which extent of injury was assessed per population.

Table 1. Characteristics of studied sites. Depth range refers to the recorded depth distribution of the yellow gorgonian *Eunicella cavolini* population at each site. Inclination characterized as "cascading" refers to slopes intercepted by smaller vertical walls.

Region	Locality	Site	Depth range Min–Max (m)	Coordinates		Habitat	Inclination	Protection level
NW Mediterranean	Marseille	Jarre	5–20	43°11'47"N	05°21'45"E	Wall	Vertical	MPA
		Castelvieille	5–35	43°12'01"N	05°29'39"E	Wall	Vertical	MPA
		Pharillons	10–45	43°12'27"N	05°20'18"E	Wall	Vertical	MPA
	Scandola	Imbuttu	15–45	42°22'41"N	08°33'05"E	Wall	Vertical	MPA
		Palazzinu	15–40	42°22'48"N	08°33'00"E	Wall	Vertical	MPA
		Gargallu	15–40	42°22'21"N	08°32'05"E	Wall	Sub-vertical	MPA
CE Adriatic	Kornati	Mana	5–60	43°48'01"N	15°15'59"E	Wall	Vertical	MPA; Natura 2000
		Balun	5–60	43°48'14"N	15°15'18"E	Wall	Vertical	MPA; Natura 2000
		Obrucan	5–55	43°50'11"N	15°13'12"E	Wall	Vertical	MPA; Natura 2000
	Pag	Paski most	12–35	44°19'07"N	15°15'38"E	Wall	Cascading	unprotected
	Rogoznica	Smokvica	15–50	43°30'38"N	15°56'32"E	Wall	Cascading	unprotected
		Planka	15–50	43°29'36"N	15°58'09"E	Wall	Cascading	unprotected
Aegean	Pelio	Lefteris	20–30	39°08'31"N	23°20'39"E	Rocky outcrop	Vertical	unprotected
		Ag.Vasso	30–50	39°05'08"N	23°07'48"E	Wall	Sub vertical	unprotected
	Chalkidiki	Ambelos	30–45	39°57'33"N	23°59'29"E	Wall	Sub-vertical	unprotected
		Nemessis	30–45	39°56'46"N	23°59'10"E	Wall	Sub-vertical	unprotected
		Spilia	32–50	39°56'38"N	23°57'31"E	Rocky outcrop	Sub-vertical	unprotected
	Lesvos	Kalloni	10–27	39°04'56"N	26°05'25"E	Rocky outcrop	Sub-vertical	Natura 2000
		Palios	30–44	39°19'42"N	26°26'10"E	Wall	Sub-vertical	unprotected

2.3 Data analysis

To assess the height frequency distribution per site, height measurements of colonies displaying <100% of injured surface were grouped into five classes: 1–10, 11–20, 21–30, 31–40, and >41 cm, and the descriptive distribution parameters of skewness (*g1*) and kurtosis (*g2*) were estimated. Coefficients of *g1* and *g2* were considered significant if the ratio to their standard error was >2 (Sokal & Rohlf 1995). The relation between mean height and density was explored using a Spearman rank order correlation.

A non-metric multidimensional scaling (MDS) ordination (Kruskal & Wish 1978) was performed to visualize patterns of population structure based on the following parameters after normalization of data: mean height, max height, proportion of the smaller (0–20 cm) and larger (>30 cm) height classes, density and upper depth distribution limit. One-way, non-parametric analysis of variance PERMANOVA (Anderson 2001), based on square root transformed data and Euclidean distances, was used to test for spatial variability in colony height and density. A three-factor hierarchical design was applied using "region" (3 levels) as a fixed factor, "locality" (8 levels) as a random factor nested within region, and "site" (19 levels) as a random factor nested within locality. Pair-wise comparisons were performed to determine specific inter or intra-regional differences when the main test indicated significant differences. Significance was confirmed based on 9999 permutations. Analyses were performed using the PRIMER v6 software with PERMANOVA+ add-on package (Clarke & Gorley 2006; Anderson et al. 2008).

3. Results

3.1 Upper depth distribution range

The upper depth distribution limit varied considerably along the longitudinal gradient (**Fig 2**). In all localities of the NW Mediterranean and CE Adriatic, the upper distribution limit of *E. cavolini* populations was found at 15 m depth or shallower, with some populations appearing at 5 m depth in the locality of Kornati (CE Adriatic). On the contrary, most populations of the N Aegean were found in waters deeper than 30 meters, with the exception of two populations that were located at 10 and 20 m depth.

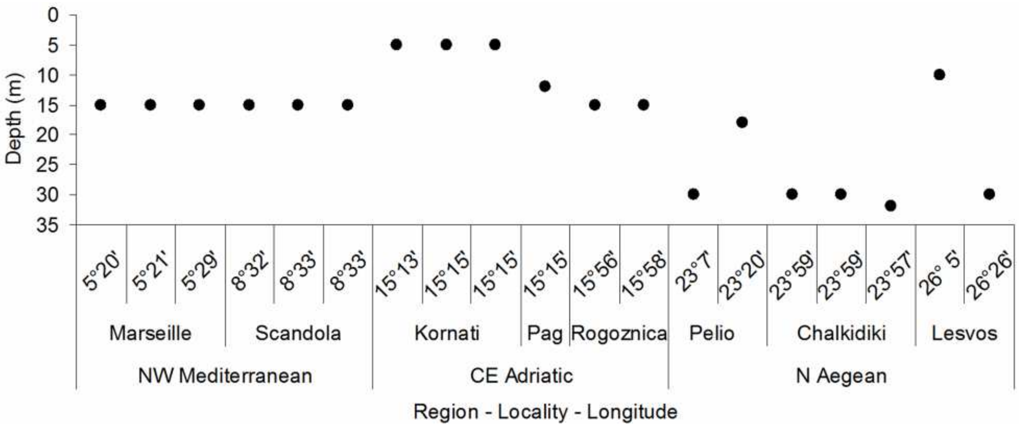

Fig 2. Upper depth distribution limits for the investigated *Eunicella cavolini* populations along a longitudinal gradient.

3.2 Demographic characteristics

Mean population density of *E. cavolini* was 14.9 ± 14.6 SD (standard deviation) per m^2. The minimum density of 4.5 colonies per m^2 was observed at Ambellos (N Aegean), while the maximum density of 62 colonies per m^2 was recorded at Jarre (NW Mediterranean, **Table 2**). Among localities (**Fig 3**), higher densities were recorded in Scandola (29.5 ± 12.9 SD per m^2) and Marseille (24.1 ± 27 SD per m^2) within the NW Mediterranean, followed by Rogoznica (17.8 ± 10.9 SD per m^2), Kornati (15.2 ± 12.8 SD per m^2), and Pag (12.9 ± 12.6 SD per m^2) within the CE Adriatic, while the lowest densities were observed in the localities of the N Aegean, namely Lesvos (10.5 ± 13.1 SD per m^2), Pelio (9.03 ± 7.1 SD per m^2), and Chalkidiki (7.5 ± 6.6 SD per m^2). PERMANOVA results suggest that a significant variability in density exists among regions and sites ($p<0.05$), but not between localities (**Table 3**). Furthermore, the greatest variation in density, indicated by the components of variation, was observed among regions. The pair-wise tests show that a significant difference in population density exists among all regions ($p<0.05$, **Table 4**) and between sites in 4 of the 7 localities analysed (**Table A**, Appendix C).

Table 2. Population characteristics of *Eunicella cavolini* per region, locality and site.

Region	Locality	Site	Sampling depth (m)	Area (m^2)	Density (m^{-2})	Height (cm)							
					Mean	N	Mean	Min	Max	SD	SE	Skewness	Kurtosis
NW Mediterranean	Marseille	Jarre	15 – 20	3.50	62.00	217	12.21	1.0	38.0	7.22	0.49	0.69*	0.20
		Castelvieille	15 – 20	6.00	12.83	76	18.28	3.0	45.0	9.21	1.06	0.49	-0.05
		Pharillons	15 – 20	4.75	10.32	49	14.20	2.0	35.0	7.79	1.11	1.02*	0.73
	Scandola	Imbuttu	15 – 20	9.50	29.47	280	13.76	1.5	28.5	5.32	0.32	0.07	-0.47
		Palazzinu	20 – 23	9.00	30.78	270	12.33	0.5	37.0	5.96	0.36	0.68*	0.73*
		Gargallu	20 – 25	8.75	28.34	245	15.12	2.0	33.0	5.72	0.36	0.29	-0.01
CE Adriatic	Kornati	Mana	9 – 28	16.75	12.24	198	10.15	1.5	43.0	4.64	0.33	1.89*	11.67*
		Balun	13 – 28	20.25	17.43	345	10.92	1.0	28.0	5.03	0.27	0.39*	0.08
		Obrucan	15 – 28	23.50	15.45	360	15.29	2.0	45.0	8.27	0.43	0.45*	-0.27
	Pag	Paski most	20 – 30	7.50	12.93	89	19.47	3.0	50.0	10.04	1.06	0.85*	0.18
	Rogoznica	Smokvica	20 – 30	7.50	17.06	126	20.66	5.0	50.0	8.43	0.75	0.72*	0.79
		Planka	23 – 30	5.50	18.91	102	17.40	4.0	50.0	10.12	1.00	1.08*	0.66
N Aegean	Pelio	Lefteris	24 – 30	11.00	10.36	113	17.13	4.0	53.0	10.29	0.97	1.13*	1.09*
		Ag.Vasso	32 – 35	12.25	7.84	95	23.66	2.0	62.0	12.08	1.24	0.37	-0.25
	Chalkidiki	Ambelos	30 – 40	26.25	4.46	114	25.06	5.0	50.0	9.16	0.86	0.21	0.03
		Nemessis	30 – 38	9.25	11.35	105	13.81	2.0	34.0	6.84	0.67	0.44	-0.44
		Spilia	35 – 40	7.75	13.29	103	23.17	3.0	51.0	10.93	1.08	0.21	-0.56
	Lesvos	Kalloni	13 – 27	6.25	23.52	127	16.71	1.0	46.0	11.11	0.98	0.49*	-0.45
		Palios	33 – 40	18.00	6.00	108	23.86	3.0	48.0	10.62	1.02	0.07	-0.88

*Statistically significant results.

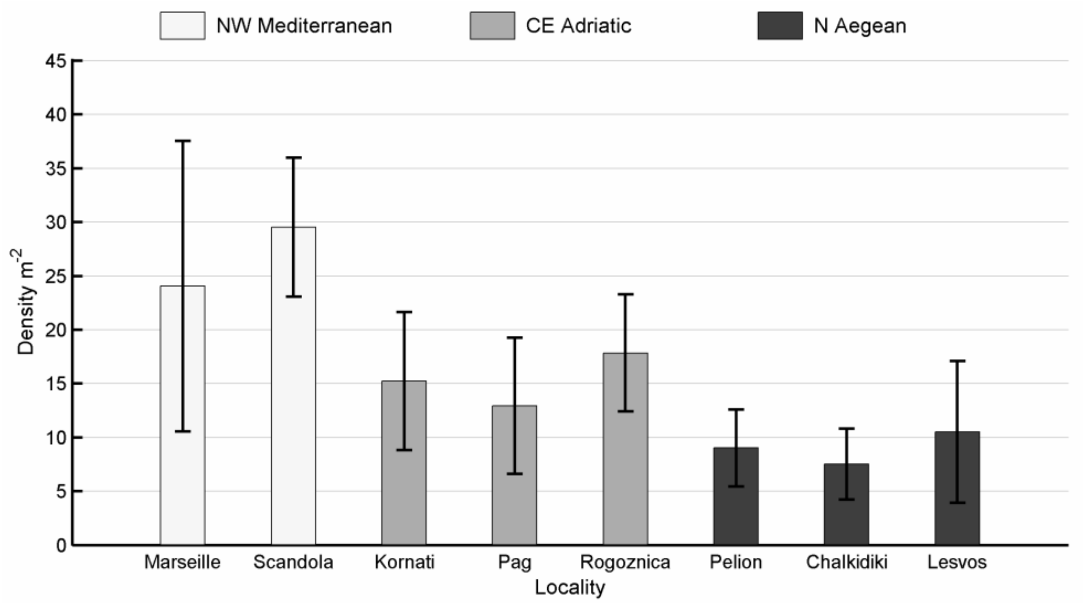

Fig 3. Mean density (colonies per m^2) of *Eunicella cavolini* populations, tabulated by locality. Whisker span indicates standard deviation. Colors denote geographic regions.

Table 3. Summary of PERMANOVA results for *Eunicella cavolini* population density.

	Source of variation					
	df	**SS**	**MS**	**Pseudo-F**	**P(perm.)**	**Unique perm.**
Region	2	726.65	363.33	21.237	0.0008*	9968
Locality(Region)	5	57.722	11.544	0.31125	0.8763	9960
Site(Locality(Region))	11	409.2	37.2	14.303	0.0001*	9944
Residuals	834	2169.1	2.6008			
Total	852	3362.7				

Tests of significance were run based on Euclidean distances for square root transformed data.
*Statistically significant differences (p<0.05).

Table 4. Summary of PERMANOVA pairwise comparisons for *Eunicella cavolini* population density among regions.

Pairwise test for regions' density	**t**	**P(perm.)**	**Unique perm.**
NW Mediterranean, CE Adriatic	2.9077	0.0183*	9970
NW Mediterranean, Aegean	7.0213	0.0019*	9965
CE Adriatic, Aegean	4.263	0.0114*	9965

Tests of significance were run based on Euclidean distances for square root transformed data.
*Statistically significant differences (p<0.05).

Overall, mean colony height was 15.6 ± 8.9 SD cm, while the maximum recorded height was 62 cm (**Table 2).** Among localities (**Fig 4**), mean colony height was greater at Chalkidiki (20.8 ± 10.3 SD cm), Pelio (20.1 ± 11.6 SD cm) and Lesvos (19.9 ± 11.4 SD cm) in the N Aegean, while equally high values were recorded at Pag (19.5 ± 10 SD cm) and Rogoznica (19.2 ± 9.3 SD cm) in the CE Adriatic. Lower height values were observed at Marseille (13.8 ± 8.1 SD cm) and Scandola (13.7

± 5.8 SD cm) in the NW Mediterranean, as well as Kornati (12.5 ± 6.8 SD cm) in the CE Adriatic. Significant differences in height were only found at the level of sites within localities (PERMANOVA test, **Table 5**; **Table B**, Appendix C).

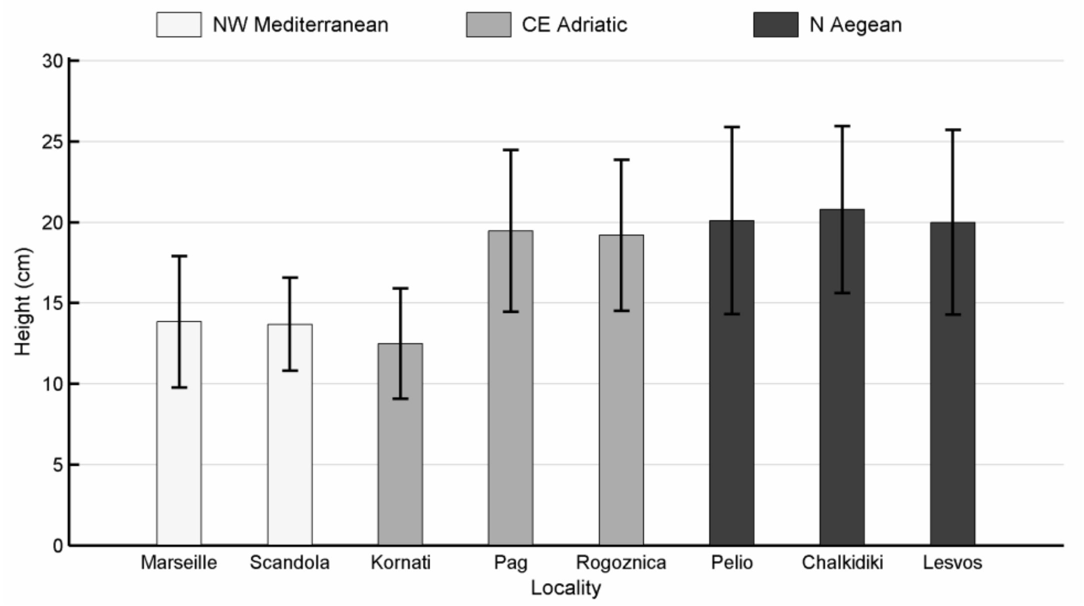

Fig 4. Mean height of *Eunicella cavolini* colonies per locality. Whisker span indicates standard deviation. Colors denote geographic regions.

Table 5. Summary of PERMANOVA results for *Eunicella cavolini* colony height.

Colony height	**Source of variation**					
Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm.)**	**Unique perm.**
Region	2	295.97	147.98	2.4786	0.1657	9955
Locality(Region)	5	176.86	35.371	1.4701	0.2791	9955
Site(Locality(Region))	11	326.65	29.695	29.73	0.0001*	9932
Residuals	3103	3099.4	0.99884			
Total	3121	3898.9				

Tests of significance were run based on Euclidean distances for square root transformed data.
*Statistically significant differences (p<0.05).

Height frequency distribution of *E. cavolini* populations appeared to be either positively skewed or relatively symmetric depending on site (**Fig 5**). A significant positive skewness, indicating a prevalence of the smaller height classes, was found for the populations of Jarre, Pharillons, and Palazzinu in NW Mediterranean, all populations of the CE Adriatic, and for the shallower sites in the N Aegean, namely Lefteris and Kalloni (**Table 2**).

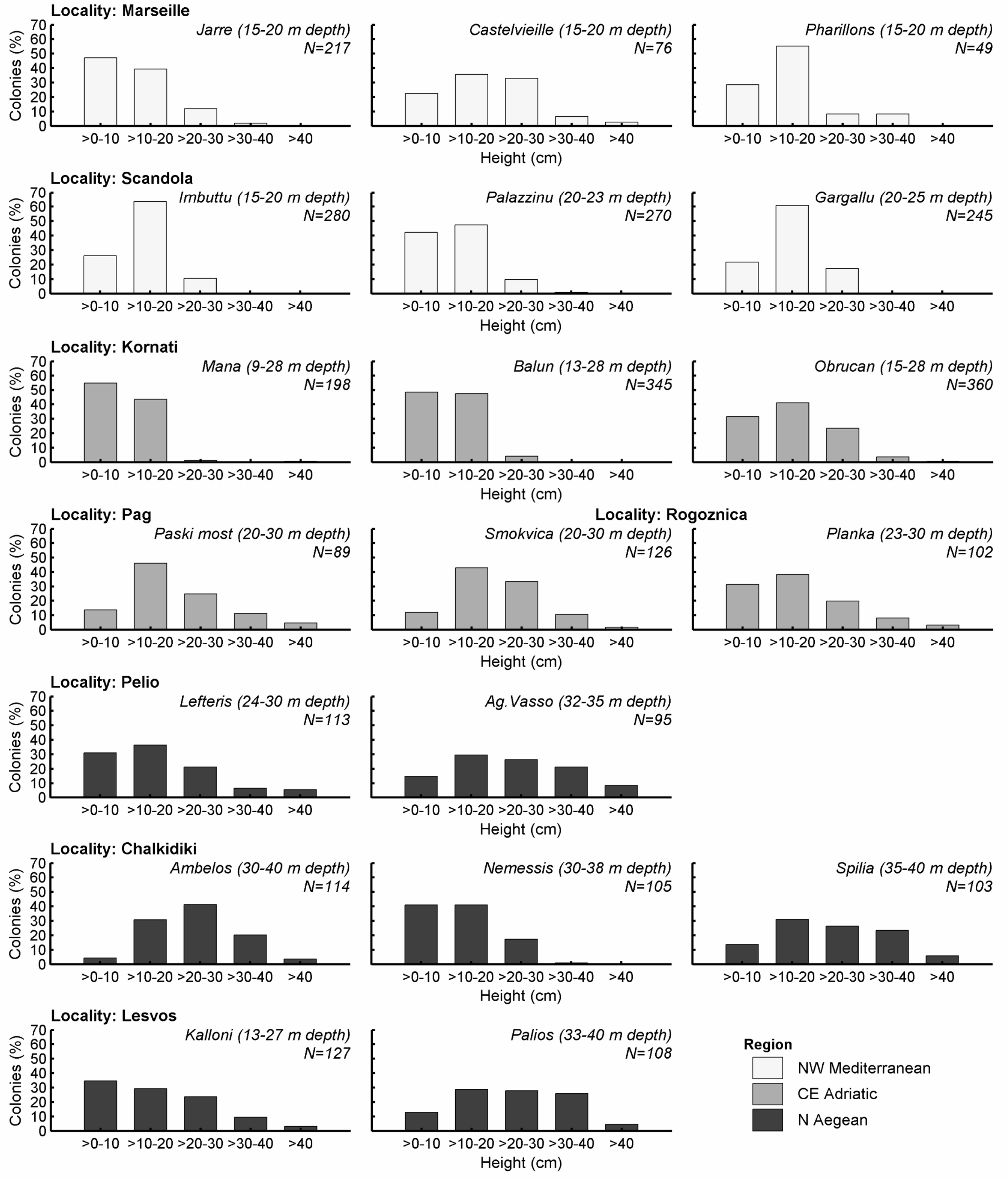

Fig 5. Height frequency distribution of *Eunicella cavolini* populations per site, grouped by locality (in bold) and region (different colors). Italics indicate site name, numbers in parentheses denote sampling depth range, and (N) corresponds to the number of colonies used.

Of these positively skewed populations, Palazzinu, Mana, and Lefteris displayed additionally a significant positive kurtosis value, suggesting a dominance of either one or both of the two smaller height classes (>0–10 and >10–20 cm). The majority of the N Aegean populations presented a non-significant negative kurtosis value. Although an important proportion of large colonies (20–30 cm) appeared in most sites, the number of colonies with height >30 cm was generally low, and more pronounced in certain sites of the CE Adriatic and N Aegean.

According to the Spearman rank order correlation values of density and mean height across sites displayed a significant inverse relation (r_s= -0.58, *p*=0.009). The MDS plot of *E. cavolini* populations according to basic demographic characteristics (**Fig 6**) produced two main clusters at a stress level of 0.06, indicating good ordination; one cluster encompassing all NW Mediteranean and CE Adriatic populations, as well as the shallower populations of the N Aegean, and a second one including the deeper populations of the N Aegean.

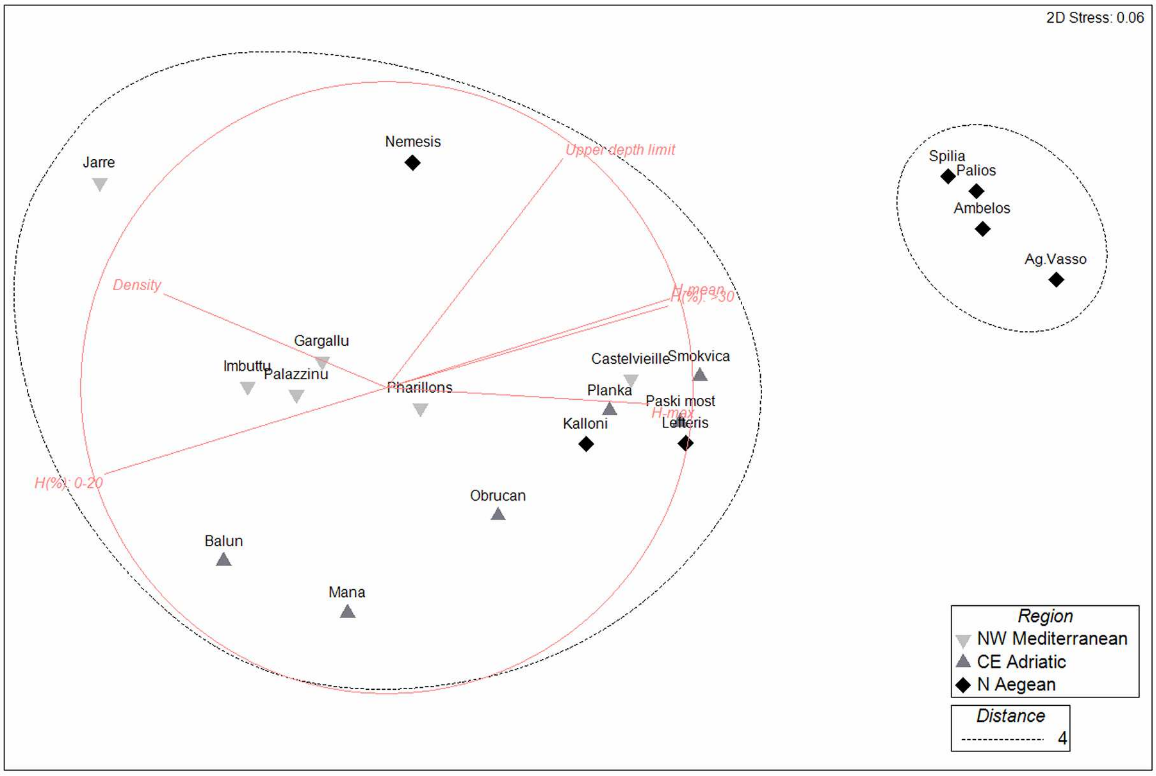

Fig 6. Non-metric multidimensional scaling (MDS) plot of *Eunicella cavolini* population structure per site. Different markers indicate different regions. Black dotted lines signify clusters formed at Euclidean distance equal to 4. The superimposed red lines denote the Euclidean distance coefficients used, after data normalization: mean height, max height, H% (proportion of height classes ≤20 cm and >30 cm), density, and upper depth distribution.

3.3 Disturbance levels

Among populations, mean extent of injury of gorgonian tissue varied substantially, ranging from 0.8% to 38.3% (**Table 6**). Most populations (14 out of 19) presented a mean extent of injury less than 10%, while higher values were observed at Planka (13%), Smokvica (16.5%) and Paski most (25.8%) in the CE Adriatic, and at Ambelos (18.6%) and Kalloni (38.3%) in the N

Aegean. The proportion of injured colonies (i.e. ≥10% to ≤99% of injured surface) ranged between 0–64%, with highest values at Paski most (37.1%) and Smokvica (39.8%) in the CE Adriatic, and Ambellos (64.1%) and Kalloni (52.4%) in the N Aegean (**Table 6**). The percentage of dead colonies was generally below 3.5% for the majority of sites, with the exception of Paski most (8.25%) and Kalloni (13.6%). Overall, the greatest proportions of healthy colonies (<10% of injured surface) were recorded in the localities of Marseille (75.3–100%), Scandola (83–91%) and Kornati (78.5–82.6%), (**Table 6**).

Table 6. Summary data on injury characteristics of *Eunicella cavolini* colonies per site. Proportion of colonies per type of injury was estimated using only colonies displaying ≥10 % of injured surface against the total number of colonies per site.

					Extent of colony injury (%)		**Proportion of uninjured, injured and dead colonies**			**Proportion of colonies per type of injury**		
Region	**Locality**	**Site**	**Year**	**N**	**Mean**	**SD**	**<10%**	**≥10 - 99%**	**100%**	**A**	**B**	**C**
NW Mediterranean	Marseille	Jarre	2005	75	6.7	10.5	85.33	14.67	0.00	10.66	2.67	9.33
		Castelvieille	2005	77	9.6	22.4	75.32	23.38	1.30	0.00	1.30	23.38
		Pharillons	2005	49	0.8	1.9	100.00	0.00	0.00	0.00	0.00	0.00
	Scandola	Imbuttu	2013	280	3.1	10.3	89.29	10.71	0.00	0.00	0.00	10.71
		Palazzinu	2013	277	7.9	21.7	83.03	14.44	2.53	0.00	0.00	16.97
		Gargallu	2013	248	3.3	14.2	91.94	6.85	1.21	0.00	0.00	8.06
CE Adriatic	Kornati	Mana	2009	205	7.9	20.7	78.54	18.05	3.41	1.46	8.78	11.71
		Balun	2009	353	5.5	18.4	89.52	8.22	2.27	0.28	1.13	9.35
		Obrucan	2009	362	5.7	15.8	82.60	16.57	0.83	0.28	3.31	13.81
	Pag	Paski most	2011	97	25.8	36	54.64	37.11	8.25	1.03	10.31	37.11
	Rogoznica	Smokvica	2009	128	16.5	26.3	58.59	39.84	1.56	0.00	1.56	38.28
		Planka	2009	104	13.3	24.2	66.35	31.73	1.92	0.00	0.00	33.65
N Aegean	Pelio	Lefteris	2011	114	8.5	16	64.91	34.21	0.85	0.00	26.32	6.14
		Ag.Vasso	2011	96	6.7	16.3	77.1	21.87	1.04	0.00	17.71	3.13
	Chalkidiki	Ambelos	2011	117	18.6	24.9	33.33	64.1	2.56	46.15	11.97	5.98
		Nemessis	2011	105	4.1	12.1	85.71	14.29	0.00	0.00	14.29	0.00
		Spilia	2011	103	6.9	15.7	78.6	21.4	0.00	0.00	19.42	1.91
	Lesvos	Kalloni	2013	147	38.3	39.1	34.01	52.38	13.61	12.24	57.82	49.66
		Palios	2011	108	2.5	8.3	89.81	10.18	0.00	0.93	9.26	0.93

The majority of affected colonies (≥10% of injured surface) in the NW Mediterranean and the CE Adriatic presented type C (old) injuries. In the N Aegean, populations mainly presented overgrowth by pioneer species (type B injury); exceptions were Ambelos, which displayed high proportion of recent tissue necrosis (type A injury: 46.15%), and Kalloni which had high levels of all types of injury. As the time of sampling varied among localities, no statistical comparisons regarding disturbance parameters were attempted.

4. Discussion

The extensive geographic distribution of *E. cavolini* and its relatively wide bathymetric range (<10 – 220 m (Russo 1985; Bo et al. 2012; Watremez 2012; Sini et al. 2014; Chapter 3) reflect its ability to adapt and survive over highly variable abiotic conditions. In this study, we carried out a comprehensive analysis of *E. cavolini* population structure and dynamics at three distinct Mediterranean regions, in order to facilitate a better understanding of the patterns observed across contrasting environmental gradients.

4.1 Upper depth distribution range

One of the most robust findings is the deeper upper bathymetric limit of populations in the N Aegean, compared to those thriving in the NW Mediterranean and CE Adriatic. In the latter regions, the upper bathymetric limit of *E. cavolini* was at 5–15 m. These observations are in line with the minimum depths reported in other localities of the western Mediterranean basin (e.g. Weinberg 1980; Russo 1985; Weinbauer & Velimirov 1995b; Bianchi et al. 2010) or the Adriatic Sea (e.g. Zavodnik et al. 2005), and the fact that the species can withstand a fairly wide range of light intensity (1–44% of surface light according to Weinberg 1980). Within the N Aegean, most populations were located at depths below 30 m. According to previous reports, gorgonian species in the Aegean Sea are generally observed in waters deeper than 40 m (Dounas et al. 2009; Salonidi et al. 2009) and are rarely found at depths shallower than 20 m (Skoufas 2006; Ioannou et al. 2009).

We hypothesize that the observed distribution patterns are related to the variability of abiotic factors that predominate in the distinct regions under study, putatively coupled with biotic interactions (Gili et al. 1989; Zabala & Ballesteros 1989). In fact, Zabala & Ballesteros (1989) suggested that in oligotrophic areas suspension feeders are restricted to deeper waters or in areas were strong currents prevail, while in shallow waters algal species can outcompete long-lived suspension feeders, such as gorgonian species. Moreover, Mediterranean gorgonian species are particularly vulnerable to temperature anomalies, which are more likely to occur in shallow waters. According to the above, the downward shift of the upper bathymetric limit observed in the N Aegean may be due to the more oligotrophic conditions and higher water temperatures characterizing this region compared to those of the NW Mediterranean and CE

Adriatic (Bosc et al. 2004; Ignatiadis 2005). The only exceptions to the bathymetric pattern of the N Aegean were the sites of Kalloni (10 m depth) and Lefteris (20 m depth), which are characterized by the presence of strong currents that are known to promote the growth of suspension feeders such as *E. cavolini* (Gili & Coma 1998).

4.2 Population structure and dynamics

E. cavolini population density ranged from 4.46 to 62 colonies per m^2, although the species may attain much greater densities (Weinbauer & Velimirov 1996b). Density was highly variable across regions, and displayed a decreasing trend from west to east. Highest values were observed in the NW Mediterranean, intermediate in the CE Adriatic, and lowest in the N Aegean, while in all regions significant differences were also detected at the level of sites within localities. Variability in density among sites within the same depth range (i.e. <40 m) has also been observed in other localities of the NW Mediterranean (e.g. for *E. cavolini*: Russo 1985; Weinbauer & Velimirov 1996b; Cigliano & Gambi 2007), as well as for other Mediterranean gorgonians (e.g. for *E. singularis*: Weinberg 1979; Linares et al. 2008, *Paramuricea clavata*: Harmelin & Marinopoulos 1994; Linares et al. 2008, and *Corallium rubrum*: Tsounis et al. 2006; Linares et al. 2010a). According to these studies, density is usually related to factors that affect reproduction and recruitment success. For example, Weinbauer & Velimirov (1996a, 1996b) justified the wide density differences observed in *E. cavolini* populations (15–180 colonies per m^2) among nearby sites at the Bay of Calvi – Corsica, on the basis of substrate availability, turbulence, abundance of large colonies and degree of colony overgrowth by other organisms. They further related these factors to the successful reproduction, settlement and survival of new colonies. On the other hand, increased densities have also been observed during periods of population recovery from MMEs, once detachment of dead colonies created free space for new recruits (e.g. Cupido et al. 2009; Linares et al. 2010b; Gambi & Barbieri 2012). In the present study, density was overall inversly related to height, supporting the idea that recruitment is driven by intra-specific competition mechanisms, where the lack of large colonies enhances recruitment success.

With regard to colony height, mean value for all examined populations was 15.7 ± 8.87 cm, with a maximum of 62 cm. Similar height values have been reported for both shallow (Russo 1985) and deep water populations of *E. cavolini* (i.e. >70 m, Bo et al. 2012). As in several other octocoral species, *E. cavolini* is known to display a high level of phenotypic plasticity (**Fig 7A** and **7B**) by modulating its structural characteristics and growth form (i.e. including fan size, shape, orientation, and polyp number) in response to water movement (Velimirov 1973, 1976; Weinbauer & Velimirov 1995a; Gori et al. 2012). It is therefore possible that the direction and velocity of prevailing water currents are the main factors determining colony height in several sites of the present study. In this respect, the greater proportion of larger colonies (>30 cm) found in the deeper sites of the CE Adriatic and N Aegean may be due to the greater environmental stability of deeper waters (Garrabou et al. 2002; Gori et al. 2011), and the decrease of hydrodynamic forces that are known to affect colony morphology. At the same time, the greater proportion of small colonies (<20 cm) observed in sites characterised by higher densities (mainly in the NW Mediterranean) may be indicative of a more dynamic environment (in terms of water flow and productivity), which reduces the optimal size of colonies, but retains highly reproductive, small sized colonies belonging to a wide range of age classes (Sebens 2002).

Although morphological plasticity may partly explain differences in population structure among sites, no significant differences were detected in colony height at the level of localities or regions. The overall patterns of height frequency distribution suggest that *E. cavolini* populations were at varying stages of development, driven by different recruitment and mortality dynamics. NW Mediterranean and CE Adriatic populations were mainly characterised by the predominance of one or both of the smaller size classes (0–10, >10–20 cm), indicating either continuous or pulse recruitment episodes. In the majority of the N Aegean populations, all size classes were almost equally represented, while the number of small colonies (especially of the 0–10 cm height class) was typically low, suggesting limited recruitment. Still, the presumably low recruitment dynamics of the N Aegean populations may be compensated by the presence of a large number of mature colonies during sporadic reproductive events, since gamete production, and hence reproductive output, increase exponentially with colony size (Yoshioka 1994, 1998; Linares 2007; Cupido et al. 2012). On the contrary, the low abundance of large colonies, or even the lack of them, observed in several studied sites across regions, may be indicative either of newly formed and expanding populations, or of the existence of additional natural and/or human-induced pressures (e.g. MMEs, mechanical damage especially caused by unregulated fisheries and recreational marine activities, or extreme wave action) which particularly affect the survivorship of larger height classes (Grigg 1975; Weinbauer & Velimirov 1996b; Cerrano et al. 2005; Linares et al. 2005; Coma et al. 2006; Tsounis et al. 2006; Cupido et al. 2009).

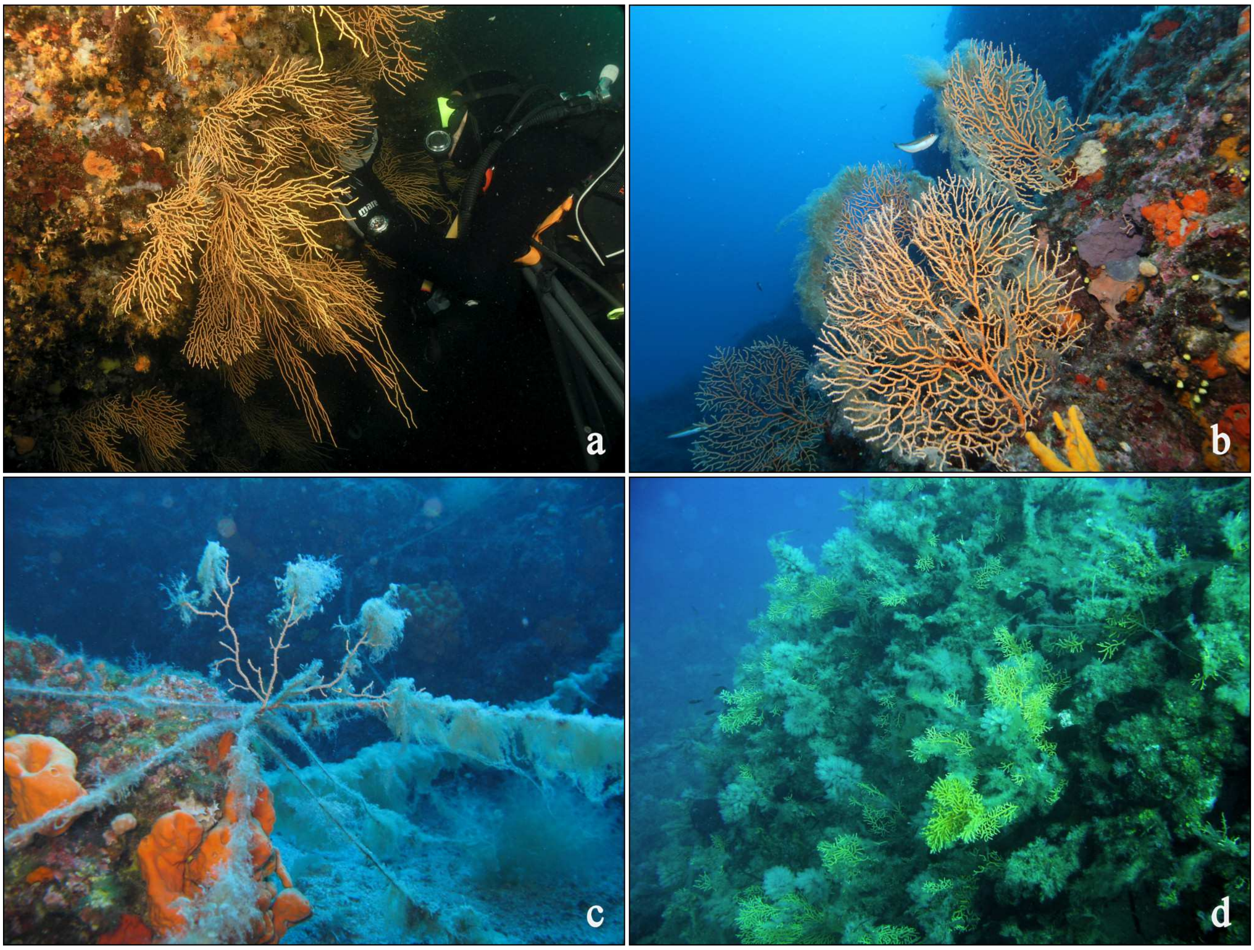

Fig 7. Colonies of the yellow gorgonian *Eunicella cavolini* exposed to different orientations and disturbances: a) in a large overhang; b) on open rock; c) under stress by fishing gear and mucilagenous algae, d) heavily overgrown during a mass mortality event.

Patterns of height frequency distribution similar to those observed herein have been documented for several gorgonian populations in other localities of NW Mediterranean and E Adriatic. A unimodal peak at the second size class –implying periodic recruitment– has been observed in populations of *E. cavolini* dwelling both shallow (<30 m, NW Corsica: Weinbauer & Velimirov 1996a) and deep waters (>70 m, S Tyrrhenian Sea: Bo et al. 2012), in shallow *P. clavata* populations off the Spanish and French coasts (<40 m, Harmelin & Garrabou 2005; Linares et al. 2008), as well as in deep *E. singularis* populations off the Spanish coasts (>50 m, Gori et al. 2011). Positively skewed populations, displaying prevalence of new recruits (0–10 cm) and low proportion of larger gorgonians, have been described for shallow *E. singularis* populations along the Spanish coasts (<25 m, Linares et al. 2008; Gori et al. 2011). Yet again, several authors (Cerrano et al. 2005; Cupido et al. 2008) have reported similar population structure for *P. clavata* in the Ligurian Sea following MMEs. On the other hand, populations characterised by a predominance of the smallest height class along with a high proportion of large colonies –reflecting well structured populations with continuous recruitment– were not observed during the present study, regardless the wide distribution range covered. Occasional reports of the latter pattern at depths <50 m include a single population of *E. cavolini* in NW Corsica (Weinbauer & Velimirov 1996a) and *P. clavata* populations in the E Adriatic (Kipson et al. 2014).

4.3 Extent of injuries: baseline for future monitoring

Injuries of gorgonian colonies are either caused by mechanical abrasion and predation or through necrosis of living tissue under stress conditions (e.g. persistence of thermal anomalies) causing partial and/or total mortality of colonies (**Fig 7c** and **7d**). Injured parts may break, regenerate or become colonised by overgrowing organisms (Bavestrello & Boero 1986; Harmelin & Marinopoulos 1994). *E. cavolini* is particularly vulnerable to such injuries, and has been affected by several MMEs related to temperature anomalies in the NW Mediterranean, some of which have led to substantial population reductions (e.g. Cerrano et al. 2000; Garrabou et al. 2009; Gambi et al. 2010). Although injury estimates were taken over different years in this study, thus not allowing for direct quantitative comparisons among regions, they do however provide insights regarding conservation status at the time of assessment, as well as baseline data for future assessments. Our assessment in Marseille and Scandola was realized two and ten years respectively, after one of the largest and best documented MME in the NW Mediterranean, which took place during late summer of 2003 (Garrabou et al. 2009). At the time of the MME, the estimated proportion of affected *E. cavolini* colonies ranged between 3–50.8% (mean: 14.5 ± 14.5) in Marseille and 4.9–34.2% (mean 17.1 ± 10.6) in Scandola (Garrabou et al. 2009). It is therefore possible that the number of affected colonies displaying old overgrowth (type C injury) in Marseille reflects the effects of the past MME given the slow recovery capacity of gorgonian species (Linares et al. 2005, 2007). This hypothesis is further supported by the high densities observed in the majority of the NW Mediterranean sites, and the low number of large colonies (>30 cm), as observed in other populations during recovery (e.g. Cupido et al. 2009; Linares et al. 2010b; Gambi & Barbieri 2012).

Within the CE Adriatic, *E. cavolini* populations found in the relative pristine conditions of Kornati presented a smaller mean extent of injury, as well as smaller proportion of affected colonies, compared to the populations of Pag and Rogoznica which are located more closely to the mainland and are potentially more exposed to human-induced stressors. As overgrowth by epibionts in all sites of the CE Adriatic was mostly old (injury type C), no recent disturbances were indicated at the time of assessment. Our observations are in agreement with reported disturbance values for populations of the red gorgonian *P. clavata* in the region (Kipson et al. 2014).

Regardless locality, the majority of N Aegean populations displayed a relatively low mean extent of injury, but overall high proportion of affected colonies. The injury values observed, combined with the generally low density and recruitment success recorded, render gorgonian populations of the N Aegean more prone to potential threats. Furthermore, in the sites of Ambelos and Kalloni, proportion of injured colonies (64.1% and 52.4% respectively) suggest increased levels of stress, while the high number of dead colonies (13.6%) in Kalloni is indicative of a strong impact. Although the reasons of the observed disturbance cannot be readily addressed through the present study, the increased levels of fishing activities (especially recreational and artisanal), and recurrent periods of high nutrient loads in the wider area (Spatharis et al. 2007, 2009), constitute some of the potential contributing stressors, especially given the shallow depth range of this population.

5. Closing remarks

Quantifying the demographic characteristics and disturbance levels of *E. cavolini* populations enabled the assessment of their conservation status and the acquisition of comparative information over a wide range of the species' known spatial distribution (Sini et al. 2014; Chapter 3). The patterns observed provide insights as to how biotic, abiotic, and anthropogenic factors may affect the structure and dynamics of populations at the spatial scales addressed in this study, and subsequently influence their adaptive capacity to environmental change. Given the widespread distribution of *E. cavolini*, further research will allow a more comprehensive view of the population trends presented herein, and enhance understanding and mitigation of potential future impacts. Extending the same kind of approaches to include other areas and species would provide key information that will help develop effective management plans for the conservation of valuable hard-bottom communities, including coralligenous assemblages, across the highly heterogeneous Mediterranean basin (Giakoumi et al. 2013).

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Κεφάλαιο 5

Ανάπτυξη και αναπαραγωγικά χαρακτηριστικά της γοργονίας *Eunicella cavolini* στο ΒΑ Αιγαίο

Περίληψη

Η εργασία διερευνά το ρυθμό ανάπτυξης και τα αναπαραγωγικά χαρακτηριστικά των αποικιών της γοργονίας *Eunicella cavolini* σε έναν πληθυσμό του ΒΑ Αιγαίου, με στόχο την κατανόηση της οικολογίας και του κύκλου ζωής του είδους. Για τη μελέτη της ανάπτυξης των γοργονιών, έγινε ποσοτική καταγραφή βασικών μορφολογικών χαρακτηριστικών σε μαρκαρισμένες αποικίες που χωρίστηκαν σε κλάσεις μεγέθους ως προς το ύψος. Σε κάθε γοργονία, μετρήθηκε το ύψος, το πλάτος, η συνολική επιφάνεια (*SA*), και η επιφάνεια του περιγεγραμμένου ορθογωνίου που περιβάλλει την αποικία (*RA*). Η εκτίμηση του ρυθμού αύξησης των μορφολογικών χαρακτηριστικών έγινε μέσω σύγκρισης φωτογραφικών δειγμάτων που συλλέχθηκαν κατά τη διάρκεια δύο δειγματοληπτικών περιόδων (Οκτώβρης 2011 και Οκτώβρης 2012). Τα βαθμονομημένα φωτογραφικά δείγματα αναλύθηκαν αξιοποιώντας διαφορετικά εργαλεία του λογισμικού photoQuad. Παράλληλα, χρησιμοποιώντας τις ίδιες κλάσεις μεγέθους, συλλέχθηκε βιολογικό υλικό με στόχο την καταγραφή των αναπαραγωγικών χαρακτηριστικών του είδους και τον προσδιορισμό του ελάχιστου μεγέθους των αποικιών που φτάνουν σε αναπαραγωγική ωριμότητα.

Η διερεύνηση των μορφομετρικών χαρακτηριστικών έδειξε πως το ύψος και το *SA* αποτελούν τους δύο πιο κατάλληλους δείκτες περιγραφής του μεγέθους και του ρυθμού ανάπτυξης της *E. cavolini*. Ο εκτιμώμενος ρυθμός ανάπτυξης του ύψους των αποικιών κυμάνθηκε μεταξύ 0.1 και 4.4 cm (1.4 cm ± 0.95, μέσος ± τυπική απόκλιση), και παρουσίασε σημαντική μείωση με την κλάση ύψους. Παράλληλα, ο απόλυτος ρυθμός αύξησης του *SA* κυμάνθηκε μεταξύ 0.1 και 69 cm^2 (14.1 cm^2 ± 16.3), ενώ ως ποσοστό της αρχικής μέτρησης, επίσης έδειξε μείωση με την κλάση ύψους. Οι σημαντικές διαφορές μεταξύ του ρυθμού ανάπτυξης των μικρότερων σε ύψος αποικιών (<20 cm) και των μεγαλύτερων, συμφωνούν με τα ευρήματα που περιγράφουν το ελάχιστο ύψος των αποικιών που φτάνουν σε αναπαραγωγική ωρίμανση. Οι μικρότερες αποικίες (ανεξαρτήτως φύλου) που έφεραν γονάδες προέρχονταν από την κλάση ύψους 10–20 cm; σε ό,τι αφορά τα επίπεδα γονιμότητας όμως, φαίνεται ότι οι αποικίες της *E. cavolini* φτάνουν σε πλήρη αναπαραγωγική

ωριμότητα αφού ξεπεράσουν το ύψος των 20 cm. Επιπλέον, παρατηρήθηκε ξεκάθαρος διαχωρισμός των φύλων μεταξύ διαφορετικών αποικιών. Οι θηλυκές αποικίες είχαν κατά μέσο όρο 4.6 ωοκύτταρα ανά πολύποδα, η διάμετρος των οποίων ήταν μεταξύ 60 και 890 μm. Οι αρσενικές αποικίες είχαν κατά μέσο όρο 25.5 σπερματοκύστες ανά πολύποδα, και η διάμετρος των σπερματοκύστεων κυμάνθηκε μεταξύ 74 και 664 μm. Η παρούσα μελέτη είναι η πρώτη προσπάθεια καταγραφής των αναπαραγωγικών χαρακτηριστικών αυτού του ευρέως γεωγραφικά κατανεμημένου είδους γοργονίας. Παρόλο που επιπλέον έρευνα είναι απαραίτητη για την αναλυτικότερη μελέτη του αναπαραγωγικού κύκλου του είδους, τα αποτελέσματα έδειξαν ότι η *E. cavolini* παρουσιάζει παρόμοια αναπαραγωγικά χαρακτηριστικά με αυτά που έχουν καταγραφεί σε άλλα Μεσογειακά είδη γοργονιών σκληρού υποστρώματος. Συγκεκριμένα, αργή αναπαραγωγική ωρίμανση, και παρατεταμένη περίοδο απελευθέρωσης γαμετών ή/και λαρβών που κορυφώνεται και ολοκληρώνεται κατά τα τέλη της άνοιξης με αρχές καλοκαιριού.

Chapter 5

Growth and reproductive characteristics of *Eunicella cavolini* in the NE Aegean Sea

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Abstract

In this study, we investigate colony growth and reproductive features of *Eunicella cavolini* colonies that thrive at an offshore reef in NE Aegean Sea (NE Mediterranean), in order to better understand the ecology of the species in this under-explored area, and contribute to the overall understanding regarding its life history traits. Growth rates of colony height, width, surface area (*SA*), and rectangular area (*RA*) were estimated in relation to colony height, by comparing sets of photographic samples acquired over two consecutive measurement seasons in the course of one year (October 2011 and October 2012). The image samples were quantitatively analysed using distance and surface area measurement tools provided by the photoQuad software. The reproductive status of colonies belonging to different height classes was also assessed, in order to define the approximate colony size at the onset of sexual maturity, and provide some first insights regarding the reproductive characteristics of *E. cavolini*. Of all morphometric parameters considered, colony height and *SA* appeared to be the most appropriate metrics for defining colony size and growth rate. The estimated mean positive growth of height ranged between 0.1 and 4.4 cm (1.4 cm ± 0.95, mean ± standard deviation), and was found to decrease with colony height. At the same time, *SA* growth ranged from 0.1 to 69 cm^2 (14.1 cm^2 ± 16.3), and when expressed as a percentage of the initial measurement, it also decreased with colony height. The significant differences between the growth rate of colonies less than 20 cm in height and the larger ones coincide with data that regard the onset of sexual reproduction. The smallest gonad-bearing colony for both sexes belonged to the height class of 10–20 cm; in terms of fecundity however, colonies appeared to reach full sexual maturity only after attaining a height of 20 cm. Furthermore, sex separation was clear among *E. cavolini* colonies. Female colonies had a mean number of 4.6 oocytes per polyp, whose diameter ranged from 60 to 890 μm. Male colonies had a mean number of 25.5 sperm sacs per polyp, with sperm sac diameter ranging from 74 to 664 μm. To our knowledge, this is the first study that assesses the reproductive characteristics of this widespread, gorgonian species. While further systematic studies are needed to investigate the annual reproductive cycle in greater detail, the results suggest that *E. cavolini* displays sexual characteristics that are also found in other hard substrate Mediterranean gorgonian species, such as delayed maturity, and a prolonged spawning period which culminates during late spring and early summer.

1. Introduction

Colony shape and size underlie several ecological processes in clonal animals, by affecting the ability of organisms to feed and reproduce (Grigg 1977; Kim & Lasker 1997; Kapela & Lasker 1999). Both from an ecological, as well as from a conservational standpoint, defining somatic growth rates and reproductive characteristics is key for understanding basic life history patterns, such as fecundity, recruitment, and mortality. The latter have great impact on population dynamics and resilience to disturbances (Gotelli 1991; Garrabou & Harmelin 2002; Linares et al. 2007), which are critical to quantify when endangered and commercially or structurally important species are considered.

Mediterranean gorgonians are important structural elements of marine benthic communities, and play an important role in the maintenance of biological diversity and biomass (True 1970; Cerrano et al. 2010; Ponti et al. 2014). Over the last few decades, the integrity of Mediterranean gorgonian forests has been greatly altered by natural and human-induced disturbances (Cerrano et al. 2000; Garrabou et al. 2009; Teixido et al. 2013). Reflecting these alterations, at least four of the most abundant –yet highly sensitive– species have been recently included in the preliminary IUCN Red List of Threatened Anthozoan Species for the Mediterranean (2015); *Corallium rubrum* has been assigned the status of “Endangered”, *Paramuricea clavata* has been characterised as “Vulnerable”*,* while *Eunicella cavolini* and *E. singularis* have been classified as “Near Threatened”. This imposes an ever-increasing pressure to compose conservation management actions at local and regional scales (UNEP-MAP RAC/SPA 2008), whose success, however, presupposes an in-depth understanding of the ecology and the species-specific responses to local conditions or stress.

While several studies have elaborated on the ecology and population dynamics of gorgonian species in the NW Mediterranean, information from other parts of the basin remains comparatively sparse (Kipson et al. 2014; Sini et al. 2015; Chapter 4). Considering the Aegean Sea in particular, evaluating the current extent and conservation status of gorgonian populations is practically hindered by the lack of historical records on past distribution and demographic characteristics (e.g. Dounas et al. 2009). The ability to predict future population trends in light of global change (Linares et al. 2007) is also limited by the absence of data on key life history parameters, such as growth and reproduction.

According to recent assessments, the yellow gorgonian *E. cavolini* is one of the widest ranging octocorals in the Mediterranean, and the most common gorgonian that thrives in coralligenous assemblages of the Aegean Sea (Sini et al. 2014, 2015; Chapter 3,4). NW Mediterranean studies have showed that *E. cavolini* is a long-lived species with an estimated maximum age of 21 years and a turnover rate (i.e. the time it takes to replace population biomass) that spans from 3.1 to 4.1 years (Weinbauer & Velimirov 1995, 1996). Similar to other gorgonians however, morphological characteristics, recruitment dynamics and mortality rates of *E. cavolini* can potentially vary even within small geographic scales, in response to local environmental conditions and natural or anthropogenic disturbances (Weinbauer & Velimirov 1996; Sini et al. 2015; Chapter 4). Moreover, the reproductive characteristics of this species have not been studied to date, regardless geographic scale.

The broader scope of this work was to contribute to a better understanding of *E. cavolini* population dynamics, and reduce existing knowledge gaps regarding the ecology of hard substrate octocorals in the Aegean Sea. In this context, we assessed morphometric parameters and reproductive features of *E. cavolini* colonies that thrive in a coralligenous assemblage at the NE Aegean Sea. Notwithstanding the temporal and geographical scale of the study, this research seeks to quantify colony growth rates, determine colony size at first reproduction, and provide some first insights into the reproductive characteristics of this widespread gorgonian, through a combined study on somatic growth and reproduction.

2. Materials and Methods

2.1 Site description

The study was conducted at Palios Reef (39°19'42"N, 26°26'10"E), NE Lesvos island, Aegean Sea. Palios Reef is part of an extensive, offshore, rocky drop-off situated along the edge of the Lesvos island plateau. The predominance of sciaphillic conditions and the continuous flow of medium-to-strong currents enhance the development of rich coralligenous assemblages along most parts of the drop-off. The study site is located at a vertical wall with NE orientation that spans a depth range of 18 to 30 m. The substrate becomes sub-vertical at the deepest part of the wall, and a population of *E. cavolini* colonies is found at 30–44 m depth. According to Chapter 4 (Sini et al. 2015), mean population density is 6 colonies per m^2 and maximum colony height is 48 cm (24 cm ± 10.6, mean ± standard deviation).

2.2 Colony morphometrics and growth

Assessment of morphometric descriptors and growth was realised using *in situ* photography of tagged colonies over a period of one year (October 2011 – October 2012). Colony height (defined as the distance between the colony base and the tip of the furthest apical branch) was initially measured *in situ* using a scale ruler, and colonies were tagged according to four predefined height classes (1st class: >0–10 cm, 2nd: >10–20 cm, 3rd: >20–30 cm, 4th: >30 cm). A total of 15 colonies per height class were marked, using uniquely-enumerated plastic tags that were secured to the base of each colony with cable ties. Tagged colonies were initially photographed during October 2011, and recovered colonies were re-photographed after one year, during October 2012. Photographs of gorgonians were taken using a DSLR camera with a 35 mm lens and external strobe lights. Photographic sampling was facilitated by a 50×50 cm white board that was annotated with calibration lines spaced at 10 cm intervals. Prior to taking a photographic sample, the board was placed behind, and parallel to, the gorgonian; this allowed a clear view of the sampled colony against the background, and permitted the calibration of images during post-processing. Facing the center of the target gorgonian, the DSLR camera was always positioned normal (i.e. perpendicular) to the colony fan.

A preliminary review of the dataset showed that, for a small fraction of images (approx. 15%), the board was not parallel to the gorgonian fan due to difficulties related to fieldwork conditions. This introduced an error in image calibration. Specifically, image calibration is achieved by placing reference marks on two points of the image that are of a known distance apart (A’B’, **Fig 1a**), and specifying the actual distance spanned by the points in centimeters (AB). In our case, AB was provided by the board’s 10 cm intervals. If the board is not positioned parallel to the fan (**Fig 1b**), image calibration marks will actually be placed on a smaller distance (A’B’, determined by the cosine of the board’s angle to the fan), yet still be specified as 10 cm apart. This effectively overestimates image measurements. The length correction factor L_{CF}, defined as the number that an image length measurement must be multiplied with to compensate for this error, is readily computed given that A’B’ = cos(θ) × AB (**Fig 1c**). Given that pixels are equal in both dimensions, area correction factor is: $A_{CF} = L_{CF}^2$. To validate this mechanism a small *ex situ* experiment was performed. Initially, the true height of a gorgonian fan was measured with a ruler. The fan was then photographed according to the *in situ* set up (**Fig 1a**), and the photograph was calibrated, verifying that the image height measurement was in agreement with the true height. Additional photographs were taken at successive board inclinations (0° – 40°, with a step of 5°), photographs were recalibrated, and the resulting image height was recorded. This verified that image height using an inclined board was overestimated, while the ratio of true height to image height as a function of the angle θ followed the theoretical curve (**Fig 1c**). An equivalent validation process was followed for area measurements.

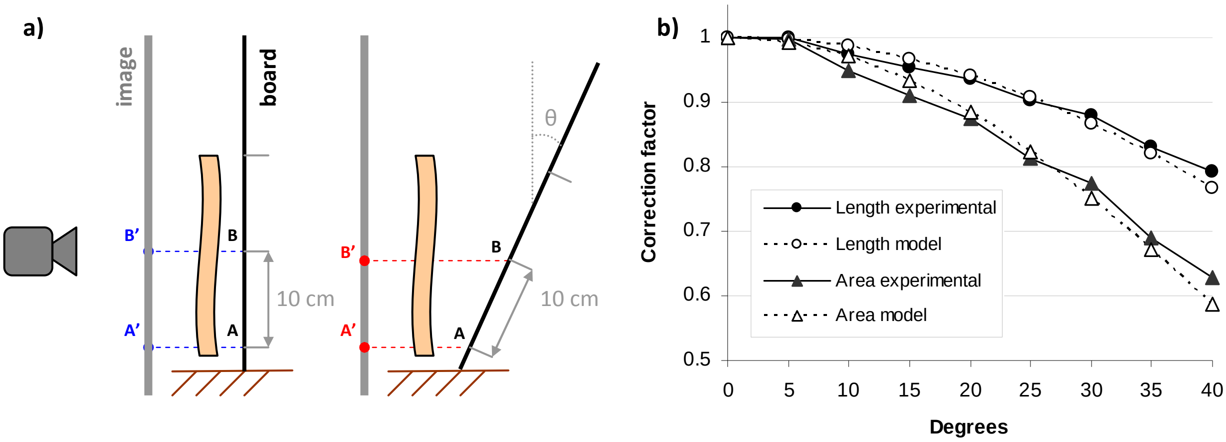

Fig 1. Correction factors for length and area measurements. a) Graphical representation of the sampling set up used to photograph gorgonian colonies. Both the colony (in orange) and the background board are projected on the image. Points A and B denote board marks placed at known intervals. The corresponding A’ and B’ calibration points directly associate pixel units to board marks. b) As in panel a), but with a background board inclined by θ˚ relative to the fan. Note that the calibration length A’B’ does not correspond to AB. c) Length and area calibration factors as a function of θ.

Photographs were preprocessed using standard image enhancement tools, and were then calibrated and analyzed using the photoQuad software (Trygonis & Sini 2012). Overall, four main colony descriptors were extracted per image sample (**Fig 2**): colony height (cm), width (cm), surface area (*SA*, cm^2), and rectangular area (*RA*, cm^2). Height was assessed by measuring the distance from the lowest visible point of the colony axis to the tip of the furthest branch; note that the lowest colony point was common for both the initial (2011) and for the follow-up

(2012) sample, and was determined after a preliminary review of the images. Width was defined as the maximum span of the gorgonian fan along a line that was perpendicular (90°) to the colony's height axis.

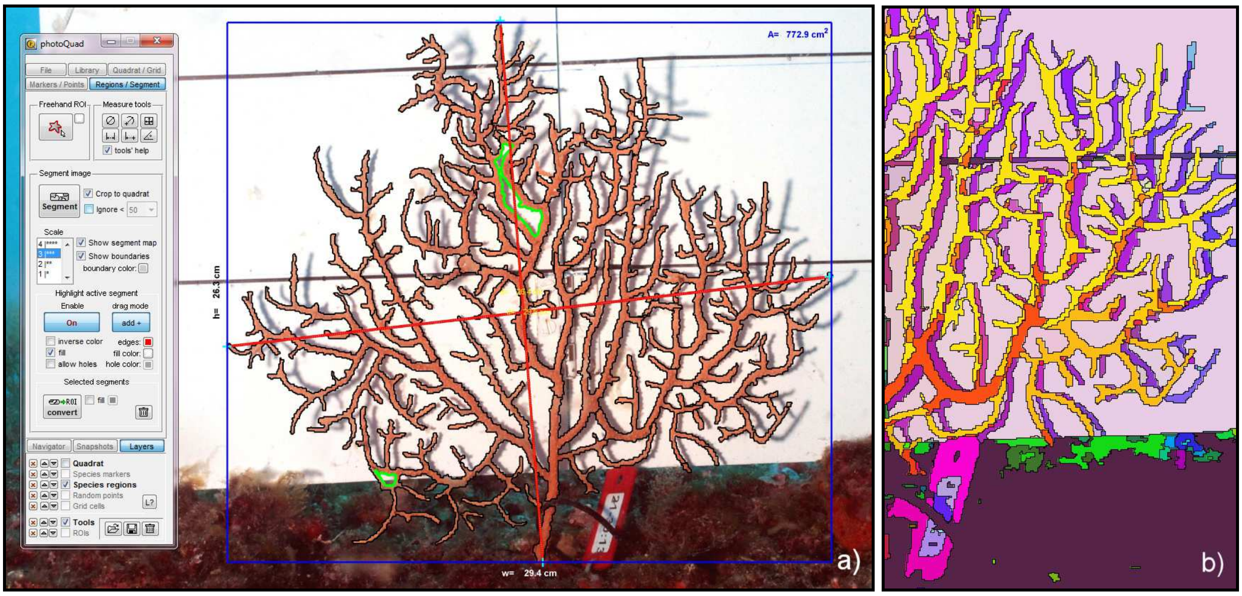
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Fig 2. Calibrated image analysis of Eunicella cavolini using the photoQuad software (Trygonis & Sini, 2012). a) Measurement tools employed to extract morphometric descriptors and growth characteristics. The black outline encompassing the E. cavolini fan indicates colony surface area (SA, cm2); inner green lines denote (internal) empty spaces that were excluded from SA measurements. The outer blue box circumscribing the fan indicates rectangular colony area (RA, cm2). Red lines represent measurements of maximum height (cm) and width (cm). Note the black calibration lines on the white board (spaced at 10 cm regular intervals) that allowed the software to convert image pixel measurements into real-world units. b) Pseudocoloured detail illustrating the image segmentation process that allows the semi-automatic selection of colony regions in order to extract the SA outline.

For each image sample, surface area *SA* was assessed by carefully outlining all colony branches, and measuring the area of the resulting patch that fully overlaid the fan; empty regions within the fan, as well as injured colony parts (i.e. regions devoid of coenchyma tissue or overgrown by other organisms) were excluded from *SA* measurements (see **Fig 2**, green regions). The selection of *SA* outlines was facilitated by photoQuad's image segmentation tool, which partitions the source image into distinct patches that share common characteristics in colour or intensity (Teixidó et al. 2011; Trygonis & Sini 2012). Segmentation occurs at four different scales (ranging from coarse to fine detail), offering individual patches that can be interactively selected and grouped to produce a unified patch (i.e. the gorgonian fan) whose surface area can be extracted. Manual outline corrections can be applied, and the software automatically converts pixel units to real-world units using the image calibration data. In case of poor contrast or colour properties, the source image was preconditioned using decorrelation stretch prior to segmentation. Decorrelation stretch is a standard technique used to exaggerate the color differences in an otherwise uniformly-toned image (Gillespie et al. 1986), producing a pseudocoloured image with clear colour separation that is easier to segment. Finally, colony rectangular area (*RA*) was assessed by manually drawing a rectangle that circumscribed the fan. By definition, the lower side of the rectangle was attached to the height axis' lower point, and rectangle sides were always parallel to the image frame regardless the fan's curvature.

For each morphometric descriptor, growth was defined as the difference between two consecutive measurements of the same colony, i.e. the measurement of 2012 minus the measurement of 2011. A negative sign indicated negative growth, i.e. reduction of the measured colony feature. When needed, morpohometric descriptors were debiased using the aforementioned calibration factors.

2.3 Reproductive characteristics

Size at first maturity

The reproductive status of *E. cavolini* colonies belonging to one of the four predefined height classes was investigated in order to determine the approximate colony size at first reproductive maturity. *E. cavolini* colonies were sampled during May 2011, based on previous reports regarding the peak in gonadal development and spawning timing of other shallow water Mediterranean gorgonian species (Coma et al. 1995; Gori et al. 2007; Ribes et al. 2007). A total of 47 colonies were sampled; 14 of the 1st height class, and 11 for each of the remaining height classes. Tagged colonies whose morphometric parameters where being monitored for the growth experiment (see section 2.2) were explicitly avoided. For each sampled colony, an apical branch tip of 3 to 5 cm in length was collected, and fixed in 10% formalin solution. A minimum of ten polyps per branch were dissected under a stereo microscope, in order to determine colony gender and quantify reproductive characteristics, i.e. percentage of fertile colonies, proportion of gravid polyps per colony, number of gonads per polyp, and gonad diameter. The minimum sample size of colonies and polyps per colony was selected according to Ribes et al. (2007). Gonads were photographed using a microscope digital camera, and measured with commercial image analysis software. Only gonads with a diameter greater than 300 μm were considered as mature, based on observations of gonad development of the congeneric species *E. singularis* (Gori et al. 2007; Ribes et al. 2007).

Final stages of gonad development

Taking advantage of the May 2011 dataset that was exclusively used to assess size at first maturity, additional samples were collected during March, April and June 2014 from the same population, increasing the temporal scale of our experiment. This was done to increase the probability of encountering (and validating) the peak of reproductive cycle, and gain some first insights regarding the final stages of gonadal development of the species. In this case, only colonies greater than 20 cm in height were sampled, given that the preliminary analysis of the May 2011 dataset suggested that full maturity is attained beyond this height. As sex could not be determined *in situ*, 30 to 45 colonies were sampled per month. Following the determination of gender in the laboratory, a minimum of ten male and ten female colonies were randomly selected and analyzed per month. The only exception was June 2014, where the absence of mature gonads did not allow determination of colony gender. To ensure a satisfactory representation of genders in this month, a slightly increased number of 25 colonies were examined. Further laboratory handling of the 2014 samples followed the same procedures applied to samples of May 2011. The final dataset for the assessment of gonadal development comprised of the aforementioned 2014 samples, pooled with samples of colonies greater than 20 cm obtained in May 2011.

2.4 Data analysis

Morphometric and reproductive parameters were initially tested for normality and homoscedasticity via the Shapiro-Wilk and Levene's tests, respectively. Datasets that did not follow a normal distribution were square root transformed. One-way Analysis of Variance (ANOVA) was the main test used for statistical comparisons, while the more robust Welsch F test was additionally performed for datasets that did not satisfy the assumption of homogeneity of variances. When the aforementioned main tests indicated significant differences, post-hoc pairwise comparisons were applied, using Tukey's test or the respective Games-Howell test for data without homogeneity of variance. The relations between different morphometric parameters, as well as the relations between their rate of growth and colony height, were further investigated through Spearman rank order correlation tests. Chi-square

(x^2) tests were applied to examine potential associations between height class and fertility, and to assess if the frequency of occurrence of colonies with negative growth depended on size.

3. Results

3.1 Morphometric descriptors and growth

A total number of 60 colonies (15 per height class) were initially tagged and photographed during October 2011; out of these, 45 colonies were successfully recovered and re-photographed a year later. An additional colony of the 4th height class was found dead due to detachment from substrate, and was excluded from analysis. During the pre-processing data review, 5 more colonies were excluded from the dataset (2 colonies of the 3rd, and 3 of the 4th height class), due to poor image quality that prohibited the objective extraction of morphometric descriptors. Based on the aforementioned inventory, the final dataset comprised of 40 colonies; their partition per height class was 8, 13, 11, and 8 colonies belonging to the 1st, 2nd, 3rd, and 4th class, respectively. The descriptive statistics of colony morphometric parameters are presented in **Table 1**, tabulated by height class and year.

Table 1. Summary statistics of *Eunicella cavolini* morphometric descriptors, tabulated by height class and year. *SA* denotes surface area; *RA* stands for rectangular area, corresponding to the rectangle circumscribing the fan (see **Fig 2** for a graphical representation of descriptors). SD: standard deviation, CV: coefficient of variation.

Height class (cm)	**Morphometric descriptor**	**2011**						**2012**					
		N	**Mean**	**SD**	**Min**	**Max**	**CV**	**N**	**Mean**	**SD**	**Min**	**Max**	**CV**
>0–10	**Height (cm)**	8	6.5	2.1	3.8	9.7	32.3	8	8.5	2.5	5.1	11.4	29.4
>10–20	**Height (cm)**	13	14.3	2.6	10.4	18.2	18.2	13	15.8	2.6	12.3	20.3	16.7
>20–30	**Height (cm)**	11	26.3	2.2	22.7	29.4	8.4	11	26.9	2.9	21.1	31.0	10.7
>30	**Height (cm)**	8	35.6	3.1	31.4	41.2	8.6	8	36.4	3.1	31.9	41.7	8.4
>0–10	**Width (cm)**	8	3.8	2.1	0.3	5.9	55.3	8	4.3	2.4	0.5	7.9	55.8
>10–20	**Width (cm)**	13	14.8	3.6	9.9	21.3	24.3	13	16.2	4.4	10.2	24.2	27.7
>20–30	**Width (cm)**	11	30	8.7	18.1	45.4	29.0	11	31.7	7.8	19.4	46.0	24.6
>30	**Width (cm)**	8	43.3	5.8	34.2	53.0	13.4	8	45.5	5.4	36.5	54.0	11.8
>0–10	***SA* (cm^2)**	8	3.0	1.5	0.2	4.9	50.0	8	4.0	2.5	0.3	7.3	62.5
>10–20	***SA* (cm^2)**	13	27.4	15.2	8.0	52.0	55.5	13	36.7	19.2	11.8	69.3	52.3
>20–30	***SA* (cm^2)**	11	118.4	51.5	46.5	224.8	43.5	11	120.8	49.1	60.0	218.0	40.6
>30	***SA* (cm^2)**	8	300.6	84.7	160.8	437.9	28.2	8	318.5	91.5	207.2	479.5	28.7
>0–10	***RA* (cm^2)**	8	24.4	16.0	0.3	50.4	65.6	8	39.2	31.5	0.9	89.1	80.4
>10–20	***RA* (cm^2)**	13	222.8	100.4	129.5	432.8	45.1	13	269.4	117.4	113.6	468.2	43.6
>20–30	***RA* (cm^2)**	11	792.2	301.7	402.7	1425.7	38.1	11	843.6	267.7	386.1	1290.8	31.7
>30	***RA* (cm^2)**	8	1532.3	383.8	1129.9	2358.7	25.0	8	1671.4	366.5	1274.2	2421.0	21.9

When all height classes were pooled, colony height ranged from 3.8 to 41.7 cm, width ranged from 0.3 to 54 cm, *SA* ranged from 0.2 to 479.5 cm^2, while *RA* ranged from 0.3 to 2421 cm^2. The one-way ANOVA tests showed that mean colony height ($F_{(3,76)} = 366.4$, $p<0.00$), width ($F_{(3,76)} = 212.3$, $p<0.00$), *SA* ($F_{(3,76)} = 238.7$, $p<0.00$), and *RA* ($F_{(3,76)} = 235.5$, $p<0.00$) were statistically different among height classes, while the post-hoc, pairwise comparisons indicated that differences existed between all height classes ($p<0.00$).

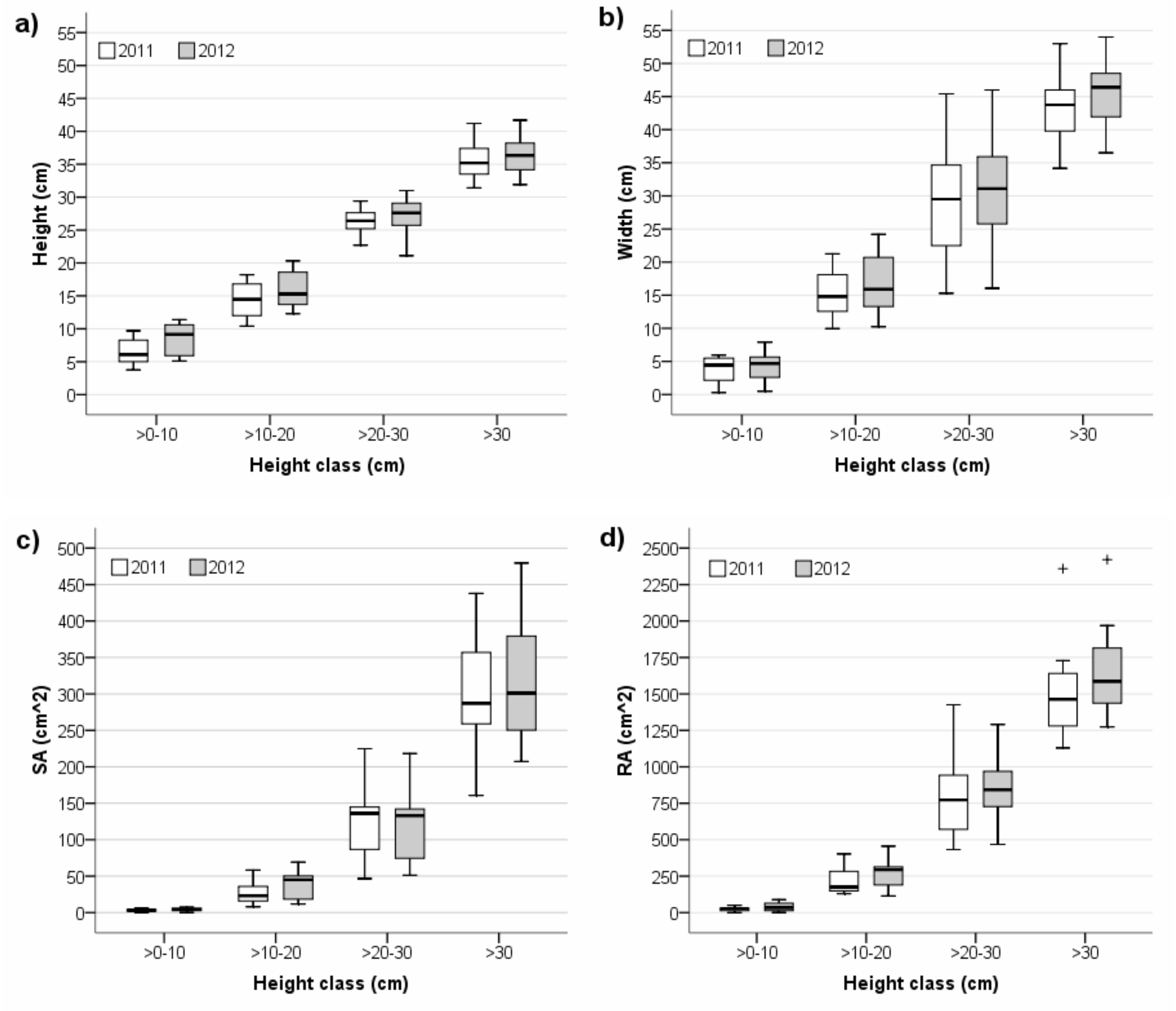

Fig 3. Box and whisker plots of *Eunicella cavolini* colony morphomentric descriptors, tabulated by height class and year: a) height; b) width; c) surface area; d) rectangular area. Horizontal lines within boxes represent the median; boxes encompass 50% of the cases, whiskers indicate non-outlier range, and cross markers denote outliers. Refer to **Table 1** for counts per height class.

All mophometric descriptors increased with height class (**Fig 3**). Excluding the largest colonies, values of colony height and width were generally comparable within classes, as also indicated by the common scale of the y-axes in **Fig 3a** and **3b**. Colony width was lower than colony height for the smallest gorgonians (1st height class), and was practically equal to height for the 2nd height class. A notable change in width variability and width-to-height ratio occurred at the larger height classes, in which colonies were greater in width than in height. In terms of surface area, differences in median *SA* increased in a non-linear fashion between consecutive height classes. Considering that *SA* is a descriptor that accounts for the development of the inner branch colony network, the pattern observed in **Fig 3c** reflects and abrupt increase in colony size after reaching approximately 20 cm in height. Colony *RA* (**Fig 3d**) followed a similar pattern to *SA*, but was an order of magnitude greater than the more realistic *SA* values.

Table 2 illustrates Spearman's rank order correlations between morphometric descriptors, using averages of measurements taken over the two observation years (2011, 2012)[1]. When tabulated by height class, descriptor correlations revealed morphological changes of the gorgonian fan, and the evolution of its overall structure. Specifically, the smallest height class (>0–10 cm) was the only case where width was not correlated with any other morphometric descriptor. At this colony size, height was the predominant structural axis of the colony, as indicated by **Fig 3a**,**b** and its strong correlation with *SA* and *RA*. Note that here, area descriptors exhibited their highest correlations found in any height class. The 2nd height class (>10-20 cm) was the only case where all morphometric descriptors were correlated with each other, and the only colony state where height and width were correlated. Taking into account that width to height ratio increased significantly between the 1st and 2nd height class (effectively reaching 1 in the latter, **Table 1**), colonies within the 2nd height class apparently exhibited a more globular increase of branches. From the 3rd height class onwards, height was not correlated with *SA*, although the latter displayed an abrupt increase in the larger height classes (**Fig 3c**). This strongly suggests that *SA* –which reflects the internal branching structure of the colony–, was not systematically related to height beyond this class. Even more so, *SA* was not correlated with any descriptor in the last height class, indicating that morphological changes in colony structure were not mirrored to any of the main colony axes (height or width). See also **Fig 4**, where width, and especially height, gradually reached a plateau in colonies of large surface area. Innate to its rectangular shape that is effectively modulated by height and/or width, *RA* was always related to the predominant colony axis per height class. Furthermore, the strongest

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[1] Within-year correlations of descriptors revealed similar patters to correlations of between-year averaged descriptors.

correlation of *RA* with *SA* was noted at the smallest height class, where colonies practically had only a single main axis (height).

Table 2. Spearman rank order correlations between colony morphometric parameters, averaged over 2011 and 2012 (N = 40 colonies).

Height class	Parameter	Av. height (cm)	Av. width (cm)	Av. *SA* (cm^2)	Av. *RA* (cm^2)
>0–10	**Av. height (cm)**	1	0.619	**0.905***	**0.952***
	Av. width (cm)		1	0.833	0.762
	Av. *SA* (cm^2)			1	**0.976***
	Av. *RA* (cm^2)				1
>10–20	**Av. height (cm)**	1	**0.709***	**0.846***	**0.912***
	Av. width (cm)		1	**0.846***	**0.890***
	Av. *SA* (cm^2)			1	**0.929***
	Av. *RA* (cm^2)				1
>20–30	**Av. height (cm)**	1	0.691	0.509	**0.773***
	Av. width (cm)		1	**0.782***	**0.982***
	Av. *SA* (cm^2)			1	**0.773***
	Av. *RA* (cm^2)				1
>30	**Av. height (cm)**	1	0.048	-0.357	0.262
	Av. Width (cm)		1	0.595	**0.929***
	Av. *SA* (cm^2)			1	0.429
	Av. *RA* (cm^2)				1
Pooled	**Av. height (cm)**	1	**0.952***	**0.965***	**0.983***
	Av. width (cm)		1	**0.973***	**0.985***
	Av. *SA* (cm^2)			1	**0.984***
	Av. *RA* (cm^2)				1

* Correlation is significant at the 0.01 level.

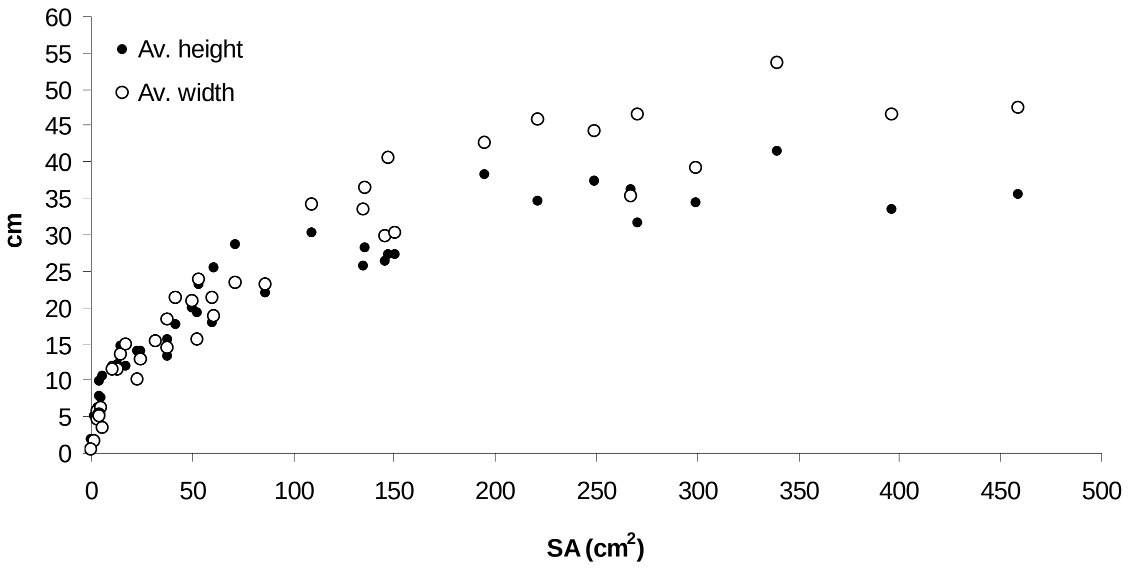

Fig 4. Between-year (2011, 2012) averaged colony height and width versus surface area (*SA*).

Out of the 40 colonies considered, 70% displayed positive growth, while 30% had negative growth in at least one of their morphometric descriptors. The chi-square test showed that colony counts with negative growth was not height dependant (x^2 = 2.93, df = 3, *p*=0.4). Identified causes of negative growth included the loss of coenchyma tissue, loss of branches, and predation or overgrowth by other organisms. Negative growth ranged from -1.2 to -1.6 cm for height, -0.4 to -2.6 cm for width, -1 to -84.5 cm^2 for *SA*, and -7.5 to -134.9 cm^2 for *RA*. In order to estimate optimum colony growth, further analysis of the data was focused on colonies displaying only positive growth. Nonetheless, **Table 3** summarises the descriptive statistics of positive growth alongside net growth to accommodate future comparisons. With regards to positive growth, height growth ranged between 0.1–4.4 cm (1.4 cm ± 0.95), and was found to decrease with height class. Growth of width ranged between 0–6.7 cm (1.9 cm ± 1.7), presented an initial increase at the 2nd height class, and remained relatively stable across the remaining height classes. In terms of colony area, both area descriptors were characterised by an overall increasing trend with height class; range of *SA* growth was 0.1–69 cm^2 (14.1 cm^2 ± 16.3), while *RA* growth was 0.6 to 241.1 cm^2 (84.8 cm^2 ± 66.9).

Table 3. Summary of *Eunicella cavolini* growth per morphometric descriptor, tabulated by height class. Net growth includes colonies displaying both negative and positive growth. The column labeled "%" expresses growth as a percentage of the initial (2011) measurement. SD: standard deviation, *SA*: surface area, *RA*: rectangular area.

Height class (cm)	**Morphometric parameter**	**Positive growth**						**Net growth**					
		N	**Mean**	**SD**	**Min**	**Max**	**%**	**N**	**Mean**	**SD**	**Min**	**Max**	**%**
0<10	**Height (cm)**	8	2.0	1.4	0.1	4.4	40.1	8	2.0	1.4	0.1	4.4	40.1
10<20	**Height (cm)**	12	1.8	0.7	0.6	3.3	13.2	13	1.5	1.1	-1.3	3.3	11.5
20<30	**Height (cm)**	10	0.9	0.6	0.1	1.6	3.3	11	0.7	0.9	-1.6	1.6	2.4
>30	**Height (cm)**	8	0.8	0.4	0.4	1.5	2.2	8	0.8	0.4	0.4	1.5	2.2
0<10	**Width (cm)**	6	1.1	1.2	0.0	3.3	41.3	8	0.5	1.7	-2.3	3.3	24.6
10<20	**Width (cm)**	11	2.0	2.2	0.1	5.9	13.5	13	1.4	2.4	-2.6	5.9	9.7
20<30	**Width (cm)**	10	1.9	1.8	0.6	6.7	7.6	11	1.7	1.8	-0.4	6.7	6.9
>30	**Width (cm)**	8	2.2	1.4	0.2	4.0	5.4	8	2.2	1.4	0.2	4.0	5.4
0<10	***SA* (cm^2)**	7	1.6	1.4	0.1	3.8	56.5	8	1.0	2.1	-3.1	3.8	41.6
10<20	***SA* (cm^2)**	11	11.7	11.8	0.8	36.3	53.8	13	9.35	12.2	-4.7	36.3	42.7
20<30	***SA* (cm^2)**	7	11.6	9.9	1.6	26.7	13.0	11	2.4	16.3	-27.6	26.7	4.5
>30	***SA* (cm^2)**	7	32.6	21.1	0.7	69.0	13.2	8	17.9	45.8	-84.5	69.0	7.9
0<10	***RA* (cm^2)**	6	23.2	16.7	0.6	38.7	126.9	8	14.8	21.0	-12.9	38.7	86.8
10<20	***RA* (cm^2)**	10	67.3	54.6	4.4	172.8	32.4	13	46.6	61.7	-32.9	172.8	22.2
20<30	***RA* (cm^2)**	8	98.5	58.3	10.3	194.5	14.6	11	51.4	97.9	-134.9	194.5	8.7
>30	***RA* (cm^2)**	8	139.1	71.6	26.1	241.1	9.7	8	139.1	71.6	26.1	241.1	9.7

The ANOVA results showed that mean growth of height ($F_{(3,34)}$ = 4.474, *p*=0.009), *SA* ($F_{(3,28)}$ = 7.267, *p*=0.001) and *RA* ($F_{(3,28)}$ = 5.412, *p*=0.005) were statistically different between height classes, while no significant differences were observed in growth of width ($F_{(3,31)} = 0.470$, *p*=0.705). The pairwise comparisons indicated that height growth had marginal differences between height classes 2 and 3 (*p*=0.47), as well as classes 2 and 4 (*p*=0.05). Significant differences in *SA* growth were due to the much higher growth displayed by height class 4 compared to height classes 1 (*p*=0.000) and 2 (*p*=0.038). Finally, significant differences in *RA* growth were only found between height classes 1 and 4 (*p*=0.003). These results should be interpreted with caution, given the low sample size per height class, especially after the exclusion of colonies with negative growth. Therefore, additional statistical comparisons were performed after regrouping the colonies into a) colonies that were less than 20 cm in height, and b) colonies that were equal to or greater than 20 cm in height. This grouping was based on the results of size at first maturity (section 3.2), which suggest that colonies attain full sexual maturity at approximately 20 cm of height. Using this grouping, the ANOVA results indicated significant differences in growth of height ($F_{(1,36)} = 14.180$, *p*=0.001), *SA* ($F_{(1,30)} = 7.947$, *p*=0.008), and *RA* ($F_{(1,30)} = 11.474$, *p*=0.002), whereas, as before, no differences were detected in width growth ($F_{(1,32)} = 0.711$, *p*=0.405).

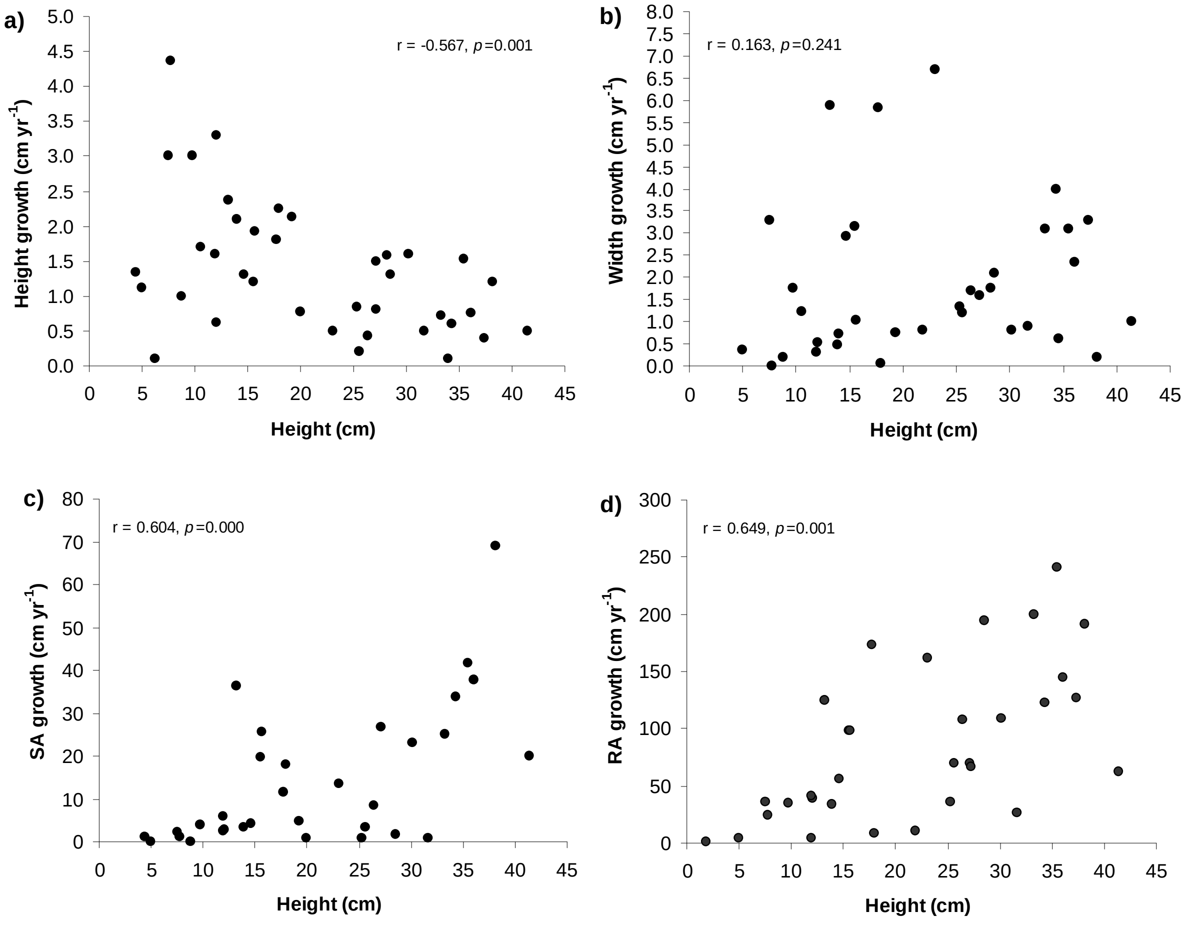

Fig 5. Growth of *Eunicella cavolini* morphometric parameters per height, over one year (October 2011, 2012). *SA*: surface area, *RA*: rectangular area. Only data of positive growth are included.

Spearman rank order correlations between colony height and positive growth parameters indicated that height growth was negatively correlated to colony height (r = -0.567, *p*=0.001, **Fig 5a**). Width growth presented no significant correlation (r = 0.192, *p*=0.277, **Fig 5b**), whereas *SA* (r = 0.604, *p*=0.000, **Fig 5c**) and *RA* (r = 0.649, *p*=0.000, **Fig 5d**) both were positively correlated with colony height.

3.2 Reproduction

Sexual maturity in relation to colony height

In order to investigate the size of colonies at the time of first reproduction, 47 branch tips of the May 2011 samples were dissected (one per colony). The proportion of gonad-bearing colonies was found to be height-dependant (x^2 = 37.5, df = 3, *p*<0.01), and increased from 72.7% in the 2nd height class to 100% in the larger classes. No gonads were observed in the 1st height class (**Fig 6a**). The number of colonies of undetermined sex that featured only small, undeveloped, gonads (less than 200 μm in diameter) peaked at the 2nd height class (45%) and dropped to 10% and 0% in the larger height classes.

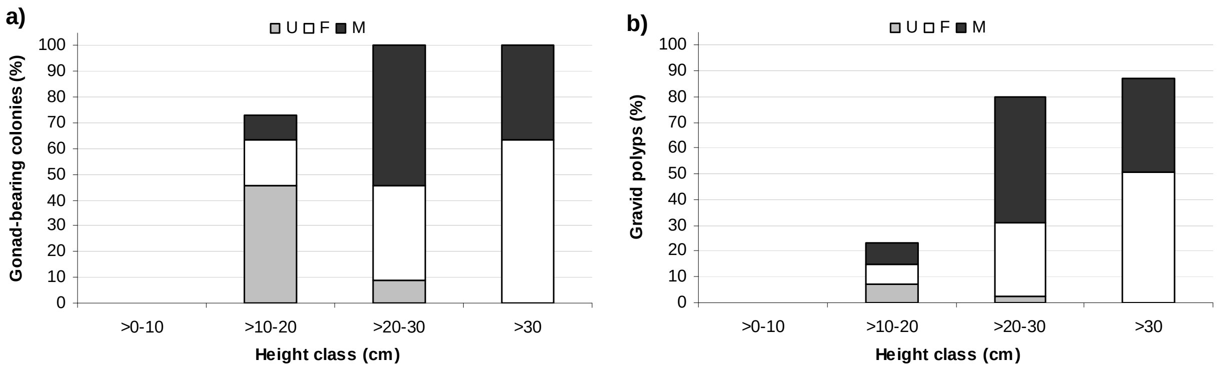

Fig 6. Proportion of *Eunicella cavolini* a) gonad-bearing colonies and b) gravid polyps, tabulated by height class and sex. Acronyms and bar shades refer to U: undetermined sex (gray), F: female (white), M: male (black).

The number of gravid polyps per colony was also statistically different among height classes ($F_{(2,30)}$ = 25.903, *p*<0.001, excluding colonies of the 1st height class where no gonads were found). The pairwise comparisons indicated that differences existed between colonies of the 2nd height class (>10–20 cm) and colonies of the larger height classes (*p*<0.001). Proportion of gravid polyps ranged from 23% in the 2nd height class to 80% and 87% in the 3rd and 4th height classes, respectively (**Fig 6b**).

The smallest fertile (female or male) colony bearing mature gonads (i.e. more than 300 µm in diameter) belonged to the 2nd height class (>10–20 cm, **Table 4**). However, mean number of female and male gonads per polyp, as well as mean number of mature gonads (>300 µm) per polyp were greater in colonies with height >20 cm. Oocyte (i.e. female gonad) diameter ranged from 60 to 830 µm, with mean and max values being generally higher in the larger gorgonians of the 3rd and 4th height classes. On the contrary, mean diameter of sperm sacs (i.e. male gonads) was relatively stable across height classes. Overall, although reproductive maturity was attained at a height of 10 to 20 cm, colony fertility displayed a substantial increase only after colonies had reached a height greater than 20 cm.

Table 4. Summary of *Eunicella cavolini* reproductive characteristics per sex and height class; SE: standard error of the mean, SD: standard deviation.

	N colonies (with gonads %)	N polyps (with gonads %)	Gonads / polyp Mean ± SE	Mature* gonads/polyp Mean ± SE	Gonad diameter (µm)	
					Mean ± SD	Min–Max
Female						
>0–10	0	-	-	-	-	-
>10–20	2 (100)	20 (45)	0.7 ± 0.2	0.2 ± 0.1	233.2 ± 119.5	91.1–498
>20–30	4 (100)	42 (76)	3.4 ± 0.5	1.2 ± 0.2	308.2 ± 250.4	59.6–831.2
>30	7 (100)	73 (80.8)	3.2 ± 0.4	2.1 ± 0.3	397 ± 194.5	69.9–772.7
Male						
>0–10	0	-	-	-	-	-
>10–20	1 (100)	11 (81.8)	3.2 ± 0.7	2.1 ± 0.6	340.3 ± 76.1	205–505.5
>20–30	6 (100)	62 (88.7)	13.6 ± 1.7	7 ± 1	313.3 ± 75.6	106.9–664.1
>30	4 (100)	43 (97.7)	13.4 ± 1.9	7.4 ± 1.1	320 ± 83.4	77–619.6
Undetermined sex						
>0–10	14 (0)	140 (0)	-	-	-	-
>10–20	8 (62.5)	82 (9.8)	0.9 ± 0.1	0	144.1 ± 70.9	80.8–268.9
>20–30	1 (100)	10 (30)	0.7 ± 0.4	0	101.3 ± 23.2	60.8–123.9
>30	0	-	-	-	-	-

*gonads >300 µm in diameter.

Final stages of gonad development and timing of spawning

During the spring months (March to May), the mean number of gonads per polyp was statistically different ($F_{(3,617)} = 369.03$, $p<0.00$) between female and male colonies of the largest height classes (>20 cm). Mean number of female gonads per polyp was 4.6 ± 0.2 SE (SE: standard error of the mean), while their diameter ranged from 60 to 830 µm. Mature female gonads were characterized by an almost spherical shape, a creamy white-yellow color, and a thick consistency (**Fig 7a,b**). On the other hand, male polyps produced numerous sperm sacs (25.5 ± 0.9 SE) that ranged between 74 and 664 μm in diameter. They were often clustered into thick clumps, and were characterised by an irregular shape, a milky-white color, and a cloudy consistency once broken (**Fig 7c,d**).

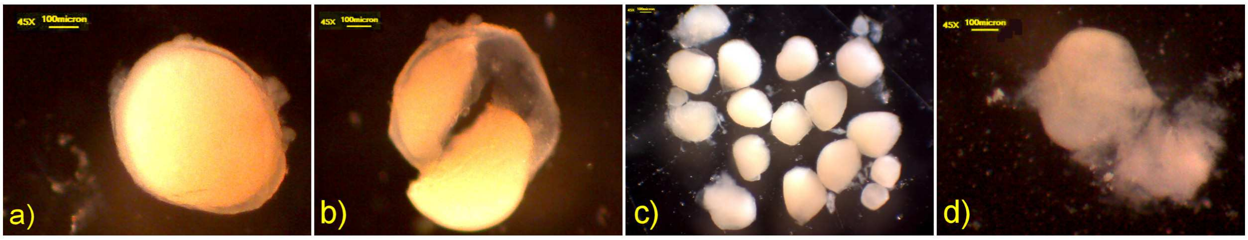

Fig 7. Characteristic images of *Eunicella cavolini* gonads; a) mature oocyte, b) broken mature oocyte, c) sperm sacs, d) broken sperm sac. Scales denote 100 μm at ×45 magnification.

Table 5. Reproductive characteristics of *Eunicella cavolini* colonies per month; SE: standard error of the mean, SD: standard deviation.

	N colonies (with gonads %)	**N polyps (with gonads %)**	**Gonads per polyp**	**Mature* gonads / polyp**	**Gonad diameter (μm)**	
			Mean ± SE	**Mean ± SE**	**Mean ± SD**	**Min–Max**
Female						
March	10 (100)	100 (100)	6.7 ± 0.3	5.3 ± 0.2	434.7 ± 138.7	90–673
April	10 (100)	102 (88)	4.3 ± 0.3	4.5 ± 0.2	547.3 ± 138.9	99–793
May	11 (100)	114 (79)	3.3 ± 0.3	2.8 ± 0.2	363.8 ± 221	60–830
June	-	-	-	-	-	-
Male						
March	10 (100)	100 (100)	30.7 ± 1.2	13.6 ± 0.8	295.9 ± 87.5	74–650
April	10 (100)	100 (100)	32.8 ± 1.3	17.3 ± 0.9	332.6 ± 85.8	86–580
May	10 (100)	105 (92)	13.5 ± 1.2	8.2 ± 0.8	316 ± 79	77–664
June	-	-	-	-	-	-
Undetermined sex						
June	25 (52)	251 (15)	0.3 ± 0.05	0	139.3 ± 41.3	55–251

*gonads >300 μm in diameter.

Although monthly samples were taken from different years, they provide some useful insights regarding the approximate timing of spawning. From March to May, both male and female colonies of the largest height classes (>20 cm) presented a high proportion of gravid polyps and a large number of well-developed gonads (**Table 5**). The frequency distribution of female gonad diameter was bimodal, with one cluster including oocytes between 50 and 300 μm in diameter, and another cluster with oocytes between 300 and 800 μm (**Fig 8a**). On the other hand, male gonad diameter was almost normally distributed across all three months (**Fig 8b**). By mid June, all reproductive characteristics presented a substantial reduction; the proportion of gravid polyps dropped to 15%, the mean number of gonads per polyp was 0.3 ± 0.05 SE, and the maximum gonad size was barely 250 µm (**Fig 8c**).

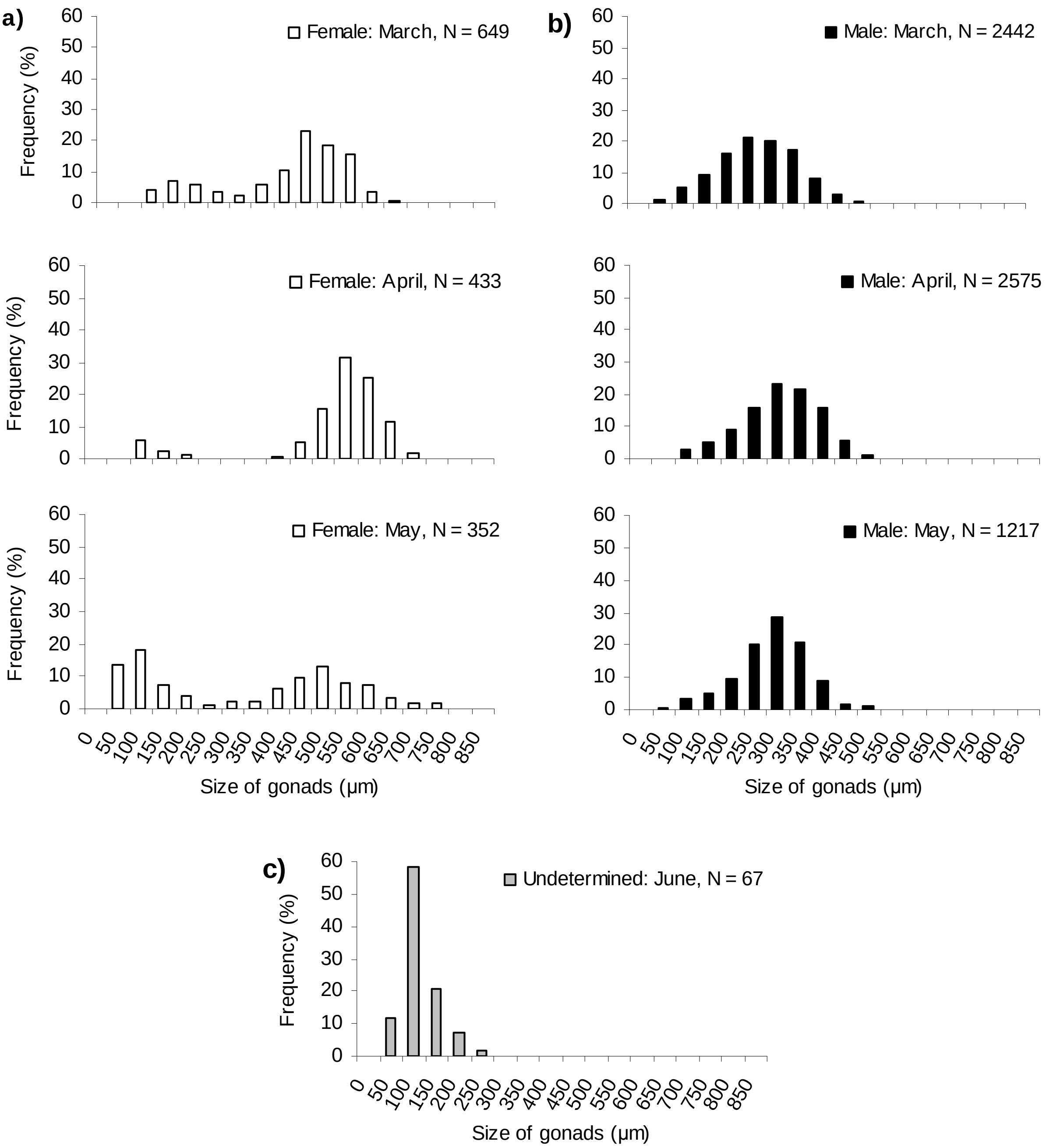

Fig 8. Frequency distribution of *Eunicella cavolini* female and male gonad diameter over the spring to early summer period. Note that monthly samples were collected over different years (May 2011, March, April, June 2014).

4. Discussion

Gorgonians are modular organisms that exhibit great morphological diversity at the species level (e.g. colony shapes include whips, plumes, fans, bushes and trees), but also present high phenotypic plasticity at the population or colony level (Velimirov 1973, 1976). In these sedentary animals, growth is achieved through the iterative replication of individual modules, referred to as branches. While new branches develop at variable rates, old ones may break or dysfunction due to partial mortality caused by mechanical damage, predation, pathogen attacks and physiological stress (e.g. Bavestrello et al. 1997; Veerland & Lasker 1989; Bally & Garrabou 2007; Previati et al. 2010; Pivotto et al. 2015); branch regeneration following a breakage event is also possible. Furthermore, several micro- or macro characteristics of the colony (including spicule morphology and fan shape, Velimirov 1976; Gori et al. 2012; Skoufas 2006) are affected by the prevailing local environmental conditions, which may limit the maximum size that a colony can attain within a given area (Sebens 2002). Ultimately, colony structure and growth are determined by interactions between population adaptations to local environmental forces –especially water flow and food availability– and genetically driven species-specific characteristics. As in other clonal organisms, therefore, gorgonian life history processes, such as survival, growth, senescence, and reproduction, are more size- than age-dependant (Hughes & Jackson 1985; Brazeau & Lasker 1992).

4.1 Growth

Given the modular structure of gorgonians, colony growth is assessed either at the level of colonies or at the level of individual branches. The former approach is based on measuring changes in height (e.g. Lasker 1990, Yoshioka & Yoshioka 1991), total branch length (Velimirov 1975; Weinbauer & Velimirov 1996), basal diameter (Mistri & Cechereli, 1993; Garrabou & Harmelin 2002), width, width×length area (Russo 1985; Skoufas 2000), and colony surface area (Coz et al. 2012), or a combination thereof. Assessing colony growth at the level of individual branches includes monitoring the changes in branch length and branching frequency (e.g. Coma et al. 1998; Rossi et al. 2011; Brazeau & Lasker 1992; Weinbauer & Velimirov 1995). In the present study, we focused on growth rates of *E. cavolini* at the colony level, using three of the most easily applied metrics in the field (i.e. height, width and rectangular area – *RA*), as well as the more detailed metric of colony surface area (*SA*).

Our results showed that a substantial proportion of the colonies sampled (approximately 30%) presented negative growth that was mainly attributed to the loss of coenchyma tissue (i.e. presence of naked colony axis), loss of branches, overgrowth by other organisms (e.g. algae, tunicates, bryozoans), and predation by the fireworm *Hermodice carunculata*. Encountering negative growth rates is common in the study of gorgonian species (e.g. Coma et al. 1998; Coz et al. 2012; Yoshioka and Yoshioka, 1991; Lasker et al. 2003), and while not always easy to spot, it can variably affect growth estimates. Specifically, branch loss from injured colonies may reduce the overall growth reported, or result to overestimates, if growth descriptors are assessed on the, faster-growing, post-breakage regenerating branches (Yoshioka & Yoshioka 1991; Lasker et al. 2003). It is thus customary in the literature to separately present positive-only, versus net growth rates; in this context, the results summarised in **Table 3** were tabulated accordingly. Overall, the number of colonies exhibiting negative growth did not statistically differ among size classes. Note, however, that considerably less colonies of the 1st height class were retrieved on the follow-up year (53%, 2012), compared to approximately 85% of retrieved colonies belonging to the larger height classes. Assuming all sampling conditions equal, this discrepancy suggests a high rate of juvenile mortality which may possibly underlie the low recruitment rate that has been observed for this population (Chapter 4, Sini et al. 2015). While further investigations are needed to validate this hypothesis, higher mortality of smaller colonies has been repeatedly reported for gorgonian species (Sebens 1983; Yioshioka 1994). Regardless height class, negative growth was primarily attributed to the reduction of area descriptors. Specifically, 20% of the total colonies had a reduction in *SA* (-21.2% mean area loss) and *RA* (-15.5%); the corresponding percentage for height was only 5% of colonies (-8% mean loss), and 15% (-12%) for width. These statistics indicate a loss of colony tissue which affects net growth, and help provide a complementary view on the health condition of sampled colonies to facilitate long-term monitoring (e.g. Brazeau & Lasker 1992; Coma et al. 1998; Coz et al. 2012).

Although based on different morphometric parameters for the estimation of growth, our estimates of mean positive height growth (1.4 cm ± 0.9) and mean net height growth (1.2 cm ± 1.1) of *E. cavolini* colonies in the NE Aegean Sea are comparable to those reported by Velimirov (1973) for the same species in Sicily (1.14 cm ± 0.4), but higher from the estimate of Weinbauer & Velimirov (1995) for the bay of Calvi, Corsica (0.85 cm ± 0.46). Intraspecific variation in growth rates is relatively common among gorgonian species (e.g. Weinberg & Weinberg 1979; Yoshioka & Yoshioka 1991; Mistri & Ceherelli 1994; Coma et al. 1998), due to intrinsic or extrinsic factors which include water movement direction and velocity, different levels of predation or competitive overgrowth, food availability, and physical condition of the colony (Weinbauer & Velimirov 1995; Coma et al. 2000; Coma & Ribes 2003; Rossi et al. 2011). Regardless this variability, the growth rate of *E. cavolini* based on height measurements falls within the range of growth values reported for other Mediterranean species (**Table 6**), as well as for other temperate and tropical gorgonians, which overall display a mean growth of 3 cm yr^{-1} (Coma et al. 1998).

Table 6. Growth rates of Mediterranean gorgonian species; SD: standard deviation.

	Growth (cm yr^{-1})					
Species	**Mean ± SD**	**Min–Max**	**Measured feature**	**Depth (m)**	**Region**	**Reference**
Eunicella singularis	2.24	0–3.3	Branch length and age	20	Banyuls-sur-Mer, NW Mediterranean	Weinberg & Weinberg (1979)
Eunicella cavolini	1.14 ± 0.44		Branch length	10–17		Weinbauer & Velimirov (1995)
Eunicella cavolini	0.85 ± 0.46		Branch length		Corsica, NW Mediterranean	Weinbauer & Velimirov (1995)
Eunicella cavolini	1.4 ± 0.95	0.1–4.4	Height	30–40	NE Aegean, NE Mediterranean	*Present study*
Eunicella verrucosa		0.6–3.3	Height	20–40	Riou Archipelago, NW Mediterranean	Sartoretto & Francour (2012)
Leptogorgia sarmentosa	2.6 ± 0.5	1.5–3	Height	16–27	Ligurian Sea, NW Mediterranean	Mistri & Cecherelli (1993)
Leptogorgia sarmentosa	2.4		Height		Banyuls-sur-Mer, NW Mediterranean	Weinberg & Weinberg (1979)
Paramuricea clavata	1.8	0.2–6.4	Height	15–27	Medes islands, NW Mediterranean	Coma et al. (1998)
Paramuricea clavata	2.7 ± 1.6	0.7–6.3	Height	28–38	Messina strait, central Mediterranean	Mistri & Cecherelli (1994)

Another characteristic frequently reported for gorgonian species is the reduction of colony growth with colony size (e.g. Grigg 1974; Velimirov 1975; Lasker 2003), or a decrease in branching rate (Weinbauer & Velimirov 1995). Our results showed that height growth was negatively correlated with mean colony height and was statistically different between colonies of the smaller (<20 cm) and larger (>20 cm) height classes (1.30 cm ± 0.4 versus 0.9 cm ± 0.3, respectively). Interestingly, these results on height growth coincide with our findings regarding the onset of reproductive maturity, according to which only colonies larger than 20 cm in height had reached full sexual maturity. Coma et al. (1995, 1998) reported similar findings regarding *P. clavata* colonies thriving in the NW Mediterranean, where the decrease in branch growth rate was linked to the onset of sexual maturity. These observations are in agreement with the research hypothesis that proposes a shift in resource allocation from growth to reproduction, once a colony has escaped a critical size of high mortality risk (Hughes & Jackson 1985; Kapela & Lasker 1999; Beiring & Lasker 2000).

Although colony height has been widely used as the primary descriptor for assessing gorgonian growth and age (Mistri & Ceccherelli 1994, Weinberg & Weinberg 1979), its suitability has been questioned; height measurements fail to account for changes in stem or branch diameter, while they ignore changes in branching rates that may be highly variable in species of increased morphological plasticity (Weinbauer & Velimirov 1995, 1996). As an alternative, Velimirov (1975) and Weinbauer & Velimirov (1996) proposed the use of total branch length and rectangular area, while more recently, Coz et al. (2012) assessed total colony surface area using computer-aided image processing. Similar to Coz et al. (2012), we used recent advances in digital image analysis tools (Trygonis & Sini 2012) to measure a series of colony descriptors complementary to height. These included width and rectangular area (*RA*), as well as the additional descriptor of total colony surface area (*SA*) that accounts for changes in the morphological structure of the gorgonian fan.

Colony width exhibited strong positive correlations with all morphometric descriptors only in the 2nd height class (>10–20 cm), in which the colony fan roughly displayed a rather circular shape. However, it was not correlated with height or *SA* in the smallest and largest height classes, due to its low effect on fan shape in the former, and its large variability in the latter. Moreover, growth of width displayed no significant differentiation with increasing height class. The lack of any systematic pattern in width growth (**Fig 5b**) is possibly due to the absence of a rigid structure or connective tissue (apart from the central colony axis) that would hold separate branches together at their outermost extent, and enable the accurate definition of maximal width along the horizontal colony axis. The “loose” branches that stem from the central colony axis may shift or sway in position. This renders consecutive measurements of maximum width difficult and subjective to acquire, even when using photographic records. Regarding *RA*, its growth was positively correlated with colony height (**Fig 5d**), and was statistically different among height classes. By definition however, *RA* is extracted from a box that circumscribes the fan, and lacks the detail needed to obtain meaningful growth area estimates; at least, in gorgonian species of similar fan shape to *E. cavolini*.

On the other hand, the analysis showed that *SA* represents a more elaborate descriptor of colony size and growth, as it quantifies the total fan area, thus providing an informative background upon which to assess height and width growth measurements. Specifically, *SA* contribution was particularly pronounced in colonies larger than 20 cm in height. In these height classes, the extensive growth of the internal branch network of the fan outcompeted growth along the height or width axis. For large colonies where height and width gradually level off, *SA* appears to be a key descriptor for better assessing *E. cavolini* growth. Furthermore, *SA* growth was positively correlated with height, and was statistically different between colonies smaller than 20 cm in height and larger ones. The former had a mean *SA* growth of 8 ± 10 cm^2 per year, while the latter 21.8 ± 19.5 cm^2. However, when *SA* growth was expressed as a percentage of the initial *SA* (2011), smaller colonies exhibited 42.5% increase, whereas larger ones grew only by 5.6%. These findings validate the growth patterns described by height and further support the resource allocation hypothesis. The relations between *SA* and height, as well as the values of *SA* reported herein are comparable to the findings of Coz et al. (2012) regarding *E. verrucosa* surface area. Although it does not provide a measure of the real 3-dimensional area of the colony, *SA* can be a valuable metric for monitoring purposes (Coz et al. 2012). However, the extraction of calibrated surface area requires specialised software and laborious post-survey analysis of digital images, especially in gorgonian species with complex fan shape.

Overall, the photographic method used is a promising tool for the study of colony morphometrics, including the measurement of total colony surface area. Although additional surveys are required to validate its accuracy and precision, it managed to detect changes in all four morphometric parameters over the course of one year, and to provide comparable growth estimates. Furthermore, additional investigation is needed with regards to its applicability on colonies of increased structural complexity. Considering the large morphological variability displayed by *E. cavolini* (Velimirov 1973, 1976), colonies of Palios Reef presented a rather simple form, characterised by a single fan per root that develops in one plane, and by a very low degree of branch overlap. To this end, the proposed method can be applied as is, provided that special care is taken to reduce potential biases, such as wrong positioning of the calibration board and camera, or obtaining images from colonies with fully expanded polyps (resulting to biased estimation of surface area). Also, the use of a black board, instead of a white one, would accommodate a faster processing of images. However, if this method is to be used for estimates of more complex colony forms (e.g. bush or tree-like colonies), additional correction factors may be needed, such as the one proposed by Coz et al. (2012) regarding branch overlap. These considerations aside, the proposed method represents a useful non-destructive tool which may be implemented for the long-term monitoring of gorgonian species.

4.2 Onset of reproductive maturity

As pointed out in section 4.1, several gorgonian species display size-dependant reproduction (Coma et al. 1995; Rossi & Gilli 2009; Torrents et al. 2005). Within a species, size is a good indicator of reproductive maturity, possibly due to a greater energy investment of smaller colonies into growth, rather than reproduction. This way, young colonies may minimize the increased risk of mortality associated with small colony size (Hughes & Jackson 1985; Harvell & Grosberg 1988; Beiring & Lasker 2000). In the present study, the smallest male or female *E. cavolini* colony bearing mature gonads was of the >10-20 cm height class. However, the majority of the fully mature colonies, which had a high proportion of gravid polyps and a large number of mature gonads, were greater than 20 cm in height. According to the mean and max estimates of positive colony growth for the two smaller height classes (see **Table 3** in section 3.1), a newly settled colony would need approximately 2.3–5 years to reach the >10-20 cm height class, and an additional 3–5.5 years to reach the height class of >20-30 cm. This sums up to a total of 5–10 years for a colony to reach full maturity from the time of settlement. These results are in line with estimates on both size (Brazeau & Lasker 1990; Coma et al. 1995; Rossi & Gili 2009) and years to first maturity (Torrents et al. 2005 and references therein) regarding other arborescent coral species. Within the Mediterranean, Coma et al. (1995) showed that the smallest *P. clavata* male or female colonies with mature gonads were 8 and 11 cm, respectively, but similar to our findings, full sexual maturity was on average delayed until colonies had reached a size of 20 cm.

4.3 Reproductive strategy

E. cavolini presented a clear separation of genders, at both the colony and polyp level, and thus appears to be a dioecious, gonochoric species which has adopted sexual reproduction as the main mode for population growth and maintenance. Gonochorism is considered as the most typical form of reproduction for shallow water Mediterranean octocorals (e.g. Tsounis et al. 2006; Rossi & Gili 2009; Cupido et al. 2012), and although instances of polyps bearing both male and female gonads have been sporadically observed in otherwise unisexual species, hermaphrodism is generally uncommon (e.g. Coma et al. 1995; Gori et al. 2007; Ribes et al. 2007). Mean number of oocytes per polyp in *E. cavolini* female colonies was 4.6, and their maximum diameter was 830 µm. In male colonies, mean number of sperm sacs per polyp was 25.5, with a maximum diameter of 664 µm. In terms of gonad diameter, values presented herein are comparable to those reported for *E. singularis* (Gori et al. 2007; Ribes et al. 2007), as well as for *Paramuricea clavata* (Gori et al. 2007; Coma et al. 1995) in the NW Mediterranean. Furthermore, similar to *E. singularis*, the number of gonads in *E. cavolini* female colonies is lower to that reported for *P. clavata*. Differences in the mean number and size of oocytes among octocoral species are linked to several factors, including reproductive strategy, and hence, whether a species is a broadcast spawner or a brooder (internal or external, Kruger et al. 1998; Gori et al. 2007). With regards to brooding, which is the prevailing strategy in shallow water Mediterranean octocorals, internal brooders, such as *E. singularis*, produce a relatively small number of large oocytes, which remain within the female polyps until finally spawned in the water column as panula larvae (Weinberg & Weinberg 1979; Ribes et al. 2007). On the other hand, external brooders, such as *P. clavata*, usually produce a large number of small-sized oocytes which are brooded within a mucus coating at the surface of the colony (Coma et al. 1995; Gori et al. 2007). Up until now, no external brooding has been reported for *E. cavolini* populations in other parts of the Mediterranean, despite the fact that the species is very abundant in the western basin, and this reproductive strategy should be relatively easy to detect by naked eye. On the other hand, no panulae larvae were detected brooding inside *E. cavolini* polyps during the present study. However, *in situ* observations of small single-branch colonies (less than 3 cm in height) approximately four months after spawning within the same population, as well as the overall similarity of *E. cavolini* reproductive features to those of its congeneric species *E. singularis*, provide some evidence in support of internal brooding.

4.4 Final stages of gonad development and timing of spawning

The assessment on the final stages of gonad development suggests that the reproductive cycle of *E. cavolini* follows a similar pattern to that of other Mediterranean gorgonians (e.g. Coma et al. 1995 and Gori et al. 2007 for *P. clavata*; Tsounis et al. 2006 for *C. rubrum*; Gori et al. 2007 and Ribes et al. 2007 for *E. singularis*; Rossi & Gili 2009 for *Leptogorgia sarmentosa*). In these species, gametogenesis is characterized by an annual maturation cycle with asynchronous development of female and male gonads, which are being released during a restricted spawning period (usually less than a month). Moreover, oocyte development is long, typically more than 12 months. This is usually evidenced by the continuous presence of oocytes in female polyps throughout the year, which form two cohorts during the peak months of development; one cohort containing mature oocytes which are ready to be released in the proximate spawning season, and one which includes small immature oocytes that are retained within the polyps to be released in the next year. On the other hand, the annual onset of spermatogenesis is delayed, but development is fast (approximately 4–8 months), enabling the synchronous release of all spermaries and mature oocytes over a single spawning event. In the present study, female and male colonies presented a large number of gonads from March to May, while oocyte frequency distribution presented two distinct cohorts; one with oocytes less than 300 μm in diameter and one with oocytes ranging from 300 to 830 μm in diameter. By mid of June, all gonads greater than 300 μm had been released, and only small immature gonads of undetermined sex were left inside the polyps. If *E. cavolini* follows a similar gonadal cycle to that described for other shallow-water Meditteranean species, we hypothesize that the gonads found in June are actually immature oocytes awaiting release during the following year.

Furthermore, the low number of small, undeveloped gonads observed during June is also indicative of the approximate time of completion of the spawning period. Given that the last colonies sampled were collected on the 13th of June, it is assumed that spawning concluded sometime before the first half of June. Although small monthly fluctuations are possible between years (Tsounis et al. 2006; Gori et al. 2007), spawning of *E. cavolini* appears to coincide with spawning of *E. singularis* and *P. clavata* during early summer in the W Mediterranean basin (Weinberg & Weinberg 1979; Coma et al. 1995). Of all environmental factors that can potentially affect gamete release in corals (e.g. tidal rhythm, lunar cycle, time of the day), seawater temperature is probably the most important cue for the initiation of spawning in gorgonian species. Several studies have showed that spatially separated populations along different geographic regions (e.g. Gutiérrez-Rodriguez & Lasker 2004; Gori et al. 2007; de Putron & Ryland 2009) and/or depth gradients (Tsounis 2006; Grigg 1977; Weinberg &

Weinberg 1979; Benayahu & Loya 1983) display differences in the timing of spawning. In all cases, populations located in warmer waters initiated spawning earlier than those inhabiting colder waters, suggesting the existence of some temperature threshold triggering gamete release. According to our estimates, spawning time of the studied *E. cavolini* population appears to coincide with an increase in seawater temperature during May and June (**Fig 9**), a pattern very similar to that observed by Gori et al. (2007).

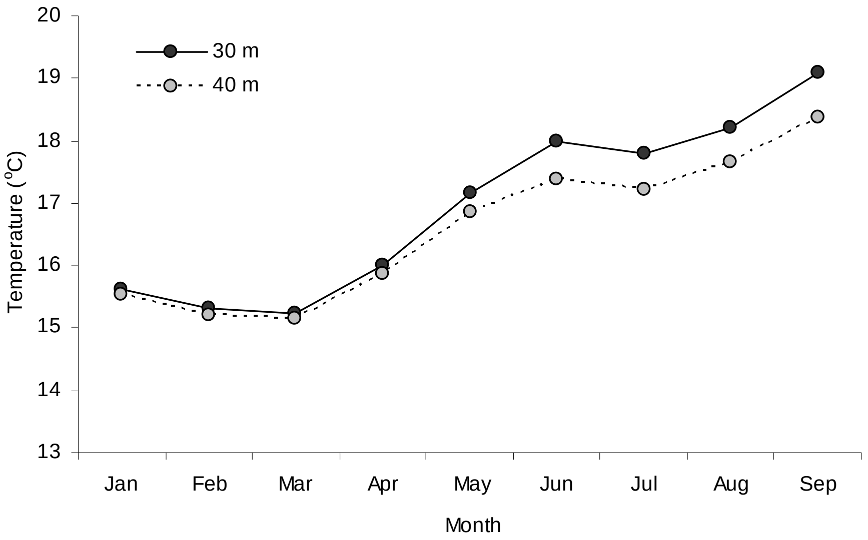

Fig 9. Seawater temperature monthly means for Palios Reef (January to September 2014) at the depth range of the studied *Eunicella cavolini* population.

Available information on Mediterranean and other temperate water gorgonians indicates that there is a relative consistency in the timing of gonad development and release (e.g. Grigg 1977 for *Muricea californica*, *Muricea fruiticosa*; Matsumoto 2004 for *Melithaea flabellifera*). This is in contrast to tropical gorgonians, which are mainly broadcast spawners and display a great variability in the duration of gonad development cycles and/or the frequency of spawning events (e.g. Kapela & Lasker 1999; Gutiérrez-Rodriguez & Lasker 2004; De Putron & Ryland 2009). The annual periodicity displayed by temperate species may be linked to the highly seasonal food availability of temperate seas, in contrast to tropical species that thrive in more stable environments and gain additional energy supplies through their symbiosis with photosynthetic zooxanthellae (Coma & Ribes 2003; Gori et al. 2007).

Although additional assessments are required to validate the present findings, our work provides important insights regarding the growth and reproductive characteristics of *E. cavolini*.

The information obtained is a first step towards understanding the population dynamics of *E. cavolini,* and the ability of this species to persist at different parts of the Mediterranean in the context of environmental change.

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Appendix A

Data sources used for mapping the distribution of coralligenous formations (**C**) and the yellow gorgonian *Eunicella cavolini* (**Ec**)

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- Giourgis Ektoras– Diver, Greece
- Poursanidis Dimitris – Marine Ecologist/Diver, Greece
- Tsantilas Christos – Diver, Greece

Appendix B

List of taxa recorded quantitatively or qualitatively in the coralligenous assemblages of the studied sites, and their current conservation status. **1.** Ag. Vasso, **2.** Lefteris, **3.** Nemessis, **4.** Spilia, **5.** Ambellos, **6.** Palios, **7.** Kalloni.

Taxa	Authority	Conservation Status	Site
Kingdom Chromista (Βασίλειο Χρωμιστά) **Phylum Ochrophyta (Φύλο Ωχρόφυτα)**			
Dictyota implexa	(Desfontaines) J.V.Lamouroux		1,3,4
Dictyota dichotoma	(Hudson) J.V.Lamouroux		3,4,6
Mucilagenous algae indet			3,4,5,6,7
Kingdom Protozoa (Βασίλειο Πρωτόζωα) **Phylum Foraminifera (Φύλο Τρηματοφόρα)**			
Miniacina miniacea	(Pallas, 1766)		2,3
Kingdom Plantae (Βασίλειο Φυτά) **Phylum Chlorophyta (Φύλο Χλωροφύκη)**			
Caulerpa cylindracea	Sonder	A	6,7
Codium bursa	(Olivi) C.Agardh		3,6,7
Codium effusum	(Rafinesque) Delle Chiaje		2,3
Cladophora pellucida	(Hudson) Kützing		1,2,3,4
Flabellia petiolata	(Turra) Nizamuddin		1,3,4,6
Halimeda tuna	(J.Ellis & Solander) J.V.Lamouroux		1,2,3,4,5,6
Pseudoclorodesmis furcellata	(Zanardini) Børgesen		3,4
Valonia macrophysa	Kützing		1,2,3,4
Phylum Rhodophyta (Φύλο Ροδοφύκη)			
Acrodiscus vidovichii	(Meneghini) Zanardini		3,4,6
Acrosymphyton pururiferum	(J.Agardh) Sjöstedt		6
Amphiroa rigida	J.V.Lamouroux		3
Laurencia chondrioides	Børgesen		6
Lithophyllum stictaephorme / cabiochiae	(J.E. Areschoug) Hauck / (Boudouresque & Verlaque) Athanasiadis		1,2,3,4,6
Mesophyllum alternans	(Foslie) Cabioch & M.L.Mendoza	O/b,c	1,2,3,4,5,6,7
Neogoniolithon mamillosum	(Hauck) Setchell & L.R.Mason	O/c	1,2,3,4,5,6
Peyssonnelia rosa-marina	Boudouresque & Denizot	O/c	1,2,3,4,6
Peyssonnelia rubra / bornetii	(Greville) J.Agardh / Boudouresque & Denizot)		1,2,3,4,6,7
Peyssonnelia squamaria	(S.G.Gmelin) Decaisne		1,2,3,4,5,6,7
Sebdenia dichotoma	Berthold		6
Sphaerococus coronopifolius	Stackhouse		1,3,4
Womersleyella setacea	(Hollenberg) R.E.Norris	A	3
Kingdom Animalia (Βασίλειο Ζώα) **Phylum Porifera (Φύλο Σπόγγοι)**			
Acanthella acuta	Schmidt, 1862		1,6,7
Agelas oroides	(Schmidt, 1864)		1,2,3,4,5,6,7
Aplysilla rosea	(Barrois, 1876)		7
Aplysilla sulfurea	Schulze, 1878		1,2,3,4,6,7
Aplysina aerophoba	(Nardo, 1833)	BC/II; O/a	3,4,6,7
Axinella cannabina	(Esper, 1794)	BC/II	1,6,7
Axinella damicornis	(Esper, 1794)		1,2,3,4,5,6,7
Axinella verucosa	(Esper, 1794)		1,2,4,5,6,7
Axinyssa aurantiaca	(Schmidt, 1864)		*6*

Taxa	Authority	Conservation Status	Site
Axinyssa digitata	(Cabioch, 1968)		7
Cacospongia molior	Schmidt, 1862		6
Calyx nicaeensis	(Risso, 1826)	O/a	6,7
Chondrosia reniformis	Nardo, 1847		2,4,6,7
Clathrina clathrus	(Schmidt, 1864)		2,7
Cliona celata	Grant, 1826		1,6
Cliona schmidtii	(Ridley, 1881)		2,3,4,6
Cliona viridis	(Schmidt, 1862)		1,3,4,6,7
Coscinoderma sporadense	Voultsiadou-Koukoura, van Soest & Koukouras, 1991		6
Crambe crambe	(Schmidt, 1862)		1,2,3,4,6,7
Crella (Grayella) pulvinar	(Schmidt, 1868)		4,6,7
Dendroxea lenis	(Topsent, 1892)		1,2,6,7
Diplastrella bistellata	(Schmidt, 1862)		6
Dictyonella incisa	(Schmidt, 1880)		1,3,4,6,7
Dysidea fragilis	(Montagu, 1814)		1,2,6,7
Dysidea avara	(Schmidt, 1862)		1,6
Fasciospongia cavernosa	(Schmidt, 1862)		1,6,7
Geodia cydonium	(Jameson, 1811)	BC/II	7
Halichondria sp.			1
Haliclona (Halichoclona) fulva	(Topsent, 1893)		1,2,4,6,7
Haliclona (Soestella) mucosa	(Griessinger, 1971)		1,2,3,5,6
Hemimycale columella	(Bowerbank, 1874)		6,7
Hexadella racvitzai	Topsent, 1896		1,2,3,4,5,6
Ircinia oros	(Schmidt, 1864)		1,3,4,6,7
Ircinia paucifilamentosa	Vacelet, 1961		4
Ircinia variabilis	(Schmidt, 1862)		1,4,6,7
Merlia sp.			4,5,6
Oscarella imperialis	Muricy, Boury-Esnault, Bézac & Vacelet, 1996		2,6
Penares euastrum	(Schmidt, 1868)		7
Penares sp.			6
Petrosia (Petrosia) ficiformis	(Poiret, 1789)	O/a	1,2,3,6,7
Phorbas fictitius	(Bowerbank, 1866)		6
Phorbas tenacior	(Topsent, 1925)		1,2,6,7
Plakina sp.	Schulze, 1880		2
Pleraplysilla spinifera	(Schulze, 1879)		6
Sarcotragus foetidus	Schmidt, 1862	BC/II	1,3,4,6,7
Sarcotragus spinosulus	Schmidt, 1862		2,6,7
Spirastrella cunctatrix	Schmidt, 1868		1,2,3,4,5,6,7
Spongia (Spongia) officinalis	Linnaeus, 1759	BC/III; Bern/III	6
Spongia (Spongia) virgultosa	(Schmidt, 1868)		6
Suberites carnosus	(Johnston, 1842)		7
Suberitidae	Schmidt, 1870		7
Terpios gelatinosa	(Bowerbank, 1866)		6
Tethya aurantium	(Pallas, 1766)	BC/II; O/a	7
Phylum Cnidaria (Φύλο Κνιδόζωα)			
Antennella secundaria	(Gmelin, 1791)		5,6
Balanophyllia (Balanophyllia) europaea	(Risso, 1826)	CITES II; IUCN/DD	6
Caryophyllia (Caryophyllia) inornata	(Duncan, 1878)	CITES/II	1,2,3,4,6,7
Cerianthus membranaceus	(Spallanzani, 1784)		3,6
Cladocora caespitosa	(Linnaeus, 1767)	BC/II; CITES/II; IUCN/En; O/a	7

Taxa	Authority	Conservation Status	Site
Eudendrium spp.	Ehrenberg, 1834		3,4,6,7
Eunicella cavolini	(Koch, 1887)	IUCN/NT	1,2,3,4,5,6,7
Eunicella singularis	(Esper, 1791)	IUCN/NT	5,7
Hoplangia durotrix	Gosse, 1860	CITES/II	2,4,6
Leptopsammia pruvoti	Lacaze-Duthiers, 1897	CITES/II	1,2,3,4,5,6
Madracis pharesnsis	(Heller, 1868)	CITES/II; IUCN/LC	1,2,5,6
Paracyathus pulchelus	(Philippi, 1842)	CITES/II	1,2,4,6
Parazoanthus axinellae	(Schmidt, 1862)	O/a	1,2,3,4,5,6,7
Penaria disticha	Goldfuss, 1820		7
Phyllangia americana mouchezii	(Lacaze-Duthiers, 1897)	CITES/II; O/a	2,3,6,7
Polycyathus muellerae	(Abel, 1959)	CITES/II	1,2,6,7
Phylum Platyhelminthes (Φύλο Πλατυέλμινθες)			
Prostheceraeus sp.			6
Pseudoceros maximus	Lang, 1884		6
Phylum Annelida (Φύλο Δακτυλιοσκώληκες) **Class Polychaeta (Κλάση Πολύχαιτοι)**			
Bispira volutacornis	(Montagu, 1804)		1,3,6
Eupolymnia nebulosa	(Montagu, 1819)		6,7
Filograna / *Salmacina*	Berkeley, 1835 / Claparède, 1870		1,2,3,4,5,6,7
Hermodice carunculata	(Pallas, 1766)		3,4,5,6,7
Myxicola infundibulum	(Montagu, 1808)		1,2,3,6
Protula tubularia	(Montagu, 1803)		5,6
Sabella pavonina	Savigny, 1822		3
Sabella spallanzanii	(Gmelin, 1791)		3,7
Spirobranchus triqueter	(Linnaeus, 1758)		4
Serpula vermicularis	Linnaeus, 1767		2,6,7
Serpulidae			1,2,3,4,5,6,7
Class Echiura (Κλάση Εχίουρα)			
Bonellia viridis	Rolando, 1821		6,7
Bryozoa (Φύλο Βρυόζωα)			
Adeonella spp.			2,3,4,7
Beania magellanica	(Busk, 1852)		3,4,6
Bugula spp.			2,3
Cellaria sp.			3,4
Caberea boryi	(Audouin, 1826)		3
Hornera frondiculata	(Lamarck, 1816)		3,4,5,6,7
Reteporella grimaldii	(Jullien, 1903)		1,2,4
Rhynchozoon neapolitanum	Gautier, 1962		1,2,3,4,5,6,7
Schizomavella (Schizomavella) mamillata	(Hincks, 1880)		1,2,3,4,6,7
Schizoporella errata	(Waters, 1878)		7
Schizoretepora serratimargo	(Hincks, 1886)		3,4,5
Schizoretepora sp.			4
Scrupocellaria sp.			6
Smittina cervicornis	(Pallas, 1766)		3,4
Phylum Mollusca (Φύλο Μαλάκια) **Class Gasteropoda (Κλάση Γαστερόποδα)**			
Calliostoma zizyphinum	(Linnaeus, 1758)		6
Caloria elegans	(Alder & Hancock, 1845)		6
Cratena peregrina	(Gmelin, 1791)		6,7
Dondice banyulensis	Portmann & Sandmeier, 1960		6,7

Taxa	Authority	Conservation Status	Site
Felimare picta	(Schultz in Philippi, 1836)		6
Felimare tricolor	(Cantraine, 1835)		4,6
Felimida luteorosea	(Rapp, 1827)		2,3,6
Flabellina affinis	(Gmelin, 1791)		6,7
Flabellina ischinata	Hirano & Thompson, 1990		6,7
Flabellina rubrolineata	(O'Donoghue, 1929)	A	7
Haminoea cyanomarginata	Heller & Thompson, 1983		6
Janolus cristatus	(Delle Chiaje, 1841)		6
Jujubinus exasperatus	(Pennant, 1777)		7
Peltodoris atromaculata	Bergh, 1880		1,6,7
Phyllidia flava	Aradas, 1847		6
Simnia spelta	(Linnaeus, 1758)		3,4
Thuridilla hopei	(Vérany, 1853)		2,3,4,5
Thylacodes arenarius	(Linnaeus, 1758)		6,7
Tritonia nilsodhneri	Marcus Ev., 1983		2
Umbraculum umbraculum	(Lightfoot, 1786)		6
Class Bivalvia (Κλάση Δίθυρα)			
Lithophaga lithophaga	(Linnaeus, 1758)	BC/II; Bern/II; CITES/II; HD/IV; O/a	6
Ostrea sp.			6
Pinna nobilis	Linnaeus, 1758	BC/II; HD IV; IUCN/VU; O/a; PD 67/1981	7
Pteria hirundo	(Linnaeus, 1758)		6
Rocellaria dubia	(Pennant, 1777)		3,6
Class Cephalopoda (Κλάση Κεφαλόποδα)			
Loligo sp. eggs			6
Octopus vulgaris	Cuvier, 1797		6,7
Phylum Arthropoda (Φύλο Αρθρόποδα) **Subphylum Crustacea (Υποφύλο Καρκινοειδή)**			
Galathea strigosa	(Linnaeus, 1761)		6
Maja squinado	(Herbst, 1788)	BC/III; Bern/III; O/a	6
Palinurus elephas	(Fabricius, 1787)	BC/III; Bern/III; IUCN/VU; O/a	6,7
Scyllarides latus	(Latreille, 1803)	BC/III; Bern/III; HD/V; IUCN/DD	6
Stenopus spinosus	Risso, 1827		6
Phylum Echinodermata (Φύλο Εχινόδερμα)			
Antedon mediterranea	(Lamarck, 1816)		3,4,5,6
Hacelia attenuata	Gray, 1840	O/a	1,3,4,5,6,7
Holothuria (Panningothuria) forskali	Delle Chiaje, 1823		7
Holothuria (Platyperona) sanctori	Delle Chiaje, 1823		7
Ophidiaster ophidianus	(Lamarck, 1816)	BC/II; Bern/II; O/a	2
Paracentrotus lividus	(Lamarck, 1816)	BC/II; Bern/III; IUCN/VU	7
Peltaster placenta	(Müller & Troschel, 1842)		3,4,5
Sphaerechinus granularis	(Lamarck, 1816		6
Stylocidaris affinis	(Philippi, 1845)		6
Phylum Chordata (Φύλο Χορδωτά) **Subphylum Tunicata (Υποφύλο Ουροχορδωτά ή Χιτωνόζωα)** **Class Ascidiacea (Κλάση Ασκίδια)**			
Aplidium elegans	(Giard, 1872)		1,2
Clavelina dellavallei	(Zirpolo, 1825)		1,2,3,4,7
Clavelina lepadiformis	(Müller, 1776)		7

Taxa	Authority	Conservation Status	Site
Cystodytes dellechiajei	(Della Valle, 1877)		7
Didemnum maculosum	(Milne Edwards, 1841)		7
Didemnum spp.			7
Diplosoma spongiforme	(Giard, 1872)		7
Halocynthia papillosa	(Linnaeus, 1767)		1,2,3,4,5,6,7
Lissoclinum perforatum	(Giard, 1872)		2,7
Microcosmus sabatieri	Roule, 1885		6
Polysyncraton lacazei	(Giard, 1872)		6
Pyura dura	(Heller, 1877)		7
Subphylum Vertebrata (Υποφύλο Σπονδυλωτά) **Class Actinopterygii (Κλάση Ακτινοπτερύγιοι)**			
Anthias anthias	(Linnaeus, 1758)		2,3,4,5,6
Chromis chromis	(Linnaeus, 1758)		1,4,7
Conger conger	(Linnaeus, 1758)		
Coris julis	(Linnaeus, 1758)		3,6,7
Dentex dentex	(Linnaeus, 1758)		6
Diplodus puntazzo	(Walbaum, 1792)		7
Diplodus sargus sargus	(Linnaeus, 1758)		4,6,7
Diplodus vulgaris	(Geoffroy Saint-Hilaire, 1817)		3,6,7
Epinephelus costeae	(Steindachner, 1878)	IUCN/DD	3,7 c
Epinephelus marginatus	(Lowe, 1834)	BC/III; Bern/II; IUCN/EN	6,7
Gobius auratus	Risso, 1810		2
Gobius vittatus	Vinciguerra, 1883		6
Labrus mixtus	Linnaeus, 1758		5
Labrus viridis	Linnaeus, 1758		6,7
Muraena helena	Linnaeus, 1758		2,6
Oblada melanura	Linnaeus, 1758		7
Phycis phycis	Linnaeus, 1766		4
Sarpa salpa	Linnaeus, 1758		7
Sciaena umbra	Linnaeus, 1758	BC/III; Bern/II; IUCN/VU	3,6
Scorpaena notata	Rafinesque, 1810		3
Scorpaena scrofa	Linnaeus, 1758		1,2,4,6
Seriola dumerili	(Risso, 1810)		6
Serranus cabrilla	(Linnaeus, 1758)		3,6,7
Serranus scriba	(Linnaeus, 1758)		6,7
Sparus aurata	Linnaeus, 1758		6,7
Spicara smaris	(Linnaeus, 1758)		3,4
Spondyliosoma cantharus	(Linnaeus, 1758)		3,6,7
Symphodus mediterraneus	(Linnaeus, 1758)		6
Symphodus melanocercus	(Risso, 1810)		6
Thorogobius ephippiatus	(Lowe, 1839)		*6*
Tripterygion delaisi	Cadenat & Blache, 1970		6
Zeus faber	Linnaeus, 1758		6

BC: Barcelona convention – **II**: Annex of endangered or threatened species, **III**: Annex of species whose exploitation is regulated. **Bern**: Convention on the conservation of european wildlife and natural habitats – **II**: Annex of strictly protected fauna species, **III**: Annex of protected fauna species. **CITES**: Convention on International Trade in Endangered Species of wild fauna and flora, 1973, Council Regulation (EC) No 338/97 – **II**: Species of Annex II. **HD**: Habitats Directive 92/43/EE on the conservation of natural habitats and of wild fauna and flora – **IV**: Animal and plant species of community interest in need of strict protection, **V**: Animal and plant species of community interest whose taking in the wild and exploitation may be subject to management measures. **IUCN**: The IUCN Red List of Threatened Species¬– **DD**: Data Deficient, **NT**: Near Threatened, **VU**: Vulnerable, **EN**: Endangered. **O**: Oceana list of threatened species (2009) – **a**: Species that are regionally threatened and included in regional or national lists, **b**: Species wholse protection is recommended by experts, **c**: Species that require protection due to their fragility or role as essential habitat creators. **PD 67/1981**: Greek Presidential Decree for the protection of wild flora and fauna. **A**: Allochthonous.

Appendix C

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Pairwise comparisons of *Eunicella cavolini* population density and colony height at different sites.

Table A. Pairwise comparisons of *Eunicella cavolini* population density between different sites.

		Density			
Region	**Locality**	**Sites**	**t**	***p*-value**	**Unique perm.**
NW Mediterranean	Marseille	Jarre, Castelvieille	8.2771	0.0001*	9234
		Jarre, Pharillons	8.491	0.0001*	8969
		Castelvieille, Pharillons	1.0518	0.3025	2836
NW Mediterranean	Scandola	Palazzinu, Gargallu	0.82342	0.4139	9815
		Palazzinu, Imbuttu	0.4661	0.6432	9811
		Gargallu, Imbuttu	0.36442	0.7144	9831
CE Adriatic	Kornati	Obrucan, Balun	1.1748	0.241	9834
		Obrucan, Mana	1.4715	0.1461	9793
		Balun, Mana	2.5824	0.0124*	9806
CE Adriatic	Rogoznica	Smokvica, Planka	0.12852	0.8986	8611
N Aegean	Pelio	Ag.Vasso, Lefteris	0.99359	0.3308	6946
N Aegean	Chalkidiki	Ambelos, Nemesis	4.7324	0.0001*	5087
		Ambelos, Spilia	7.6613	0.0001*	3348
		Nemesis, Spilia	1.8253	0.0688	6718
N Aegean	Lesvos	Palios, Kalloni	4.9877	0.0001*	6517

*Statistically significant difference (*p*<0.05).

Table B. Pairwise comparisons of *Eunicella cavolini* colony height between different sites.

		Height			
Region	**Locality**	**Sites**	**t**	**p-value**	**Unique perm.**
NW Mediterranean	Marseille	Jarre, Castelvieille	5.5745	0.0001*	9815
		Jarre, Pharillons	1.8146	0. 0712	9822
		Castelvieille, Pharillons	2.5223	0.0126*	9846
NW Mediterranean	Scandola	Imbuttu, Palazzinu	3.2787	0.0012*	9825
		Imbuttu, Gargallu	2.7148	0.0074*	9836
		Palazzinu, Gargallu	5.6487	0.0001*	9844
CE Adriatic	Kornati	Mana, Balun	1.4603	0.1468	9824
		Mana, Obrucan	7.3821	0.0001*	9824
		Balun, Obrucan	7.4461	0.0001*	9835
CE Adriatic	Rogoznica	Smokvica, Planka	3.1893	0.0018*	9848
N Aegean	Pelio	Ag.Vasso, Lefteris	4.1543	0.0001*	9831
N Aegean	Chalkidiki	Ambelos, Nemesis	10.24	0.0001*	9844
		Ambelos, Spilia	1.7248	0. 0914	9822
		Nemesis, Spilia	7.0881	0.0001*	9842
N Aegean	Lesvos	Palios, Kalloni	5. 299	0.0001*	9821

*Statistically significant differences (*p*<0.05).

Greek glossary of scientific terms

Γλωσσάρι επιστημονικών όρων

A

Abiotic parameters / abiotic factors (Αβιοτικοί παράγοντες) – Τα περιβαλλοντικά στοιχεία (εκτός των ζωντανών οργανισμών) που συνθέτουν ένα οικοσύστημα, π.χ. φωτισμός, τύπος υποστρώματος, αλατότητα, ρεύματα, θερμοκρασία, θρεπτικά συστατικά.

Acclimatisation (Εγκλιματισμός) – Η αλλαγή στη συμπεριφορά ή στη φυσιολογία ενός οργανισμού ως αντίδραση στις αλλαγές των περιβαλλοντικών συνθηκών υπό τις οποίες ζει.

Adaptation (Προσαρμογή) – Κάθε αλλαγή στη δομή, στις φυσιολογικές λειτουργίες, ή στη συμπεριφορά ενός οργανισμού που τον κάνει καλύτερα προσαρμοσμένο στο περιβάλλον του και αυξάνει τις πιθανότητες επιβίωσης και αναπαραγωγής μέσω της φυσικής επιλογής.

Adaptability / adaptive capacity (Δυνατότητα προσαρμογής) – Η δυνατότητα προσαρμογής ενός οργανισμού, πληθυσμού, βιοκοινότητας ή οικοσυστήματος σε νέες περιβαλλοντικές συνθήκες που μπορεί να έχουν προκληθεί από κάποια διατάραξη ή μεταβολή του οικοσυστήματος, όπως συμβαίνει με τη σταδιακή αύξηση της θερμοκρασίας της θάλασσας.

Ahermatypic corals (Μη-ερματυπικά ή ασυνεργά κοράλλια) – Κοράλλια που δεν συμβάλλουν στη δημιουργία κοραλλιογενών υφάλων.

Allochthonous, exotic, non-native species (Αλλόχθονο, εξωτικό, εισαγόμενο, μη-αυτόχθονο είδος) – Είδος το οποίο εμφανίζεται σε ένα οικοσύστημα ή σε μία γεωγραφική περιοχή που βρίσκεται πέραν των ορίων της ιστορικής γεωγραφικής του κατανομής. Η παρουσία ενός αλλόχθονου είδους σε μια νέα περιοχή μπορεί να οφείλεται σε φυσικά (π.χ. θαλάσσια ρεύματα) ή ανθρωπογενή αίτια (π.χ. ναυσιπλοΐα, υδατοκαλλιέργειες, κ.λ.π.). Στην περίπτωση που το αλλόχθονο είδος καταφέρει να επιβιώσει, εγκατασταθεί και αναπαραχθεί στο νέο περιβάλλον, μπορεί να επιφέρει αρνητικές οικολογικές συνέπειες στους πληθυσμούς των αυτόχθονων ειδών και στους μηχανισμούς λειτουργίας των οικοσυστημάτων˙ Τα είδη αυτά χαρακτηρίζονται ως **"Εισβολικά είδη" – "Invasive species"**.

Anthropogenic (Ανθρωπογενές) – Αυτό που προέρχεται από ανθρώπινες δραστηριότητες.

Arborescent (Δενδροειδές) – Αυτό που παρουσιάζει διακλαδώσεις.

Assemblage / species assemblage (Συνάθροιση ή συνεύρεση / συνάθροιση ή συνεύρεση ειδών) – Η μικρότερη λειτουργική βιοκοινοτική μονάδα. Η συνάθροιση μπορεί να είναι έκφραση αναπαραγωγικών προτύπων, κοινωνικής συμπεριφοράς, ή αποτέλεσμα της απόκρισης των οργανισμών σε διαφορές του ενδιαιτήματος / οικοτόπου και σε ημερήσιες ή εποχιακές περιβαλλοντικές αλλαγές.

Asexual / vegetative reproduction (Αγενής / βλαστητική αναπαραγωγή) – Αναπαραγωγή ενός οργανισμού που γίνεται χωρίς το σχηματισμό γαμετών (βλ. αντιθ. *Sexual reproduction*).

B

Benthos (Βένθος) – Οι οργανισμοί που έχουν στενή εξάρτηση από το βυθό (ζουν και κινούνται επί (επιβενθικά είδη), εντός (ενδοβενθικά είδη) ή πλησίον (παραβενθικά είδη) του βυθού).

Bio-construction (Βιο-οικοδόμηση, βιο-κατασκευή) – Η δημιουργία ή διαμόρφωση ενός ενδιαιτήματος από φυτικούς ή ζωικούς οργανισμούς (π.χ. κοραλλιογενείς ύφαλοι).

Bio-constructors (Είδη βιο-κατασκευαστές) – Οι οργανισμοί που συμμετέχουν στη δημιουργία ενδιαιτήματος, όπως είναι τα κοραλλιοειδή ροδοφύκη, οι σπόγγοι, τα ερματυπικά κοράλλια, και τα βρυόζωα (βλ. και *Ecosystem engineers*).

Biodiversity, biological diversity (Βιοποικιλότητα, βιολογική ποικιλότητα) – Η γενετική, ταξινομική και οικολογική ποικιλία σε όλες τις χρονικές και χωρικές κλίμακες. Στην οικολογία ο όρος συνήθως χρησιμοποιείται για να περιγράψει το συνολικό αριθμό των διαφορετικών ειδών που ζουν σε μία συγκεκριμένη γεωγραφική περιοχή ή σε ένα τύπο οικοτόπου.

Bio-erosion (Βιο-διάβρωση) – Η διάβρωση του υποστρώματος που προκαλείται από τη δράση οργανισμών, όπως π.χ. από είδη σπόγγων, εχινόδερμων, πολυχαίτων, μαλακίων (βλ. *Erosion, Weathering*).

Bio-eroders (Βιο-διαβρωτές, διατρητικοί οργανισμοί) – Οργανισμοί που διατρυπούν ή θρυμματίζουν το υπόστρωμα, προκαλώντας έτσι τη διάβρωση του. Τέτοιοι οργανισμοί είναι για παράδειγμα οι σπόγγοι του γένους *Cliona*, το μαλάκιο *Lithophaga lithophaga* (πετροσωλήνας), και ορισμένα είδη αχινών.

Biogenic formation (Βιογενής σχηματισμός) – βλ. *Biogenic substrate, Bioherm*.

Biogenic substrate (Βιογενές υπόστρωμα) – Ο τύπος υποστρώματος που δημιουργείται από τις αποθέσεις βιολογικού υλικού, όπως οι σκελετοί και τα όστρακα νεκρών και ζωντανών οργανισμών.

Bioherm (Βιογενές ανάγλυφο) – Υπόστρωμα που αποτελείται κυρίως από βενθικά ασπόνδυλα (όπως π.χ. ροδοφύκη, κοράλλια, μαλάκια), καθώς και ίζημα ή πετρώματα διαφορετικής προέλευσης.

Biological cycle / life cycle (Βιολογικός κύκλος / κύκλος ζωής) – Το σύνολο των διαφορετικών βιολογικών σταδίων ή φάσεων που περνά ένας οργανισμός κατά τη διάρκεια της ζωής του.

Biomass (Βιομάζα) – Το συνολικό βάρος της οργανικής ύλης που προέρχεται από ζωντανούς οργανισμούς. Συνήθως υπολογίζεται ως ξηρό βάρος.

Biotic environment (Βιοτικό περιβάλλον) – Το σύνολο των βιοτικών παραγόντων (φυτά και ζώα) του φυσικού περιβάλλοντος.

Biotope (Βιότοπος) – Η περιοχή, ο συγκεκριμένος τόπος ή χώρος όπου ζει και αναπαράγεται ένας οργανισμός ή τα μέλη μίας βιοκοινότητας. Συνήθως αφορά στο αβιοτικό μέρος του οικοσυστήματος (π.χ. τύπος υποστρώματος, ωκεανογραφικά και χημικά χαρακτηριστικά νερού). Για παράδειγμα ο βιότοπος του αστακού (δεκάποδο καρκινοειδές) είναι οι θαλάσσιες βραχώδεις περιοχές που φέρουν αρκετές τρύπες, ενώ ο βιότοπος του ψαριού λύχνος είναι οι αμμώδεις βυθοί.

Bloom (Άνθιση) – Η απότομη αύξηση της αφθονίας ενός είδους ή πολλών ειδών, συνήθως φυτοπλαγκτονικών οργανισμών.

Broadcast spawning species (Είδη που απελευθερώνουν γενετικό υλικό στην υδάτινη στήλη) – Τύπος εξωτερικής αναπαραγωγής, κατά την οποία γίνεται ταυτόχρονη απελευθέρωση θηλυκών και αρσενικών γαμετών ή σπορίων στην υδάτινη στήλη (βλ. *Spawn*).

Brooding species (Επωάζον είδος) – Είδος που επωάζει αβγά. Στην περίπτωση των κοραλλιών, η επώαση χωρίζεται σε: α) **εσωτερική (internal brooding)**, όπου η γονιμοποίηση και επώαση των αβγών γίνεται εντός των σωματικών κοιλοτήτων του οργανισμού, και β) **εξωτερική (external brooding)**, όπου η επώαση των αβγών γίνεται έξω από το σώμα του οργανισμού. Στην εξωτερική επώαση, τα αβγά εναποθέτονται στην επιφάνεια του γονικού σώματος (συνήθως του μητρικού), στο οποίο συγκρατούνται με τη βοήθεια βλέννας. Εναλλακτικά, κάποια άλλα είδη ασπόνδυλων (όπως οι σπόγγοι και τα κοράλλια) επιλέγουν την εξωτερική αναπαραγωγή μέσω της ταυτόχρονης απελευθέρωσης θηλυκών και αρσενικών γαμετών στην υδάτινη στήλη (βλ. *Spawn, Broadcast spawning species*).

C

Calcareous (Ασβεστώδες / αασβεστολιθικό) – Οργανισμός ή υπόστρωμα που αποτελείται από ανθρακικό ασβέστιο ($CaCO_3$).

Calcareous algae / Coralline algae (Ενασβεστωμένα μακροφύκη / κοραλλιοειδή μακροφύκη) – Μακροφύκη που αποθηκεύουν ανθρακικό ασβέστιο στο θαλλό τους.

Carrying capacity (Φέρουσα ικανότητα) – Η μέγιστη δυνατότητα αντοχής των μηχανισμών φυσιολογικής λειτουργίας ενός οικοσυστήματος. Ο όρος επίσης χρησιμοποιείται για να περιγράψει το μέγιστο ανώτερο όριο στο μέγεθος ενός πληθυσμού, και καθορίζεται από τη διάθεση τροφής, την παρουσία θηρευτών, ή άλλων περιορισμών του ενδιαιτήματος.

Climate change (Κλιματική αλλαγή) – Η μεταβολή του κλιματικού προτύπου σε τοπική ή παγκόσμια κλίμακα, η οποία σχετίζεται άμεσα ή έμμεσα με ανθρωπογενείς δραστηριότητες που επηρεάζουν τη σύνθεση της παγκόσμιας ατμοσφαίρας, καθώς και με τη φυσική διακύμανση του κλίματος.

Coelenteron (Κοιλέντερο) – Η σωματική κοιλότητα των κνιδόζωων.

Colony (Αποικία) – Χωρικά ευδιάκριτος πληθυσμός ή υποπληθυσμός ενός είδους.

Colonial / Clonal species (Αποικιακά είδη) – Είδη που αναπτύσσονται σε μορφή αποικίας γενετικά πανομοιότυπων οργανισμών ή κυττάρων μέσω αγενούς ή βλαστιτικής αναπαραγωγής, όπως για παράδειγμα οι γοργονίες και οι σπόγγοι (βλ. συνών. *Modular*).

Community (Βιοκοινότητα / κοινότητα) – Το σύνολο των φυτικών και ζωικών οργανισμών που συνυπάρχουν σε μία περιοχή ή σε ένα βιότοπο και αλληλεπιδρούν μεταξύ τους μέσω τροφικών και χωρικών σχέσεων – Το βιοτικό μέρος του οικοσυστήματος.

Competition (Ανταγωνισμός) – Ο τύπος αλληλεπίδρασης μεταξύ δύο ή περισσοτέρων οργανισμών που εκμεταλλεύονται κοινούς φυσικούς πόρους, στην προσπάθεια απόκτησης των οποίων ο ένας οργανισμός βλάπτει τον άλλον. Ο ανταγωνισμός μπορεί να συμβαίνει ανάμεσα σε άτομα του ίδιου είδους **(Ενδοειδικός ανταγωνισμός – Intraspecific competition)**, ή ανάμεσα σε άτομα διαφορετικού είδους **(Διαειδικός ανταγωνισμός – Interspecific competition)**.

Conservation (Διατήρηση) – Οι διαφορετικές ανθρωπογενείς ενέργειες και τα θεσμικά πλαίσια που στοχεύουν στην εξασφάλιση και διατήρηση της καλής απόδοσης και συνεχούς λειτουργίας των οικοσυστημάτων και του βιόκοσμου που τα εποικίζει.

Coralligenous formations / coralligenous outcrops / coralligène / coralline reefs (Κοραλλιγενείς σχηματισμοί) – Βιογενείς σχηματισμοί που αναπτύσσονται σε σκληρό υπόστρωμα υπό συνθήκες μειωμένου φωτισμού, μέσω της απόθεσης ανθρακικού ασβεστίου από τους σκελετούς των κοραλλιοειδών ροδοφυκών και άλλων βενθικών οργανισμών (όπως τα κοράλλια, τα βρυόζωα, κλπ). Πρόκειται για έναν ενδημικό τύπο οικοτόπου της Μεσογείου που διαφέρει από τους κοραλλιγενείς υφάλους των τροπικών θαλασσών ως προς το ότι αναπτύσσεται κυρίως σε βαθιά νερά όπου επικρατούν έντονα ρεύματα και χαμηλές εντάσεις φωτισμού. Επιπλέον, οι βασικοί οργανισμοί (βλ. *Foundation species, Ecosystem engineers*) που δημιουργούν τους κοραλλιγενείς σχηματισμούς της Μεσογείου είναι κατά κύριο λόγο τα κοραλλιοειδή ροδοφύκη, και όχι τα κοράλλια, τα οποία συνήθως διαδραματίζουν δευτερεύοντα ρόλο.

Coralligenous banks / platform coralligenous (Κοραλλιγενείς σχηματισμοί σε μορφή πλατφόρμας) – Κοραλλιγενείς σχηματισμοί σε μορφή υφάλων οι οποίοι περιβάλλονται από κινητό υπόστρωμα.

Coralligenous rims / coralligenous of the littoral rock (Κοραλλιγενείς σχηματισμοί ως προεξοχές βράχων) – Κοραλλιγενείς σχηματισμοί που αναπτύσσονται ως ανάγλυφο πάνω σε βραχώδεις περιοχές.

D

Dominant Species (Κυρίαρχα Είδη) – Τα είδη που διαθέτουν τη μεγαλύτερη αφθονία ή βιομάζα σε μία βιοκοινότητα.

Degradation (Υποβάθμιση) – Η απλοποίηση της δομής και των λειτουργιών ενός οικοσυστήματος και η μείωση της βιοποικιλότητας που προκαλούνται από διαταράξεις (βλ. *Biodiversity, Disturbance*) η συχνότητα ή/και η σφοδρότητα των οποίων δεν επιτρέπει την ανάκαμψη του οικοσυστήματος. Η υποβάθμιση σταδιακά μειώνει την παραγωγικότητα και την οικολογική ακεραιότητα των οικοσυστημάτων.

Disturbance (Διατάραξη) – Η απότομη αλλαγή των φυσικών και βιοτικών παραγόντων ενός οικοσυστήματος που επιφέρει μερική ή σημαντική οικολογική μεταβολή, επηρεάζοντας τη ποικιλότητα, τη δομή και τις λειτουργίες των πληθυσμών, βιοκοινοτήτων και οικοσυστημάτων. Η διατάραξη μπορεί να οφείλεται σε φυσικά αίτια, όπως η πτώση ενός βράχου, ή σε ανθρωπογενή αίτια, όπως η ρίψη μπάζων στο βυθό στα πλαίσια εκτέλεσης παράκτιων έργων.

E

Ecological status (Οικολογική κατάσταση) – Η αξιολόγηση της λειτουργίας ενός οικοσυστήματος ή της υγείας ενός πληθυσμού βάσει δεικτών περιγραφής συγκεκριμένων βιοτικών και αβιοτικών παραμέτρων (βλ. *Reference conditions*).

Ecosystem (Οικοσύστημα) – Μία οργανωμένη και αυτορρυθμιζόμενη ενότητα αβιοτικών στοιχείων και έμβιων όντων που συνυπάρχουν στο χώρο, αλληλεπιδρούν μεταξύ τους και ανταλλάσσουν υλικά ή πληροφορίες με κινητήρια δύναμη την ενέργεια.

Ecosystem Based Management Approach (Οικοσυστημική Προσέγγιση Διαχείρισης Περιβάλλοντος) – Διαχειριστική προσέγγιση που θέτει ως βάση το οικοσύστημα ως σύνολο, και όχι μεμονωμένα επιμέρους συστατικά του (όπως ένα είδος-στόχος).

Ecosystem engineers (Μηχανικοί του οικοσυστήματος) – Οργανισμοί που «χτίζουν» το οικοσύστημα, δηλαδή δημιουργούν, διαμορφώνουν και συντηρούν τα φυσικά στοιχεία των ενδιαιτημάτων. Χωρίζονται στους α) **Αλλογενείς μηχανικούς του οικοσυστήματος (Alogenic ecosystem engineers)**, οι οποίοι διαμορφώνουν και προκαλούν αλλαγές στο φυσικό περιβάλλον μέσω μηχανικής δραστηριότητας (όπως είναι οι πετροσωλήνες *Lithophaga lithophaga* που διατρυπούν το σκληρό υπόστρωμα), και στους β) **Αυτογενείς μηχανικούς περιβάλλοντος (Autogenic ecosystem engineers)**, ή αλλιώς **Ιδρυτικά είδη (Foundation species)** που διαμορφώνουν και προκαλούν αλλαγές στο φυσικό περιβάλλον λόγω της μορφής τους (όπως είναι τα μακροφύκη του γένους *Cystoseira* που φέρουν πυκνό φύλλωμα, τα ερματυπικά κοράλλια που δημιουργούν υφάλους, οι έντονα διακλαδισμένες γοργονίες).

Ecosystem services (Οικοσυστημικές υπηρεσίες) – Τα αγαθά και οφέλη που αποκομίζει ο άνθρωπος από τις διεργασίες και λειτουργίες των φυσικών οικοσυστημάτων.

Egg (Αβγό ή ωάριο) – Ο θηλυκός γαμέτης, το θηλυκό γεννητικό κύτταρο.

Enclave (Θύλακας) – Η παρουσία ενός τύπου βιοκοινότητας εντός μίας άλλης βιοκοινότητας σε μία περιοχή, λόγω ύπαρξης μικρο-ενδιαιτήματος (βλ. *Microhabitat*) που παρέχει κατάλληλες συνθήκες για την ανάπτυξή της. Για παράδειγμα, οι σκιερές τρύπες μίας βραχώδους ακτής προσφέρουν κατάλληλες συνθήκες για την ανάπτυξη σκιόφιλων βιοκοινοτήτων, ανάμεσα στις κατά τ' άλλα φωτόφιλες βιοκοινότητες που αναπτύσσονται στις οριζόντιες επιφάνειες των βράχων.

Encrusting (Κρουστώδη) – Φυτικοί και ζωικοί οργανισμοί που αναπτύσσονται ως κρούστα πάνω σε βράχους ή άλλες επιφάνειες.

Endemic (Ενδημικό) – Είδος οργανισμού ή τύπος οικοτόπου που εξελίχθηκε και υπάρχει αποκλειστικά σε ένα συγκεκριμένο γεωγραφικό χώρο.

Erosion (Διάβρωση) – Το σύνολο των διεργασιών που έχει ως αποτέλεσμα τη σταδιακή αποσύνθεση του υποστρώματος. Μπορεί να προκαλείται από φυσικούς (π.χ. κυματισμός, ρεύματα) ή/και βιολογικούς παράγοντες (π.χ. διάτρηση ή θρυμματισμός βιογενούς υποστρώματος από τη δράση οργανισμών). (βλ. *Bio-erosion, Substrate, Weathering*).

Evolution (Εξέλιξη) – Η αλλαγή της γενετικής σύνθεσης ενός βιολογικού πληθυσμού μεταξύ διαδοχικών γενεών που μπορεί να οφείλεται σε αίτια όπως η φυσική επιλογή, η διασταύρωση μεταξύ γενετικά συγγενικών ατόμων, και οι γενετικές μεταλλάξεις (βλ. *Adaptation*).

F

Facies (Φάση) – Η οικολογική κατάσταση μίας βιοκοινότητας στην οποία συγκεκριμένες βιοτικές και αβιοτικές συνθήκες ευνοούν την επικράτηση ενός είδους ή μίας μικρής ομάδας ειδών.

Fecundity (Παραγωγικότητα, αναπαραγωγικότητα) – Η ικανότητα ενός οργανισμού να παράγει απογόνους. – Η μέγιστη δυνατή αναπαραγωγική απόδοση ενός ατόμου κατά τη διάρκεια της ζωής του. Σχετίζεται κυρίως με την αναπαραγωγική απόδοση των θηλυκών ατόμων (Αντιθ. Στειρότητα).

Fertility (Γονιμότητα) – Τρόπος μέτρησης της αναπαραγωγικής απόδοσης ενός οργανισμού ή ενός πληθυσμού σε μία συγκεκριμένη χρονική στιγμή. Μετριέται ως ο αριθμός των αβγών ή απογόνων που παράγει ένας οργανισμός ή πληθυσμός κατά τη εγγενή αναπαραγωγή (βλ. *Sexual reproduction*) ή ο αριθμός των σπορίων ή εκβλαστήσεων κατά την αγενή αναπαραγωγή (βλ. *Asexual reproduction*). (Αντίθ. Μη-γονιμότητα).

Fertilization (Γονιμοποίηση) – Η διαδικασία ένωσης γαμετών. Χωρίζεται σε: α) **Εσωτερική (Internal fertilization)** όταν λαμβάνει χώρα μέσα στο γονικό σώμα, και β) **Εξωτερική (External fertilization)** όταν οι θηλυκοί και αρσενικοί γαμέτες έχουν απελευθερωθεί από το γονικό σώμα και η γονιμοποίηση λαμβάνει χώρα στην υδάτινη στήλη (βλ. και *Broadcast spawning species*).

G

Gamete (Γαμέτης) – Αναπαραγωγικό κύτταρο, το οποίο ενώνεται με έναν άλλο γαμέτη για το σχηματισμό του ζυγώτη. Παράδειγμα γαμετών είναι τα ωάρια και σπερματοζωάρια.

Gonad (Γονάδα) – Αναπαραγωγικό όργανο (ωοθήκη ή όρχις) που παράγει τα αναπαραγωγικά κύτταρα (βλ. *Gamete*).

Gonochoristic / dioecious species (Γονοχωριστικό / δίοικο είδος) – Είδος με διακριτά θηλυκά και αρσενικά άτομα (βλ. αντιθ. *Hermaphroditic species*).

Good Environmental Status, GES (Καλή Περιβαλλοντική Κατάσταση) – Κατηγορία ευνοϊκής περιβαλλοντικής κατάστασης, όπως αυτή καθορίζεται βάσει κριτηρίων της Ευρωπαϊκής Οδηγίας 2008/56/ΕΟΚ για τη Θαλάσσια Στρατηγική.

Gorgonian (Γοργονία) – Αποικιακά ανθόζωα οκτακτινωτής συμμετρίας (Octocorallia) τα οποία εκκρίνουν σκελετό που περιέχει την πρωτεΐνη γοργονίνη.

H

Habitat (Ενδιαίτημα, οικότοπος) – Ο χώρος, και τα αβιοτικά/βιοτικά χαρακτηριστικά αυτού, στον οποίο διαβιεί ένα είδος, πληθυσμός ή βιοκοινότητα. Συχνά, χρησιμοποιείται εναλλακτικά και ο όρος "οικότοπος", κυρίως σε Περιβαλλοντικές Οδηγίες της Ευρωπαϊκής Ένωσης και σε Διεθνείς Συμβάσεις. Ως "Τύποι Οικοτόπων" νοούνται διακριτές μονάδες χώρου που ορίζονται με βάση κυρίαρχα αβιοτικά και βιοτικά (φυτά και ζώα) στοιχεία.

Habitat restoration (Αποκατάσταση ενδιαιτήματος) – Ανάκαμψη ενός ενδιαιτήματος που έχει υποστεί υποβάθμιση ή έχει καταστραφεί.

Habitats Directive (Οδηγία για την Προστασία των Οικοτόπων) – Η Ευρωπαϊκή Οδηγία 92/43/ΕΟΚ που έχει ως στόχο τη διατήρηση των φυσικών οικοτόπων και της άγριας χλωρίδας και πανίδας.

Hard bottom substrate (Σκληρό υπόστρωμα) – Υπόστρωμα που αποτελείται από συμπαγές υλικό. Μπορεί να είναι φυσικό (όπως ο βράχος), ή τεχνητό (όπως το τσιμέντο και το μέταλλο).

Hermaphroditic species (Ερμαφρόδιτο είδος) – Ο οργανισμός του οποίου το κάθε άτομο περιέχει το θηλυκό και το αρσενικό αναπαραγωγικό σύστημα (βλ. αντιθ. *Gonochoristic species*). Ο ερμαφροδιτισμός εκφράζεται ως α) **Ταυτόχρονος ερμαφροδιτισμός** με παράλληλη παραγωγή γαμετών διαφορετικού φύλου από το ίδιο άτομο, β) **Ερμαφροδιτισμός με αντιστροφή φύλου** ή **Διαδοχικός ερμαφροδιτισμός** όπου ο οργανισμός παράγει αρχικά μόνο θηλυκούς (πρωτογυνία) ή αρσενικούς γαμέτες (πρωτανδρία) και σε κάποια φάση του κύκλου ζωής το φύλο αντιστρέφεται.

Hermatypic corals (Ερματυπικά κοράλλια ή συνεργά κοράλλια) – Κοράλλια που σχηματίζουν κοραλλιογενείς υφάλους στις θερμές τροπικές θάλασσες του πλανήτη.

Heterotroph (Ετερότροφος) – Οργανισμός που εξασφαλίζει τροφή (θρεπτικά και ενέργεια) καταναλώνοντας άλλους οργανισμούς ή τα οργανικά συστατικά τους.

I

Indicator species (Είδος δείκτης) – Είδος που μπορεί να χρησιμοποιηθεί ως έμμεσος δείκτης περιγραφής κάποιας φυσικής διεργασίας ή συγκεκριμένων περιβαλλοντικών συνθηκών. Τα χαρακτηριστικά ενός είδους δείκτη (όπως η παρουσία, η αφθονία και ο ρυθμός ανάπτυξης) δύναται να εκφράζουν την οικολογική κατάσταση μεγαλύτερων ομάδων οργανισμών, μίας βιοκοινότητας, ή του οικοτόπου μίας περιοχής, και να προειδοποιούν για την παρουσία μίας επικείμενης διατάραξης.

Invasive species (Εισβολικό είδος) – Το είδος που έχει εισαχθεί σε μία περιοχή έξω από τα γνωστά γεωγραφικά όρια εξάπλωσης του, και το οποίο έχει καταφέρει να εγκατασταθεί, να αναπαραχθεί και να εξαπλωθεί εις βάρος των αυτόχθονων ειδών (βλ. *Allochthonous species*).

Iteroparity (Πολυγονία / Επανατοκία) – Πρότυπο αναπαραγωγής κατά το οποίο ένα είδος γεννά πολλές φορές κατά τη διάρκεια του κύκλου ζωής του, σε μία σειρά διακριτών αναπαραγωγικών γεγονότων (βλ. αντίθ. *Semelparity*).

IUCN – International Union for the Conservation of Nature and Natural Resources (Διεθνής Ένωση Προστασίας της Φύσης) – Παγκόσμια περιβαλλοντική οργάνωση που ιδρύθηκε το 1948 στη Γαλλία με στόχο τη διατήρηση των ειδών και την προστασία της φύσης, και εκδίδει τον Ερυθρό Κατάλογο (Red List) των απειλούμενων ειδών του κόσμου.

K

Keystone species (Θεμελιώδες είδος) – Είδος που ασκεί έντονο έλεγχο στη δομή μίας βιοκοινότητας μέσω τροφικών αλληλεπιδράσεων και όχι απαραίτητα λόγω αυξημένης αφθονίας.

L

Larva (Προνύμφη) – Το ανώριμο στάδιο στον κύκλο ζωής ενός ασπόνδυλου, κατά το οποίο η μορφολογία του οργανισμού συνήθως διαφέρει σημαντικά από τη μορφολογία των ώριμων σταδίων (βλ. και *Planula*).

M

Marine conservation planning (Θαλάσσιος χωροταξικός σχεδιασμός) – Συστηματικός σχεδιασμός με στόχο τη διατήρηση του θαλάσσιου περιβάλλοντος και τη βιώσιμη διαχείριση των ανθρωπογενών δραστηριοτήτων που το επηρεάζουν.

Marine Protected Areas, MPAs (Θαλάσσιες Προστατευόμενες Περιοχές, ΘΠΠ) – Γεωγραφικά καθορισμένες θαλάσσιες περιοχές που βρίσκονται υπό καθεστώς προστασίας, με στόχο τη βιώσιμη διαχείριση ή/και αποκατάσταση των θαλάσσιων βιολογικών και φυσικών πόρων. Εντός των ορίων μίας ΘΠΠ, συγκεκριμένες ανθρώπινες δραστηριότητες (όπως η αλιεία) μπορεί να απαγορεύονται ή να υπόκεινται σε διαχειριστικούς περιορισμούς.

Marine Reserve (Θαλάσσιο καταφύγιο) – Κατηγορία Θαλάσσιας Προστατευόμενης Περιοχής που προσφέρει το υψηλότερο επίπεδο προστασίας. Σε ένα θαλάσσιο καταφύγιο απαγορεύεται κάθε ανθρώπινη δραστηριότητα που αφαιρεί κάτι από (ή απορρίπτει κάτι στο) θαλάσσιο οικοσύστημα. Παράδειγμα τέτοιων δραστηριοτήτων είναι η αλιεία, η εξόρυξη ή η αγκυροβόληση.

Marine Strategy Framework Directive (Οδηγία για την Θαλάσσια Στρατηγική) – Στρατηγική για την προστασία και διαχείριση του θαλάσσιου περιβάλλοντος βάσει της Οδηγίας 2008/56/ΕΟΚ. Στοχεύει στη διατήρηση των θαλάσσιων οικοσυστημάτων, στην προστασία των θαλάσσιων φυσικών πόρων, και στην προαγωγή της αειφόρου χρήσης των θαλασσών. Στα πλαίσια της Οδηγίας, τα Κράτη Μέλη καλούνται να εφαρμόσουν τα απαραίτητα μέτρα ώστε να επιτύχουν ή να διατηρήσουν την Καλή Περιβαλλοντική Κατάσταση των θαλάσσιων υδάτων της ΕΕ έως το 2020 (βλ. *Good Environmental Status*).

Mass mortality events, MMEs (Περιστατικά μαζικής θνησιμότητας) – Η ξαφνική και απότομη θνησιμότητα μεγάλου αριθμού οργανισμών ενός πληθυσμού ή μίας βιοκοινότητας σε μία περιοχή.

Model species (Είδος μοντέλο) – Οργανισμός που χρησιμοποιείται ως μοντέλο ή πρότυπο σε μελέτες βιολογίας, φυσιολογίας και συμπεριφοράς.

Microhabitat (Μικρό-ενδιαίτημα) – Ενδιαίτημα μικρής έκτασης (συνήθως μικρότερο του 1m^2) που περιβάλλεται από ένα μεγαλύτερης έκτασης ενδιαίτημα, π.χ. οι τρύπες των βράχων στα ρηχά νερά, τα κανάλια των σπόγγων ή τα κλαριά των γοργονιών που προσφέρουν επιπλέον υπόστρωμα σε πληθώρα μακροβενθικών οργανισμών.

Modular organisms – Αποικιακοί οργανισμοί που αναπτύσσονται με την επαναληπτική παραγωγή πανομοιότυπων μελών ή υπομονάδων (modules), όπως τα κλαριά ενός φυτού, οι πολύποδες των αποικιακών κοραλλιών και τα ζωίδια των βρυοζώων. Αν και κάποιες υπομονάδες μπορεί σε κάποια στιγμή να αποκοπούν από τη γονική αποικία, συνήθως μπορούν να συνεχίσουν τις φυσιολογικές λειτουργίες ζώντας ανεξάρτητα (βλ. *Colonial* / *Clonal species, Ramet*).

Monoecious species (Μόνοικο είδος) – Στους αποικιακούς και φυτικούς οργανισμούς (βλ. *Colonial / Clonal species*) μόνοικο ονομάζεται το είδος στο οποίο τα θηλυκά και αρσενικά όργανα βρίσκονται σε ξεχωριστά άτομα πάνω στην ίδια αποικία, ή σε ξεχωριστά άνθη του ίδιου φυτού. Όταν τα θηλυκά και αρσενικά όργανα βρίσκονται μέσα στα ίδια άτομα, τότε ο οργανισμός αποκαλείται ερμαφρόδιτος (βλ. *Hermaphroditic species*).

O

Ovary (Ωοθήκη) – Η θηλυκή γονάδα (βλ. Gonad).

P

Passive suspension feeder (Παθητικός αιωρηματοφάγος) – Οργανισμός που χρησιμοποιεί βλέννα ή βλεφαρίδες για να παγιδεύσει τα μερίδια τροφής που αιωρούνται στο νερό (βλ. και *Suspension feeder*).

Perennial (Πολυετής) – Οργανισμός που ζει για παραπάνω από δύο χρόνια, σε αντίθεση με τους μονοετείς ή διετείς οργανισμούς.

Planula (Πλάνουλα) – Η βλεφαριδοφόρος προνύμφη των κνιδόζωων που κινείται ελεύθερα. Η πλάνουλα τελικά εγκαθίσταται σε μία κατάλληλη επιφάνεια και εξελίσσεται σε πολύποδα (βλ. *Larva, Polyp*).

Polyp (Πολύποδας) – Το προσκολλημένο στάδιο ζωής ενός κνιδόζωου. Έχει μικροσκοπικό κυλινδρικό ή ασκοειδές σώμα που η μία άκρη του είναι προσαρμοσμένη για να προσκολλάται στο υπόστρωμα, και στο αντίθετο άκρο φέρει ένα στόμα το οποίο περιβάλλεται από ακτινωτά διατεταγμένες κεραίες για τη σύλληψη τροφής.

Population (Πληθυσμός) – Όλα τα άτομα ενός είδους που ζουν σε μία συγκεκριμένη περιοχή και βρίσκονται σε σχετική απομόνωση από άλλα άτομα ή ομάδες ατόμων του ίδιου είδους.

Population dynamics (Δυναμική πληθυσμού) – Το σύνολο των ποσοτικών μεταβολών ενός πληθυσμού στο χρόνο, οι οποίες σχετίζονται με τον αριθμό των ατόμων που προστίθενται μέσω γεννήσεων και εποικισμού, και τον αριθμό των ατόμων που απομακρύνονται μέσω θανάτωσης και μετανάστευσης.

R

Ramet (Ανεξάρτητο μέλος κλώνου) – Ένα άτομο που προέρχεται από αποικία γενετικά πανομοιότυπων οργανισμών, όπως για παράδειγμα ο πολύποδας μίας γοργονίας ή ενός ερματυπικού κοραλλιού (βλ. *Colonial* / *Clonal species, Modular*).

Recruitment (Ενσωμάτωση, νεοεισδοχή) – Η ενσωμάτωση μίας νέας ηλικιακής κλάσης σε έναν ενήλικο πληθυσμό, διαδικασία που είναι απαραίτητη για την ανανέωση και βιωσιμότητα του πληθυσμού ενός είδους.

Recruitment success (Επιτυχία ενσωμάτωσης) – Ο ετήσιος αριθμός των νεαρών ατόμων που καταφέρνουν να εγκατασταθούν και να ενσωματωθούν στον ενήλικο πληθυσμό.

Reference conditions (Συνθήκες αναφοράς) – Συγκεκριμένες φάσεις/καταστάσεις ενός βιολογικού/φυσικού πόρου ή ενός ενδιαιτήματος που χρησιμοποιούνται για την αξιολόγησή του. Τυπικά, οι συνθήκες αναφοράς προσδιορίζονται βάσει δεικτών περιγραφής που προέρχονται από επιστημονικά πρωτόκολλα ή/και μοντέλα (βλ. *Ecological status*).

Reproduction (Αναπαραγωγή) – (βλ. *Asexual / vegetative reproduction* και *Sexual reproduction*).

Reproductive effort (Αναπαραγωγική προσπάθεια) – Ο τρόπος και ο χρόνος με τον οποίο ένας οργανισμός κατανέμει την ενέργεια του προς όφελος της αναπαραγωγής, έτσι ώστε να συνεισφέρει τα μέγιστα στις μέλλουσες γενιές και να εξασφαλίσει τη δική του μελλοντική επιβίωση. Ο όρος συμπεριλαμβάνει το συγχρονισμό της αναπαραγωγής (απλοτοκία ή επανατοκία) σε σχέση με τα υπόλοιπα στάδια του βιολογικού κύκλου, τη σχέση ηλικίας ή σωματικού μεγέθους του οργανισμού με τη γονιμότητα, την ηλικία κατά την αναπαραγωγική ωρίμανση, τη γονική επένδυση και τον αριθμό απογόνων, και γενικότερα τη στρατηγική του βιολογικού κύκλου του οργανισμού σύμφωνά με τη θεωρία της επιλογής r- ή K-.

Reproductive maturity (Αναπαραγωγική ωριμότητα) – Η βιολογική φάση στον κύκλο ζωής ενός οργανισμού κατά την οποία ξεκινάει η περίοδος της αναπαραγωγικής δραστηριότητας.

Reproductive strategy (Αναπαραγωγική στρατηγική / στρατηγική του ζευγαρώματος) – Ο τρόπος αναπαραγωγής. Ο όρος συμπεριλαμβάνει τον τύπο αναπαραγωγής (π.χ. αγενής ή εγγενής αναπαραγωγή), το σύστημα ζευγαρώματος (μονογαμία ή πολυγαμία, πολυγυνία ή πολυανδρία), και την επιλογή αναπαραγωγικού συντρόφου.

Reproductive success (Αναπαραγωγική επιτυχία) – Ο αριθμός γεννήσεων ανά θηλυκό άτομο συγκεκριμένης ηλικίας (ή ηλικιακής κλάσης) ανά μονάδα χρόνου. – Η αναπαραγωγική επιτυχία ενός οργανισμού ή ενός πληθυσμού σε κάποια συγκεκριμένη χρονική περίοδο, που κυρίως σχετίζεται με την ηλικία ή το μέγεθος των ατόμων, τη φυσιολογική τους κατάσταση, και περιβαλλοντικούς παράγοντες.

Resilience / ecological resilience (Ανθεκτικότητα / οικολογική ανθεκτικότητα) – Η δυνατότητα ενός είδους, οικοτόπου ή οικοσυστήματος να ανταποκρίνεται σε διαταραχές, δηλαδή να αντιστέκεται στις ενδεχόμενες καταστροφές και να έχει γρήγορη ανάκαμψη.

S

Sedimentation (Ιζηματαπόθεση) – Η διεργασία εναπόθεσης αιωρούμενου υλικού ως ίζημα.

Semelparity (Μονογονία / Απλοτοκία) – Πρότυπο αναπαραγωγής κατά το οποίο ένα είδος γεννά μόνο μία φορά κατά τον κύκλο ζωής του. Ένα τέτοιο είδος, συνήθως πεθαίνει μετά την ολοκλήρωση της αναπαραγωγικής περιόδου (βλ. αντίθ. *Iteroparity*).

Sexual reproduction (Αμφιγονία, εγγενής αναπαραγωγή) – Τύπος αναπαραγωγής που περιλαμβάνει την ένωση γαμετών (βλ. αντιθ. *Asexual / vegetative reproduction*).

Spawn (Γεννώ, παράγω, αποθέτω αβγά) – Η απελευθέρωση γεννητικού υλικού (θηλυκών και αρσενικών γαμετών) από θαλάσσιους / υδρόβιους οργανισμούς στο νερό.

Sperm cell / Spermatozoa (Σπερματοζωάριο) – Ο αρσενικός γαμέτης. – Το αρσενικό γεννητικό κύτταρο.

Spermatocysts (Σπερματοκύστη) – Σπερματοφόρος σάκος.

Species richness (Πλούτος ειδών, αριθμός ειδών) – Ο συνολικός αριθμός ειδών που βρίσκεται σε μία βιοκοινότητα ή σε έναν οικότοπο.

Spicule (Σκληρίτες) – Μικρά ασβεστώδη ή πυριτικά σκελετικά στοιχεία που βρίσκονται ανάμεσα στα κύτταρα και τους ιστούς ορισμένων ασπόνδυλων, όπως σε σπόγγους, ανθόζωα και ασκίδια.

Stress (Πίεση) – Η διαταραγμένη κατάσταση ενός είδους, πληθυσμού ή οικοσυστήματος (π.χ. μείωση του μεγέθους ενός πληθυσμού, κατακερματισμός ενδιαιτημάτων) που έχει προκληθεί από φυσικές ή ανθρωπογενείς παραμέτρους.

Substrate (Υπόστρωμα) – Το υποκείμενο υλικό. – Το υλικό πάνω στο (ή μέσα) στο οποίο διαβιεί ένας οργανισμός. Συνήθως χωρίζεται σε α) **πρωτογενές υπόστρωμα (primary substrate)**, π.χ. βράχος, ίζημα, τεχνητή κατασκευή, και β) σε **δευτερογενές υπόστρωμα (secondary substrate)** το οποίο αφορά στην επιφάνεια που παρέχουν φυτά και ζώα προς εγκατάσταση άλλων οργανισμών.

Suspension feeder (Αιωρηματοφάγο) – Ζώο που τρέφεται με τα μερίδια τροφής που αιωρούνται στο νερό (βλ. και *Passive suspension feeder*).

T

Threatened species (Επαπειλούμενο είδος) – Είδος που απειλείται η επιβίωσή του, και μπορεί να διατρέχει τον κίνδυνο εξαφάνισης. Η IUCN έχει κατατάξει τα επαπειλούμενα είδη σε διαφορετικές κατηγορίες κινδύνου. Οι 4 κατηγορίες που τυπικά αφορούν στα επαπειλούμενα είδη είναι:

Critically Endangered species (Κρισίμως κινδυνεύον είδος) – Είδος που αντιμετωπίζει εξαιρετικά υψηλό κίνδυνο εξαφάνισης από το φυσικό του χώρο στο άμεσο μέλλον.

Endangered species (Κινδυνεύον είδος) – Είδος που αντιμετωπίζει πολύ υψηλό κίνδυνο εξαφάνισης από το φυσικό του περιβάλλον στο άμεσο μέλλον.

Vulnerable species (Τρωτό είδος) – Είδος που αντιμετωπίζει υψηλό κίνδυνο εξαφάνισης στο μεσοπρόθεσμο μέλλον.

Near Threatened species (Σχεδόν απειλούμενο είδος) – Είδος που ενδέχεται να μπει σε κατηγορία κινδύνου στο άμεσο μέλλον.

Tolerance limits (Όρια αντοχής) – Οι ακραίες τιμές (ανώτατη και κατώτατη) συγκεκριμένων αβιοτικών συνθηκών, όπως η θερμοκρασία, η αλατότητα ή το pH, μεταξύ των οποίων εξασφαλίζεται η εκτέλεση των φυσιολογικών λειτουργιών ενός είδους ή ενός οικοσυστήματος.

Threat (Απειλή) – Παράγοντας (συνήθως ανθρωπογενής) που μπορεί να επιφέρει μερική μεταβολή ή ολοκληρωτική κατάρρευση ενός πληθυσμού, οικοσυστήματος, ή την εξαφάνιση ενός είδους.

U

Understory (Υποόροφος) – Το σύνολο των φυτικών και ζωικών οργανισμών που αναπτύσσονται κάτω από τον θόλο άλλων φυτών ή δενδροειδών οργανισμών.

W

Weathering (Αποσάθρωση, αποσύνθεση, διάβρωση) – Η σταδιακή καταστροφή ενός συστήματος ή ενδιαιτήματος από φυσικά αίτια, όπως η σταδιακή διάβρωση των βράχων από τη μηχανική δράση του κυματισμού (βλ. *Erosion, Bioerosion*).

Z

Zooxanthellae (Ζωοξανθέλλες) – Δινομαστιγωτά που ζουν συμβιωτικά μέσα στους ιστούς ορισμένων ασπόνδυλων, όπως σε κοράλλια και σπόγγους.

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