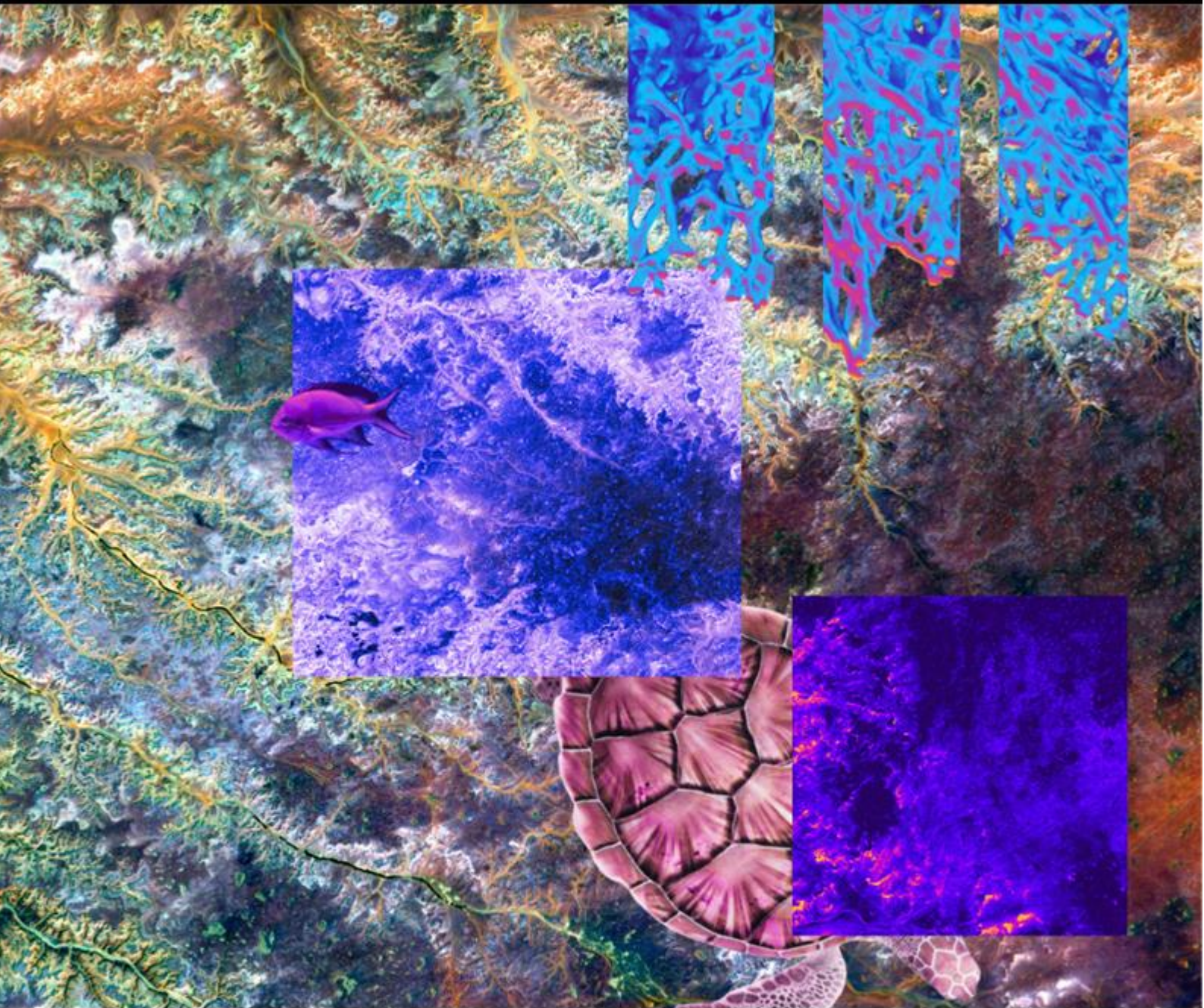


Aristotle University of Thessaloniki

Faculty of Sciences

School of Biology

Department of Ecology



Investigating climate change impacts on marine biodiversity
integrating characteristics of lifecycle, biology and behaviour of
species

Anastasia Chatzimentor
PhD Dissertation

Thessaloniki, January 2024



**ARISTOTLE UNIVERSITY OF THESSALONIKI
FACULTY OF SCIENCES
SCHOOL OF BIOLOGY
DEPARTMENT OF ECOLOGY
DOCTORATE STUDIES**



***Investigating climate change impacts on marine
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PhD DISSERTATION

ANASTASIA CHATZIMENTOR
Graduate of the School of Biology AUTH

Thessaloniki, January 2024



ΑΡΙΣΤΟΤΕΛΕΙΟ ΠΑΝΕΠΙΣΤΗΜΙΟ ΘΕΣΣΑΛΟΝΙΚΗΣ
ΣΧΟΛΗ ΘΕΤΙΚΩΝ ΕΠΙΣΤΗΜΩΝ
ΤΜΗΜΑ ΒΙΟΛΟΓΙΑΣ
ΤΟΜΕΑΣ ΟΙΚΟΛΟΓΙΑΣ
ΔΙΔΑΚΤΟΡΙΚΕΣ ΣΠΟΥΔΕΣ



*Διερευνώντας τις επιπτώσεις της κλιματικής αλλαγής
στη θαλάσσια πανίδα
ενσωματώνοντας χαρακτηριστικά του κύκλου ζωής
και της βιολογίας και συμπεριφοράς των ειδών*

ΔΙΔΑΚΤΟΡΙΚΗ ΔΙΑΤΡΙΒΗ

ΑΝΑΣΤΑΣΙΑ ΧΑΤΖΗΜΕΝΤΩΡ
Πτυχιούχος Τμήματος Βιολογίας ΑΠΘ

Θεσσαλονίκη, Ιανουάριος 2024

Εγώ, η Αναστασία Χατζημέντωρ, βεβαιώνω ότι είμαι συγγραφέας της παρούσας εργασίας και ότι έχω αναφέρει ή παραπέμψει σε αυτήν, ρητά και συγκεκριμένα, όλες τις πηγές από τις οποίες έκανα χρήση δεδομένων, ιδεών, προτάσεων ή λέξεων, είτε αυτές μεταφέρονται επακριβώς (στο πρωτότυπο ή μεταφρασμένες) είτε παραφρασμένες.

Η έγκριση της παρούσης διπλωματικής εργασίας υπό του Τμήματος Βιολογίας της Σχολής Θετικών Επιστημών του Αριστοτελείου Πανεπιστημίου Θεσσαλονίκης δεν υποδηλοί αποδοχή των γνώμων του συγγραφέως (Ν.5343/1932, άρθρ. 202, παρ. 2).

Εξεταστική Επιτροπή

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Προτεινόμενος τρόπος αναφοράς της Διδακτορικής Διατριβής

Χατζημέντωρ Αναστασία (2024) Διερευνώντας τις επιπτώσεις της κλιματικής αλλαγής στη θαλάσσια πανίδα ενσωματώνοντας χαρακτηριστικά του κύκλου ζωής και της βιολογίας και συμπεριφοράς των ειδών. Διδακτορική διατριβή. Αριστοτέλειο Πανεπιστήμιο Θεσσαλονίκης, Ελλάδα

Chatzimentor Anastasia (2024) Investigating climate change impacts on marine biodiversity integrating characteristics of lifecycle, biology and behaviour of species. PhD dissertation. Aristotle University of Thessaloniki, Greece

ΕΝΙΣΧΥΣΗ ΕΡΕΥΝΑΣ



Η συγγραφέας της παρούσας διδακτορικής διατριβής έχει λάβει οικονομική ενίσχυση από το Ελληνικό Ίδρυμα Έρευνας και Καινοτομίας (ΕΛ.ΙΔ.Ε.Κ.) στο πλαίσιο της Δράσης «1η Προκήρυξη ερευνητικών έργων ΕΛ.ΙΔ.Ε.Κ. για την ενίσχυση των μελών ΔΕΠ και Ερευνητών/τριών και την προμήθεια ερευνητικού εξοπλισμού μεγάλης αξίας» (Αριθμός Έργου: 2340) με τίτλο: "Συστηματικός σχεδιασμός διαχείρισης υπό το πρίσμα της κλιματικής αλλαγής: αναπτύσσοντας μια ολιστική προσέγγιση για την χαρισματική θαλάσσια μεγαπανίδα".

Ευχαριστίες

Σε αυτήν την πολύχρονη προσπάθεια για την ολοκλήρωση της διατριβής δεν ήμουν μόνη, αλλά πλαισιώθηκα από πολλούς καλούς ανθρώπους, τους οποίους θα ήθελα να ευχαριστήσω για τη βοήθεια, τη συμπαράσταση και την ολότελη παρουσία τους.

Αρχικά, θα ήθελα να ευχαριστήσω τον επιβλέπων καθηγητή της διατριβής, κ. Αντώνιο Μαζάρη, για την καθοδήγηση που μου παρείχε όλα αυτά τα χρόνια, την έμπνευση, τη δυνατότητα να συμμετέχω σε όμορφες ερευνητικές πρωτοβουλίες και έργα, την ελευθερία να αναλαμβάνω πρωτοβουλίες και την πίστη, την υπομονή και ενθάρρυνση σε αυτά που κάνω και κάνουμε ως ομάδα. Ευχαριστώ πολύ και τα υπόλοιπα μέλη της Τριμελούς Επιτροπής, τον κ. Στέλιο Κατσανεβάκη και τον κ. Αθανάσιο Τσίκληρα για τις πολύτιμες υποδείξεις τους στις εργασίες της διατριβής μου. Επίσης, θα ήθελα να ευχαριστήσω τα υπόλοιπα μέλη της Επταμελούς Επιτροπής, κ. Δρόσο Κουτσούμπα, κ. Γεώργιο Κόκκορη, κ. Αθανάσιο Καλλιμάνη και κ. Αθανάσιο Δάμιαλη, για την αξιολόγηση της διατριβής, τις εύστοχες ερωτήσεις τους και το γόνιμο διάλογο και συζήτηση που είχα τη χαρά να κάνουμε στην παρουσίαση της διατριβής. Θα ήθελα να ευχαριστήσω την κ. Αγγελική Δόξα για τη βοήθειά της σε κάθε βήμα αυτής της διατριβής και την ουσιαστική, καθοριστική και ανθρώπινη παρουσία της. Επίσης, καθότι είχα τη χαρά να συνεργαστώ με την κ. Βασιλική Αλμπανίδου στην αρχή της διατριβής, αλλά και πριν από αυτή, θα ήθελα να την ευχαριστήσω για όλα αυτά που μου έμαθε, σε επιστημονικό και ανθρώπινο επίπεδο. Θα ήθελα επίσης να ευχαριστήσω την κ. Στέλλα Βαρελτζίδου για τη φιλία, τη συνεργασία και την αμέριστη υποστήριξη και πίστη της σε εμένα για όλα αυτά τα χρόνια πριν και κατά τη διάρκεια της διατριβής.

Θα ήθελα φυσικά να ευχαριστήσω τους γονείς μου, Αλεξάνδρα και Γαβριήλ, και τα αδέρφια μου, Ρέα και Αντώνη, για την αμέριστη και γεμάτη υπομονή συμπαράσταση και ψυχολογική υποστήριξη στις χαρούμενες και τις πιο δύσκολες στιγμές αυτής της προσπάθειας. Θα ήθελα να ευχαριστήσω φίλους και συγγενείς με τους οποίους μοιράστηκα τους προβληματισμούς μου και τις χαρές μου όλα αυτά τα χρόνια. Και φυσικά θα ήθελα να ευχαριστήσω τους συναδέλφους μου και τις συναδέλφισσες μου για την ένθερμη συμπαράσταση, τις ατέλειωτες συζητήσεις, τα πολλά γέλια και την όμορφη παρέα. Θα ήθελα επομένως να ευχαριστήσω τον κ. Αθανάσιο Χαραλαμπίοπουλο, την κ. Νατάσα Τσαβδαρίδου, τον κ. Παναγιώτη Πέτσα, την κ. Αμαλία Κυπριώτη, την κ. Βαλεντίνη Σταματιάδου, τον κ. Αντρέα Κωνσταντινίδη, την κ. Μαρία Παπαζέκου, την κ. Ιλάειρα Γιατρουδάκη, την κ. Δάφνη Χατζηνικολάου, την κ. Κατερίνα Κώνστα και την κ. Δήμητρα Δάλλα. Για την εικόνα του εξώφυλλου θα ήθελα να ευχαριστήσω θερμά την κ. Έρικα Τσιουκαντάνα.

Περίληψη

Ο βαθμός της επίδρασης της κλιματικής αλλαγής στους θαλάσσιους οργανισμούς αποτελεί ένα ζήτημα πολύπλοκο, καθώς εξαρτάται από τη συνέργεια πολλαπλών παραγόντων. Ακόμη και αν η έκθεση τους στις μεταβαλλόμενες συνθήκες είναι παρόμοια, ο κίνδυνος των οργανισμών μπροστά στην κλιματική αλλαγή ποικίλει και διαφέρει. Με βάση την τρέχουσα οικοθέση των ειδών, είναι δυνατόν να προβλέψουμε τη μελλοντική πιθανή κατανομή της στο χώρο και να αξιολογήσουμε πιθανές νέες περιοχές καταλληλότητας αλλά και περιοχές όπου η κλιματική καταλληλότητα προβλέπεται να περιοριστεί. Ωστόσο, οι πιθανές αλλαγές στη χωρική κατανομή και την αφθονία τους εξαρτώνται και από άλλους παράγοντες, όπως είναι η συμπεριφορά, η φυσιολογία και ο κύκλος ζωής τους.

Μπροστά στην κλιματική αλλαγή, υπάρχουν χαρακτηριστικά τα οποία καθιστούν τους οργανισμούς περισσότερο ευάλωτους στις αλλαγές των περιβαλλοντικών τους παραγόντων, όπως είναι το στενό θερμοκρασιακό εύρος. Ενώ, αντίστοιχα, κάποια από τα χαρακτηριστικά αυτά μπορούν να προσδώσουν υψηλή ικανότητα για προσαρμογή, όπως είναι για παράδειγμα η υψηλή ικανότητα διασποράς. Στην αξιολόγηση της πιθανής απόκρισης των ειδών μπροστά στην κλιματική αλλαγή, είναι σημαντικό να λαμβάνονται υπόψιν τα αντίστοιχα χαρακτηριστικά που μπορεί να συνδέονται άμεσα με τις αναμενόμενες περιβαλλοντικές μεταβολές.

Στην παρούσα διατριβή επιχείρησα να συμβάλλω στην τρέχουσα επιστημονική συζήτηση σχετικά με την επίδραση της κλιματικής αλλαγής στη θαλάσσια βιοποικιλότητα, σε μία προσπάθεια να βελτιώσω τις προβλέψεις και τις αξιολογήσεις που πραγματοποιούνται για τους διάφορους οργανισμούς. Στην προσπάθεια αυτή, έλαβα υπόψιν οικολογικά και συμπεριφορικά χαρακτηριστικά των ειδών, τον κύκλο ζωής τους καθώς και τα ενδιατήματα που χρησιμοποιούν. Η διατριβή επικεντρώθηκε στη χωρική κλίμακα της Μεσογείου, μίας περιοχής που φιλοξενεί και αναμένεται να φιλοξενήσει σημαντικές μεταβολές στα πρότυπα κατανομής και αφθονίας της θαλάσσιας βιοποικιλότητας της. Η διερεύνησή μου εστίασε τόσο σε ήδη καλά μελετημένα, μεμονωμένα είδη, όπως οι θαλάσσιες χελώνες *Caretta caretta*, όσο και σε ευρύτερες ομάδες θαλάσσιων ειδών, συμπεριλαμβάνοντας θαλάσσια θηλαστικά και χελώνες, θαλάσσια ασπόνδυλα, καρχαρίες, σελάχια και ψάρια.

Πιο συγκεκριμένα, στην παρούσα διατριβή (Chapter B), προσδιόρισα πιθανές αλλαγές στην καταλληλότητα των θαλάσσιων ενδιατημάτων των θαλάσσιων χελωνών λόγω αύξησης της μέσης θερμοκρασίας της επιφάνειας της θάλασσας, λαμβάνοντας υπόψιν διάφορα στάδια του κύκλου ζωής τους. Ενήλικα και ανώριμα άτομα διαφοροποιούνται στη συμπεριφορά τροφοληψίας και τις οικολογικές τους απαιτήσεις. Χρησιμοποιώντας παρουσίες ατόμων που πραγματοποιούσαν τροφοληψία στη Μεσόγειο, εφάρμοσα συζευγμένα μοντέλα κλιματικής καταλληλότητας, με τα οποία προβλέφθηκε η κατανομή των θερμοκρασιακά κατάλληλων περιοχών των δύο σταδίων ζωής για τις παροντικές και μελλοντικές κλιματικές συνθήκες. Οι προβλέψεις αυτές διέφεραν, γεωγραφικά και τοπογραφικά. Ενώ οι κατάλληλες περιοχές των ανώριμων ατόμων εντοπίστηκαν κυρίως στην κεντρική και δυτική Μεσόγειο, οι κατάλληλες περιοχές των ενήλικων ατόμων εντοπίστηκαν κυρίως στο κεντρικό και ανατολικό τμήμα της λεκάνης. Ένα ενθαρρυντικό εύρημα της έρευνας ήταν ότι η έκταση των κατάλληλων περιοχών προβλέπεται να αυξηθεί και νέες κατάλληλες περιοχές προβλέφθηκαν στη δυτική Μεσόγειο στο μέλλον, ενώ η έκταση των κατάλληλων περιοχών των ανώριμων

ατόμων παραμένει σχετικά σταθερή. Λαμβάνοντας υπόψιν τα διαφορετικά στάδια του κύκλου ζωής των θαλάσσιων ειδών στις προβλέψεις μπορεί να συνεισφέρει στην αξιολόγηση των αποκρίσεών τους στην κλιματική αλλαγή, ακόμη και για τα ανώριμα στάδια που είναι περισσότερο ευάλωτα και λιγότερο μελετημένα.

Παρόλα αυτά, οι θαλάσσιες χελώνες αποτελούν είδη με υψηλή κινητικότητα σε όλη τη στήλη του νερού, ένα χαρακτηριστικό της συμπεριφοράς τους το οποίο αγνοείται στις προβλέψεις για τις επιπτώσεις της κλιματικής αλλαγής στη χωρική τους καταλληλότητα. Βασιζόμενη σε αυτόν τον προβληματισμό, επιχείρησα στο επόμενο κεφάλαιο της διατριβής (Chapter C) να προβλέψω τις πιθανές αλλαγές στη θερμοκρασιακή καταλληλότητα των θαλάσσιων χελωνών σε διαφορετικά βάθη, για τα ανώριμα και ενήλικα άτομα στη Μεσόγειο θάλασσα. Επιχείρησα να προσδιορίσω τρισδιάστατες περιοχές κλιματικής καταλληλότητας, χρησιμοποιώντας παρουσίες των θαλάσσιων χελωνών στη Μεσόγειο, καθώς και προβλέψεις για τη θερμοκρασία της θάλασσας σε τρεις βαθυμετρικές ζώνες. Η κατανομή των ενδιατημάτων διέφερε για κάθε στάδιο του κύκλου ζωής, αντικατοπτρίζοντας τη στρατηγική τροφοληψίας που ακολουθείται από τα ανώριμα και τα ενήλικα άτομα. Η ανάλυση κατέδειξε μία πιο εκτενή κατανομή των ανώριμων ατόμων σε περιοχές κοντά στην επιφάνεια της θάλασσας σε σχέση με βαθύτερες περιοχές και με περιοχές που εκτείνονται σε όλη τη στήλη του νερού. Στο μέλλον, οι προβλέψεις των μοντέλων διέφεραν για τα διακριτά ενδιατήματα. Ενώ για το νοτιοανατολικό άκρο της κατανομής των ανώριμων ατόμων προβλέφθηκε συρρίκνωση των περιοχών κοντά στην επιφάνεια της θάλασσας, ωστόσο στην κεντρική και βόρεια Μεσόγειο προβλέφθηκε αύξηση της καταλληλότητας για περιοχές σε όλη τη στήλη του νερού. Από την άλλη, για τα ενήλικα άτομα προβλέφθηκε κυρίως εξάπλωση των θερμοκρασιακά κατάλληλων περιοχών κοντά στην επιφάνεια της θάλασσας προς τη δυτική Μεσόγειο. Καθώς τα παραγόμενα πρότυπα θερμοκρασιακής καταλληλότητας διαφέρουν ανάλογα με το βάθος που αντιπροσωπεύουν για τις παροντικές και μελλοντικές συνθήκες, καθίσταται αναγκαία η ενσωμάτωση του τρισδιάστατου χαρακτήρα των ενδιατημάτων των θαλάσσιων ειδών.

Στο επόμενο κεφάλαιο της διατριβής (Chapter D), διεύρυνα το εύρος της μελέτης από ένα μεμονωμένο είδος σε μία ευρύτερη ομάδα ειδών της Μεσογείου. Στόχος του κεφαλαίου ήταν η αξιολόγηση του κινδύνου μπροστά στην κλιματική αλλαγή μίας ομάδας θαλάσσιων ειδών που διατρέχει υψηλό κίνδυνο εξαφάνισης, όπως τα απειλούμενα θαλάσσια ζώα της Μεσογείου με βάση την Κόκκινη Λίστα της IUCN. Επιχείρησα να εκτιμήσω τα επίπεδα του κινδύνου που διατρέχουν διαφορετικά είδη, όπως επίσης να προσδιορίσω περιοχές στις οποίες φιλοξενούνται είδη που προβλέπεται να διατρέχουν τον υψηλότερο κίνδυνο. Για το σκοπό αυτό επέλεξα ένα σύνολο χαρακτηριστικών που υποδηλώνουν τρωτότητα και ικανότητα προσαρμογής στις επιπτώσεις της κλιματικής αλλαγής, αλλά και δείκτες έκθεσης της κατανομής των διαφορετικών ειδών απέναντι στην προβλεπόμενη αύξηση της θερμοκρασίας της θάλασσας σε διαφορετικές βαθυμετρίες. Η ανάλυση προσδιόρισε ένα σημαντικό αριθμό θαλάσσιων ειδών με υψηλό κίνδυνο κινδύνου, με αντιπροσώπους σε ποικίλες ταξινομικές ομάδες, όπως τα θαλάσσια ασπόνδυλα, κορυφαίους θηρευτές όπως ψάρια, καρχαρίες, σελάχια, θηλαστικά και θαλάσσιες χελώνες. Περιοχές με αυξημένη παρουσία ειδών με υψηλό κλιματικό κίνδυνο βρέθηκαν στη δυτική Μεσόγειο, την Αδριατική θάλασσα και το βόρειο Αιγαίο πέλαγος. Καθώς όλες οι θαλάσσιες προστατευόμενες περιοχές της Μεσογείου φιλοξενούσαν μέρος της κατανομής τουλάχιστον ενός είδους με υψηλό κλιματικό κίνδυνο, οι μελλοντικές διαχειριστικές ενέργειες μπορούν να δομηθούν με προτεραιότητα στα είδη αυτά, βασιζόμενες σε βάση

μία οικοσυστημική προσαρμοστική προσέγγιση η οποία θα λαμβάνει υπόψιν την τρωτότητα, τα επίπεδα έκθεσης αλλά και την προσαρμοστική τους ικανότητα.

Τέλος, επιχείρησα να διερευνήσω πιθανές αλλαγές στη σύνθεση βασικών λειτουργικών χαρακτηριστικών της ιχθυοπανίδας των ρηχών υφάλων σχετικών με την ιστορία ζωής, την αύξηση και την αναπαραγωγή τους. Για το σκοπό του πέμπτου κεφαλαίου της διατριβής (Chapter E), συνδύασα προβλέψεις τους μελλοντικής αφθονίας των ψαριών των ρηχών υφάλους της βορειοανατολικής Μεσογείου έτσι ώστε να προσδιορίσω αλλαγές στη μέση σύνθεσή τους στην περιοχή μελέτης, για ένα μεσοπρόθεσμο και ένα μακροπρόθεσμο μελλοντικό σενάριο. Η ανάλυση προέβλεψε ότι οι μελλοντικές συνθήκες είναι πιθανόν να ευνοήσουν μία μετατόπιση της λειτουργικής σύνθεσης προς είδη με μικρότερο σωματικό μέγεθος, μικρότερη διάρκεια ζωής και μικρότερη ηλικία ωρίμανσης στα ψάρια των ρηχών υφάλων στις παράκτιες περιοχές της βορειοανατολικής Μεσογείου. Αυτή η πιθανή αλλαγή στα λειτουργικά πρότυπα μπορεί με τη σειρά της να επηρεάσει τις οικοσυστημικές υπηρεσίες. Για αυτό, πέρα από τη διερεύνηση των μεταβολών στην κατανομή και στην αφθονία των ειδών, είναι σημαντικό να εξετάζονται και οι επιδράσεις που μπορεί να έχουν και στη σύνθεση των μέσων χαρακτηριστικών των θαλάσσιων βιοκοινοτήτων.

Συμπερασματικά, η ενσωμάτωση της γνώσης μας για τις οικολογικές απαιτήσεις, τα ενδιατήματα, τη φυσιολογία, τη συμπεριφορά και τον κύκλο ζωής των θαλάσσιων ειδών μπορεί να παράγει νέα αποτελέσματα, ενημερωμένα ως προς τη διάσταση της βιολογίας των θαλάσσιων ειδών. Τα ευρήματα αυτά μπορούν να βελτιώσουν ακόμη περισσότερο τις προβλέψεις μας για τις μελλοντικές κατανομές των ειδών, τις αξιολογήσεις του κινδύνου που πραγματοποιούμε για τις ομάδες ειδών και για τα μελλοντικά λειτουργικά πρότυπα προστά στην κλιματική αλλαγή. Με βάση τα παραπάνω, μπορούμε να διευρύνουμε και να εμπλουτίσουμε τα μεθοδολογικά πλαίσια μοντελοποίησης και αξιολογήσεων που χρησιμοποιούμε, με τα χαρακτηριστικά των ειδών να αποτελούν αναγκαίες παραμέτρους που πρέπει να λάβουμε υπόψιν για τα τρέχοντα και τα μελλοντικά σχέδια διατήρησης.

Abstract

Climate change impacts on marine organisms constitutes a highly complex issue, as it depends on the interaction of multiple factors. Even if species are exposed to similar environmental changes, their risk in face of climate change varies and differs. Based on their current ecological niche, it is possible to predict new potential areas of suitability for species as well as areas where climatic suitability might be decreased. However, potential changes in their spatial distribution and abundance also depends on other factors, such as their behavioral characteristics, physiological mechanisms and life cycle.

Certain characteristics could render species vulnerable to environmental changes, such as a narrow thermal range. Others, however, could in turn, confer a high capacity for adaptation, such as a high dispersal ability. In order to predict species' response to changing conditions, it is important to take also into account the corresponding characteristics of species that could be directly linked to environmental changes in face of climate change.

In the present thesis, I attempted to contribute to the current scientific discourse regarding the potential effect of climate change on marine biodiversity, in an effort to improve predictions and assessments undertaken for organisms. In this endeavor, I took under consideration their interaction with species ecological and behavioral characteristics, their life cycle, as well as the habitats they utilize. The spatial scale of the thesis referred to the Mediterranean sea, a region that already hosts and is expected to undergo significant changes in distribution patterns and abundance of its biodiversity. My investigation focused on both the impacts on well-studied species, such as the loggerhead sea turtle (*Caretta caretta*), and broader groups of marine species, including marine mammals and turtles, marine invertebrates, sharks, rays, and fish.

Specifically, in Chapter B of the thesis, I identified potential changes on the suitability of marine foraging habitats of sea turtles under the predicted increase in sea surface temperature, taking into account both the immature and adult stages of their life cycle. Adult and immature individuals differ in foraging behavior and ecological requirements. Using presences of foraging adult and immature individuals in the Mediterranean sea, I applied an ensemble of climate suitability models that predicted the distribution of suitable areas for the two life stages under current and future climatic conditions. These predictions differed geographically and topographically. While suitable areas for immature individuals were mainly identified in the central and western Mediterranean, suitable areas for adult individuals were mainly located in the central and eastern basin. An encouraging finding of this research was that adults' suitable areas were predicted to increase in extent, and shift towards the western Mediterranean in the future, while the extent of areas for immature individuals was predicted to remain relatively stable. Consideration of the different stages of the life cycle of marine species in predictions could improve the assessment of their responses to climate change, even for immature stages that are more vulnerable and less-studied.

Nevertheless, sea turtles constitute species with high mobility throughout the water column, a characteristic of their behavior that is overlooked in predictions for the

impacts of climate change on their spatial suitability. Based on this consideration, in the next chapter of the thesis (Chapter C), I attempted to assess the predicted changes in thermal suitability for loggerhead sea turtles at different depths under the projected increase in sea temperature, for immature and adult individuals in the Mediterranean Sea. I intended to identify three-dimensional areas of climatic suitability, utilizing the presences of sea turtles in the Mediterranean, as well as predictions for sea surface temperature in three depth zones. The distribution of suitable areas differed for each life stage, reflecting the foraging strategy followed by immature and adult individuals. The analysis revealed a more extensive distribution of immature individuals for near-surface habitats compared to deeper habitats and water-column habitats. Future model predictions differed along distinct bathymetric habitats. While immatures' near-surface areas were predicted to contract in the south and central Mediterranean, an increase in suitability was predicted for water-column areas in the central and northern Mediterranean. As the resulting patterns of thermal suitability differed according to respective depth, the incorporation of the three-dimensional nature of marine species' habitats becomes essential for present and future predictions and assessments.

In the following chapter of the thesis (Chapter D), I expanded the scope of the research from an individual species to a broader group of marine species in the Mediterranean. The aim of this chapter was to assess the risk faced by a group of marine species that undergo great danger of extinction, the threatened marine animals of the Mediterranean Sea based on the IUCN Red List. I attempted to estimate the levels of risk faced by different species, as well as to identify marine areas where species of high risk are hosted. For this purpose, I selected a set of species characteristics indicating vulnerability and adaptive capacity to climate change impacts, as well as exposure indices of species distributions to the predicted increase in sea temperature at different depths. The analysis identified a significant number of marine species at high climate risk, representing various taxonomic groups, such as marine invertebrates, top predators like fish, sharks, rays, mammals, and sea turtles. Areas with increased presence of species with high climate risk were found in the western Mediterranean, the Adriatic Sea, and the northern Aegean Sea. As all marine protected areas in the Mediterranean were predicted to host part of the distribution of at least one species with high climate risk, management actions should be articulated prioritizing the identified high-risk species, based on an ecosystem-based approach taking into account vulnerability, exposure levels and adaptive capacity.

Finally, I attempted to explore potential changes in the future synthesis of key functional characteristics of the fish fauna in shallow coastal areas related to their life history, growth, and reproduction. For the purpose of the fourth chapter of the thesis (Chapter E), I combined predictions of future abundance of shallow-water fish in the northeastern Mediterranean to identify changes in their average functional composition across the entire study area for the mid-term and long-term future. The analysis predicted that future conditions might favor a shift in the functional composition towards species with smaller body size, shorter lifespan, and earlier maturation in shallow-water fish in the coastal areas of the northeastern Mediterranean. This potential change in functional patterns may, in turn, affect ecosystem services. Therefore, it is necessary to investigate how changes in the distribution and abundance of species may also impact the synthesis of functional characteristics of marine biota.

In conclusion, the integration of our knowledge about the ecological requirements,

habitats, physiology, behavior, and life cycle of marine species could generate novel and more biologically informed results. These findings could further improve our predictions for the future distributions of species, risk assessments in face of climate change and future functional patterns, enriching the methodological frameworks of modelling and assessments we use, with species characteristics constituting necessary parameters that must be taken into account for current and future conservation plans.

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Chapter A. Introduction – State of the art

A.1 Climate change and potential impacts on marine biodiversity

Historically, marine ecosystems have been continuously exposed to changes in their climatic conditions, either as part of the ongoing geological and climatic history of the planet (Nogués-Bravo et al., 2018) or as significant fluctuations in climatic conditions shorter in duration, such as the El Niño phenomenon or seasonal variations (Dowd et al., 2015; Slein et al., 2023). Species encounter variations in their environmental conditions within their distribution range (Bertrand et al., 2020), and most of them demonstrate an ability to adapt to these changes. In recent decades, the ongoing climate change stands apart from previous shifts. The current alterations in climatic conditions primarily result from human activities, particularly the intense industrial activity over the last 200 years (Barnett et al., 2001; Hansen & Stone, 2016). Changes in mean air temperature and greenhouse gas concentrations are rapid, and the impacts of these changes are often combined with various existing anthropogenic pressures on marine and terrestrial ecosystems (Henson et al., 2017). The oceans continually absorb the additional heat resulting from the increase in mean air temperature and the released carbon dioxide, having profound impacts on the conditions that support marine life. This phenomenon results in increasing sea temperature, alterations in the intensity and frequency of extreme weather events, rising sea level, and a decrease in ocean pH (Garcia-Soto et al., 2021).

Marine organisms respond to gradients in physicochemical parameters in their environment based on a curve of optimal conditions and resources that allow them to maintain a sustainable population, grow and reproduce. These conditions represent the ecological niche of a species and involve a range of environmental parameters and their corresponding values within which the species are capable of surviving. The realized niche of a species includes also its biotic interactions with other organisms, and collectively, these parameters determine species distributions world-wide. So, an increase in sea temperature could positively or negatively impact the realized niche of species (Hillebrand et al., 2018). Species ecological niche could be achieved in a new area outside their distribution range when conditions there meet their minimum temperature requirements, after a sea temperature increase. This would allow individuals to populate the area, as observed for certain tropical whale species in colder waters (Kerosky et al., 2012). However, when temperatures exceed the maximum tolerable temperatures of a species, the niche is theoretically not accomplished. This poses the survival of the species at risk, as for example a reduction in larval survival was observed for commercially important fish species like *Sparus aurata* (Madeira et al., 2016). Cumulative impacts also may affect the physiological tolerances of species compromising their functions, as sea temperature increase interacts with changes in other physicochemical factors, such as decrease in oxygen availability and reduction in sea pH (Garcia-Soto et al., 2021).

As highlighted, species survive within a range of environmental parameters. However, for other processes such as reproduction, suitable environmental conditions and essential necessary resources may be restricted to a smaller portion of the niche (Bykova et al., 2012). Therefore, if temperature increase is not expected to threaten the

survival of a species, it does not exclude the possibility of impacting other processes, such as reproduction and fertility. For instance, sea turtles' eggs can survive up to a critical maximum temperature (Howard et al., 2014), while the prolonged exposure of female sea turtles to higher temperatures is linked to lower rates of conception, with similar effects on their reproductive success (Albouy et al., 2020). Similarly, for sea urchins, a reduction in their respiratory activity (e.g., *Paracentrotus lividus* (Yeruham et al., 2020)) and negative impacts on their fertilization (e.g., *Lytechinus variegatus* (Lenz et al., 2019)) have been observed. Corals, on the other hand, exhibit bleaching when exposed to higher temperatures (Hughes et al., 2018).

Apart from an optimal temperature range, marine species niche involves a variety of environmental factors within which species survive, grow, and reproduce, such as seawater pH (Talukder et al., 2022). For example, experiments have shown that changes in environmental pH impact the metabolic activity of Antarctic fish and the phenology of their reproduction (Todgham & Mandic, 2020). This is also observed in the mobility and sperm velocity of marine stars (Uthicke et al., 2013) and the respiratory rate of cold-water corals like *Lophelia pertusa* (Hennige et al., 2015). Certain taxonomic groups in marine environments exhibit increased vulnerability to changes in temperature and ocean acidity, such as mollusks, compared to others like nematodes and flatworms (Hale et al., 2011; Ricevuto et al., 2015). However, some species may experience positive effects, as seen in the increased survival of immature stages of *Ruditapes decussatus* (Range et al., 2011). The combined effects of ocean temperature increase and acidification can adversely affect the survival of certain organisms, as observed in the coral-producing algae *Lithophyllum cabiochae*. Its mortality increased 2-3 times under higher CO₂ pressure due to tissue dissolution of its skeleton (Martin & Gattuso, 2009; Diaz-Pulido et al., 2012). Similar impacts may arise from the synergistic effects of rising temperature and decreasing oxygen availability (hypoxia) in marine ecosystems, negatively affecting the survival and embryonic development of species like the catshark *Scyliorhinus canicula*, leading to reduced survival and decreased length and mass of newly hatched individuals (Musa et al., 2020).

In case that conditions become more favourable for a species, it can colonize a region by expanding its current distribution range. Alternatively, if conditions become more favourable in an area where the species already exists, local population abundance may increase. Climate change has been associated with the redistribution and abundance changes of numerous marine species worldwide (Hastings et al., 2020). For instance, many fish and marine invertebrate species have exhibited contractions or expansions of their distribution ranges in the southern Australia region (Wernberg et al., 2011). The drivers behind these changes are not solely attributable to temperature increases but also involve alterations in the circulation and intensity of local sea currents, along with historically existing anthropogenic pressures in the area (Wernberg et al., 2011). In a literature review by Simpson et al. (2011), 72% of the 177 studied marine species were impacted by temperature changes, in the northeast Atlantic. Increased abundance was observed near the polar end of their distribution, while decreased abundance was encountered towards the equator-side of their distribution (Hastings et al., 2020). For example, the tropical and subtropical whale *Balaenoptera brydei* has been observed in colder waters near California over the past decade (Kerosky et al., 2012). In contrast, the white-beaked dolphin *Lagenorhynchus albirostris*, which prefers colder waters, has experienced a reduction in both its range and abundance (Albouy et al., 2020). This shift occurs at faster rates at their leading edges compared to their trailing edges, a

phenomenon linked, among other factors, to the magnitude of changes in these regions (Poloczanska et al., 2013).

Furthermore, some of the most important species in the sea, such as corals, have limited dispersal ability. The adaptation of these species in front of the shifting favourable conditions presents a challenging endeavor. Organisms like seagrasses, mangrove forests, salt marshes, and oysters represent formations on which multiple species depend on for both habitat and resources. So, impacts on them could affect hundreds of species that rely upon them (Gutiérrez et al., 2011). For example, mass bleaching of corals and their mortality due to increased temperatures have already influenced the reduction in the diversity and density of fish in coral reef areas (Hoegh-Guldberg & Bruno, 2010). These organisms, due to their sessile lifestyle, are simultaneously the most exposed ones to extreme temperature events and long-term trends in sea temperature increase (Smale et al., 2019). So far, marine heatwaves of the last decades in the Mediterranean Sea have caused massive mortality events, impacting various species, such as seagrasses, macroalgae, and corals, along with their associated fish and invertebrates (Garrabou et al., 2022). As these complex and extensive formations on the seafloor serve as substrates, food sources, and breeding grounds for the early life stages of many fish species, impacts on them trigger a series of cascading effects on other species. Depending on the characteristics and functions of each species, impacts on community's functions and ecosystem services were analogous, with negative consequences for commercial fishing, the survival of charismatic species, reduction of carbon sequestration by primary producers, and the deterioration of water quality due to the decline of filter-feeding organisms (Smith et al., 2021).

Understanding the aforementioned impacts of climate change on species, at both the level of individuals and populations, at the community and ecosystem level, will contribute to a comprehensive assessment of their vulnerability and adaptive capacity within their respective communities. Such insights will be crucial in constructing useful material for proposing more effective and specific strategies and measures for the adaptation of organisms and marine ecosystems to both climate change and the broader environmental changes occurring in ecosystems.

A.2 The mediating role of species characteristics in their response to climate change

The response of marine organisms to the changing climate is complex and dependent on the synergy of multiple factors. Their exposure to environmental changes is expected to vary, according to the magnitude of changes at the local level (Walther et al., 2002; Tingley et al., 2012; Pinsky et al., 2013), or even management measures that may be taken (O'Regan et al., 2021). For instance, there may be areas within the range of a species that could undergo considerable changes in their climatic conditions due to local topography and interactions with pre-existing environmental pressures (Helmuth et al., 2006). Thus, local populations could face different levels of risk, with exposure to a combination of environmental and existing anthropogenic pressures implying higher vulnerability to stress and lower adaptive capacity (He & Silliman, 2019).

However, even under similar environmental conditions, organisms' responses vary depending on their functions and behaviour, which differ based on their life history, genetic variability, and ecological requirements (Poloczanska et al., 2016). Under altering climate conditions, there are three possible cases for species response: either species distribution will shift as they follow their favourable conditions (Perry et al., 2005), local populations do not shift their position but adapt to changes (Hoffmann & Sgrò, 2011), or local populations experience a decrease to the point of local or even total disappearance (Wiens, 2016). Depending on their position along their distribution range and whether the new environmental conditions align with their ecological requirements, environmental changes may be favourable for them.

Based on the current distribution of species, we can predict their future potential distribution and evaluate possible new areas suitable for species as well as areas where their climatic suitability is limited (Elith & Leathwick, 2009). However, potential changes in their spatial distribution and/or abundance also depend on other factors, such as their behaviour, physiological mechanisms, and life cycle. As a first point, while adult individuals are usually the focus of studies, some species have complex life cycles and early life stages before the adult phase may be more vulnerable to the impacts of climate change (Dahlke et al., 2020; Crozier et al., 2021). For example, vulnerability in immature life stages constitutes a crucial factor in the distribution of adult stages in marine invertebrates (Pandori & Sorte, 2019). Therefore, for a comprehensive assessment of species potential responses to climate change, incorporating species life cycle can contribute to improving our predictions and determine the climatically vulnerable life stages of each species.

Ecological requirements, physiological functions and life cycle characteristics are expected to play an intermediate role in differentiated responses of marine organisms to environmental changes (Foden et al., 2019). For instance, narrow thermal tolerance of some species renders them susceptible to a potential increase in temperature and extreme weather events (Crabbe, 2008). While the high dispersal ability of pelagic species may provide increased adaptive capacity compared to benthic species (Poloczanska et al., 2016). Physiological functions, ecological requirements, life cycle, and behaviour of species can be summarized into broader categories of measurable traits (Violle et al., 2007). Knowledge of these characteristics can enrich and enhance predictions of species responses and their ability to adapt to a changing climate. For instance, stenothermal species are at a higher risk compared to eurythermal species, as

their temperature tolerance range is smaller, rendering them more susceptible to temperature changes (Foden et al., 2019). For certain species' functions are directly correlated with climate change. For example, the predicted decrease in seawater pH and the concentration of carbonate ions and biologically important calcium carbonate salts is expected to affect organisms that construct their skeletons and shells using calcium carbonate as a structural element (Fabry et al., 2008; Doney et al., 2020). Organisms relying on calcification processes, such as calcifying corals, mollusks, and echinoderms, are much more vulnerable to such changes, followed by crustaceans and fish, whereas marine mammals are not expected to be directly affected.

In addition, the life cycle of a species and its distinct characteristics can be a valuable source of information for our climate change assessments. Marine organisms go through discrete life stages during their life cycle, with varying vulnerability of each life cycle stage (Dahlke et al., 2020). Specifically, for immature stages, temperature influences the survival and development of larvae for some marine invertebrates and fish (Fredston-Hermann et al., 2020), and the use of marine habitats may vary spatially and bathymetrically (e.g., marine turtles and fish (Juan-Jordá et al., 2013; Casale et al., 2018)). The majority of predictions of climate change impacts are based on an examination of impacts only on the adult life stage, however, stages before reproductive maturity, which are often the most vulnerable ones, could be greatly affected by climate change (Russell et al., 2012).

The life cycle of the majority of marine organisms unfolds across various bathymetric layers in relation to the sea surface, which is almost exclusively analyzed and for which data are generally available. Many organisms continuously move among habitats at different depths (Derville et al., 2022; Schaber et al., 2022), with certain of them inhabiting and foraging in habitats of varying depths at different stages of their life cycle, such as marine turtles and benthic fish with a larval pelagic form (Leis & McCormick, 2002; Petitgas et al., 2013; Casale et al., 2018). Climate change will affect physiological functions of organisms as well as species habitats, with some habitats being more exposed to change than others (Donner, 2009). Based on habitat type used by a species and its geography, it may be more exposed compared to other ones. Environmental factors that determine habitat use by organisms, such as temperature, vary with depth (Venegas-Li et al., 2018). Specifically, the increase in sea surface temperature is expected to induce changes at different depths in both temperature and other abiotic factors (Levin & Le Bris, 2015). As changes in climate conditions across different depths are projected to be disproportionate (Brito-Morales et al., 2020), the suitability of three-dimensional habitats of marine organisms may be altered in the future, affecting the vertical migration of species (Jorda et al., 2020). However, only few studies explore the delineation of marine areas with vertical coherence (Brito-Morales et al., 2022; Doxa et al., 2022). Including different habitats used by species throughout their life cycle in predictions is an important next step, as use of deeper habitats in the sea may represent a trait supportive of species adapting to the increased sea surface temperature.

In conclusion, predictions and assessments of marine biodiversity, encompassing individual species or broader groups of species, need to consider various additional factors that influence the future vulnerability or adaptive capacity of marine organisms, ensuring a comprehensive understanding of climate change impacts. This includes considering their life cycle, habitats they move along the horizontal and vertical axis, as well as their physiology and behaviour.

A.3 Current research challenges

In a changing climate, range shifts and/or changes in population abundance have been observed and are also predicted for multiple species and taxonomic groups (Pinsky et al., 2020; Poloczanska et al., 2016). Current management efforts are focused on establishing marine protected areas (MPAs) and actively or passively managing a portion or the entire range of species distributions under protection. In this context, there is an urgent need for mapping the significant areas of species in the marine environment (e.g., IMMAs for marine mammals, Corrigan et al., 2014), especially migratory species utilizing multiple habitats in space and time. Sea turtles constitute such a group, and efforts have been made to spatially define their distributions in the Persian Gulf and the Indian Ocean (Pilcher et al., 2014; Hays et al., 2014). However, a systematic effort for the spatial determination of their important areas in the Mediterranean Sea is still lacking. Even if we manage to identify important areas for their conservation, these may change over the years due to potential shifts caused by individuals seeking more favourable conditions due to climate change (O'Regan et al., 2021). Therefore, besides spatially determining important areas under current climatic conditions, it is essential for a long-term and meaningful species conservation to consider potential future shifts. Predictions of the suitability of these important areas under future climate change scenarios can help identify vulnerable areas of change and potential new areas that may already be inhabited by smaller local populations. Incorporating the elements of change over time, new areas could be identified as candidate protection zones or connectivity nodes between existing marine areas (Rilov et al., 2019).

While most predictions regarding species suitability focus almost exclusively on information of environmental variables at the sea surface for which data are available, a large number of marine species possess a broader bathymetric range due to either active movement along the vertical axis or the ability to disperse into deeper waters (Brierley, 2014; Doherty et al., 2019). Specifically, marine turtles perform daily movements across various bathymetric layers for performing migration, foraging, and reproduction (Casale et al., 2018). Therefore, a step closer to a more comprehensive determination of their important areas, both at present and future conditions, involves the inclusion of all bathymetric layers they move along. Such information would be valuable in designing a three-dimensional spatial conservation plan, especially as anthropogenic activities intensify throughout the entire water column (Fanelli et al., 2021). Additionally, it could serve as input for investigating the vertical displacement of suitable climatic conditions for species and exploring their potential for adaptation. Therefore, it is essential to collect predictions for species suitability along the bathymetry and the potential impacts of climate change on them, especially considering that human activities, whether extracting minerals or biological resources, shift focus on deeper waters.

Taking a step further on, predictions about the impacts of climate change on individual species, as demonstrated earlier for marine turtles, are equally crucial for informing assessments of the vulnerability of larger groups of species. The Mediterranean Sea, being the second, largest region hosting a significant portion of global species richness (Coll et al., 2010), already experiences reported impacts of the changing climate on its marine biodiversity (Marbà et al., 2015; Garrabou et al., 2022). These include alterations in fish assemblage composition (Albouy et al., 2012), habitat loss and the

shifting distributions of many emblematic indicator species such as seagrasses (Chefaoui et al., 2018) and coastal fish (Albouy et al., 2013). Species face pressures from existing anthropogenic threats, causing a loss of biodiversity and historically leading to a declining trend in populations of 93 out of the 104 threatened species in the Mediterranean (IUCN, 2021). However, there is no systematic and comprehensive assessment of the risk they face under the pressure of a changing climate. Their overall vulnerability is predicted to depend on a combination of traits that confer susceptibility or adaptation to change and their overall exposure to changing conditions (Foden et al., 2019). Such a species-specific approach allows for comparisons among different species under a common set of characteristics related to physiological functions, ecological requirements, and behaviours, for which their vulnerability may differ. This approach is essential in order to consider additional important factors, beyond temperature requirements, in our ecological modelling assessments.

Research connecting species traits to anticipated responses to climate change is still limited but growing (Green et al., 2022). Within a marine community, when species with decreasing abundance share common traits with species whose abundance is increasing, a functional overlap occurs (Fonseca & Ganade, 2001). In such cases, the overall ecosystem functions remain largely unaltered, a phenomenon known as functional redundancy (Fonseca & Ganade, 2001). However, if their traits differ, and either the functions of species with decreasing abundance disappear or new functions appear or are added in the community, a functional change, a shift in the functional patterns within ecosystem, occurs. This can have implications for the provided ecosystem services and biotic interactions within community. Examples of such changes are documented, mainly concerning the alteration of macrophytic ecosystems in the Southern Aegean and Levantine Sea due to the grazing impact of invasive species such as *Siganus rivulatus* and *Siganus luridus*. This change is facilitated by increasingly favourable conditions for their population establishment, inherent traits of high competitiveness and the absence of top predators due to overfishing (Rilov, 2016; Nikolaou et al., 2023). Particularly for the Mediterranean, environmental changes are expected to favour the spread and increase in abundance of thermophilic species towards the north, transforming marine communities into more tropical-like ecosystems (Coll et al., 2012). Winter temperatures and temperature seasonality play a crucial role in this transition (Titelboim et al., 2019). Some areas in the Mediterranean may act as thermal refugia due to cooler conditions they will host, such as the Gulf of Lions, the northern Adriatic Sea and the North Aegean Sea until the mid-21st century, providing a refuge for cold-adapted species. However, by the end of the century, these areas are predicted to function as potential traps leading to their extinction as climatic conditions shift northward (Ben Rais Lasram et al., 2010). Therefore, beyond identifying potential species shifts and abundance changes in front of climate change, evaluating the likelihood of a functional change in the community and the ecosystem due to certain prevailing or disappearing characteristics is equally important (Levin & Möllmann, 2015; Möllmann et al., 2015).

In conclusion, in the present thesis, I attempted to address the aforementioned gaps and research questions, focusing spatially on the Mediterranean Sea, a global biodiversity hotspot that has already started to be significantly affected by the changing climate conditions, predicted to cause a 'tropicalization' of its climate, with a faster pace than other marine areas (Marbà et al., 2015). Results of the present thesis aim to contribute to a much more efficient planning for marine biodiversity protection.

A.4 Goals and thesis diagram

Although the literature on predictions for climate change impacts on marine life is extensive and continually expanding, at this stage, the integration of information on life cycle, physiology and behaviours of marine species can provide significant insights for an improved assessment of their vulnerability to climate change. In this direction, such steps can contribute to a much more comprehensive and holistic methodological approach in the way we assess the impacts of climate change, taking into account the complexity of the above-mentioned characteristics of marine animals, as well as the complexity of the habitats they use in the Mediterranean Sea. Therefore, in this doctoral thesis, I aim to investigate the following research questions:

1. Assessing the impact of changing sea temperature conditions on the spatial distribution and extent of marine habitats for Mediterranean sea turtles, considering different suitability predictions for adult and immature individuals.
2. Assessing the effect of selecting different bathymetric layers on the final suitability prediction for the marine areas of sea turtles in the Mediterranean Sea under current and future conditions, considering different suitability predictions for adult and immature individuals.
3. Evaluating the risk of threatened marine species to changing temperature conditions based on the combination between their vulnerability and adaptive capacity, considering both their life cycle and the bathymetric range of species distribution in the Mediterranean Sea.
4. Assessing the predicted impacts of changing environmental conditions on the patterns of mean functional characteristics of the fish fauna. Using field data on the abundance of shallow-water species in the Aegean and Ionian Seas I run predictions for their future abundance, combining information on the functional characteristics of these species, to evaluate possible changes in functional patterns due to climate change.

The first research objective was explored through Chapter B, where I developed a modelling methodology, combining information on the presence of marine turtles for both immature and adult individuals, current average sea surface temperature in the Mediterranean, and projections for the future. The models developed allowed the spatial determination of climatically suitable marine areas for the present and the future in the Mediterranean Sea. Comparing the results of the models for the present and the future allowed me to identify changes in the suitability of areas (loss, gain, maintenance of suitability) and assess the different predictions for different life stages.

The second research objective was explored through Chapter C. Based on a climate suitability modeling framework, using the presence of immature and adult marine turtles and predictions for sea surface temperature in three depth zones, I attempted to identify areas of climate suitability that extend across more than one depth zone. In addition, I assessed future predictions on their thermal suitability and projected changes in the climate change scenario.

The third research objective was explored through Chapter D. Using information on the vulnerability and adaptive capacity of species, as well as their exposure to increased sea temperatures within their bathymetric range, I built a methodological framework for

assessing the climate risk of threatened Mediterranean species. This framework allowed me to incorporate information on their life cycle, functions, and behaviour representing characteristics of increased or decreased vulnerability.

The fourth research objective was explored through Chapter E and aimed to evaluate possible changes in functional patterns of shallow-water fish species due to the changing climate, based on present and future community mean weighted traits of shallow reef fish. For this, I combined information on present-day abundance and predictions I performed for their future abundance coupled with information on the functional characteristics of respective species.

Chapter B. Projected redistribution of sea turtle foraging areas reveals important sites for conservation.

Publication:

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B.1 Introduction

Marine ecosystems globally have experienced significant loss in biodiversity, with around one-third of large migratory marine species currently facing extinction risk (Pimiento et al., 2020). They possess critical roles in marine communities (Estes et al., 2016) and their wide-ranging distributions expose them to different resources (Learmonth et al., 2006). However, they are susceptible to human-induced pressures within their broadly distributed habitats, threatening their long-term survival (Albouy et al., 2017). Consequently, many species of the charismatic marine megafauna are under high risk, underscoring the urgent need for targeted and adaptable management strategies (Lascelles et al., 2014).

A first step fostering our conservation efforts is the identification of key areas for migratory marine species (Hays et al., 2019). There have been endeavors towards this direction, delineating significant areas to prioritize actions in species important habitats (Corrigan et al., 2014). However, distribution shifts and significant habitat loss in front of the changing climate (Learmonth et al., 2006; Willis-Norton et al., 2015; Birkmanis et al., 2020) could pose challenges in determining crucial areas for conservation actions (Gissi et al., 2019). Nonetheless, the precise effects of climate change across their various habitats remain uncertain (Albouy et al., 2020; Payne et al., 2016). Thus, identifying key areas under different climate change scenarios emerges as a critical focus for ongoing and future conservation efforts to protect these species.

Sea turtles, with their complex life cycle and migratory behavior, utilize various habitats for breeding, development, and foraging, often distinct from one another (Bolten et al., 2003). Foraging habitats are particularly vital for population persistence, serving as areas where individuals replenish energy reserves, promote population growth, and facilitate successful breeding migrations. However, identifying important foraging habitats for different life cycle stages of sea turtles remains unclear. Sea turtles employ diverse foraging strategies and consume a variety of food resources. Additionally, individuals hatched from the same site may disperse to different foraging grounds (Hays et al., 2010), and mature animals breeding at a particular rookery may also utilize distinct and distant foraging sites (Schofield et al., 2013).

Limited efforts have been made to determine important areas for sea turtles within the marine environment, such as in the Arabian region (Pilcher et al., 2014), the Caribbean for hawksbill sea turtles (Nivière et al., 2018), and the Indian Ocean for green sea turtles (Hays et al., 2014). However, these studies have typically been conducted on a smaller spatial scale compared to regional management units, which are spatially defined areas hosting sea turtle populations with distinct genetic, demographic, and behavioral characteristics (Wallace et al., 2010). In the Mediterranean, previous studies have aimed to delineate important foraging habitats for sea turtles, offering either a general overview based on literature synthesis (e.g., Hawkes et al., 2009) or focusing on specific foraging grounds (e.g., through genetic analyses, Clusa et al., 2014). While there's a consensus that climate change could impact sea turtle distribution (Poloczanska et al., 2009; Hawkes et al., 2009), research evaluating how climate change projections might alter the distribution of potential foraging habitats on a broad scale remains limited (Payne et al., 2016) (but see Patel et al., 2016; Maffucci et al., 2016).

In this study, my aim was to delineate important foraging habitats for loggerhead sea turtles (*Caretta caretta*) in the Mediterranean basin. The loggerheads in the

Mediterranean face numerous anthropogenic pressures at sea, highlighting the need for their protection (Rees et al., 2013). To achieve this goal, I compiled a digital database of all published data on foraging individuals collected through satellite telemetry in the Mediterranean region. Using this dataset, I developed and applied a modeling framework to identify climatically suitable marine habitats under current conditions, focusing on two distinct life stages of loggerheads: juveniles and adults. Additionally, I explored potential shifts in these habitats due to climate change. This approach, which considers both life-cycle specific and climatically stable habitats of sea turtles, could provide new insights into the spatial configuration of the species' habitats and valuable information for future conservation planning that accounts for the impacts of climate change.

B.2 Methodology

I applied the following methodology, in order to determine important foraging areas for loggerhead sea turtles in the Mediterranean. At first, I compiled a digital database based on collected and digitized data of satellite tracked sea turtles, juvenile and adult individuals foraging. As a second step I extracted data of sea surface temperature (SST) with which I constructed a set of bioclimatic variables. Based on previously collected information I developed a series of climatic niche models for the different life stages and with their final projections I was able to produce maps of climatically suitable areas for the species under current and future conditions.

Species presence data

I performed an extensive literature review in relevant scientific papers and grey literature (e.g., technical reports, conference proceedings, book chapters) included in the search engine of Google Scholar, in order to collect presence information of juvenile loggerhead sea turtles in the Mediterranean. The search strategy involved the terms: (“marine turtle*” OR “sea turtle*”) AND “Mediterranean” AND (“subadult*” OR “juvenile*” OR “immature*”). I identified 248 references for juvenile satellite-tracked sea turtles by July 2020. I only included sources that met the following criteria: i) the geographical extent of the provided data should be within the Mediterranean Sea, ii) data should have been obtained through satellite telemetry for greater accuracy and precision in spatial occurrence information, iii) spatial information should be provided in the form of a map or coordinates, and iv) sea turtles caught should have been alive and healthy to maximize the likelihood that they actually used the area for foraging and minimize the possibility of being carried away passively due to injury. For sources that did not explicitly mention tracked individuals as juveniles, a threshold value based on the reported curved carapace length (CCL) was used to select presence data. Individuals with a CCL equal to or less than 66.5 cm were defined as juveniles, representing the minimum of the range of means of the size of loggerhead sea turtles found nesting in the Mediterranean (Casale et al., 2018). The size of individuals ranged from 26 cm to 66.5 cm CCL. Individuals above 40 cm CCL are considered subadults, capable of swimming more independently of sea currents (Casale et al., 2018). However, due to unclear distinctions and complexity among different life stages, individuals both above and below 40 cm CCL were included to avoid setting arbitrary thresholds. Therefore, the search yielded 10 source papers [list of papers; Supp. Methods], including data for 51 juvenile loggerhead sea turtles.

The collected tracks of juvenile sea turtles were georeferenced and digitized using ArcGIS 10.1 (ESRI, 2011). Initially, the entire track line was digitized. Then, to convert the line to presence points, the digitized route was overlaid with a grid of cell size $0.0625^{\circ} \times 0.0625^{\circ}$ (approximately 7km x 7km), consistent with the resolution of climatic data (see section 2.2). If the tracked line intersected a cell of the grid, a presence point was assigned to the centroid of that cell. This process resulted in 3105 presence points for juvenile sea turtles.

On what concerns adults, presence points were derived from 126 satellite-tracked foraging individuals, extracted through a literature review following similar procedures and rules as for juveniles. A total of 1300 references concerning satellite-tracked sea turtles in the Mediterranean were identified and reviewed [list of papers; Supp.

Methods]. The extracted locations of foraging adult loggerheads were georeferenced and digitized. For data on post- or pre-nesting migration, the end or start point of the route that each tracked individual followed to reach the foraging area was considered as a presence point. When multiple satellite telemetry points were provided for a tracked animal exhibiting foraging behavior, the presence point was determined as the centroid of the 50% data distribution isopleth derived from kernel density estimations. If a specific point was indicated as the location of a foraging turtle, this information was extracted for use as a presence point.

Climatic data

I obtained the climatic information from the Centro Euro-Mediterraneo sui Cambiamenti Climatici (CMCC), which provided climatic data on SST for the Mediterranean region (Cavicchia et al., 2015). The dataset included historical and projected mean daily SST data covering the Mediterranean Sea for the period from 1950 to 2100, at a 0.0625° spatial resolution. Present climatic conditions were defined based on SST data for the period of 1991 – 2020, while future climatic conditions were based on SST data covering the period of 2051 – 2080, based on projections of the Fifth Assessment Report of the Intergovernmental Panel on Climate Change and the rcp8.5 worst-case emission scenario.

I used year-round SST data for juveniles for the construction of the bioclimatic variables, as they actively forage during the whole year (Bolten et al., 2003; Hawkes et al., 2009), whereas for adults, that forage areas during all year, except for their reproduction and post- and pre-migration phase (Rees et al., 2013), I used SST data from September (i.e., after the completion of the nesting season) to March (i.e., before the beginning of pre-nesting migration).

As a next step, I constructed bioclimatic variables based on SST data (sensu (Hijmans et al., 2011) so as to have an ecological meaning for sea turtles, whose viability is linked to temperature (Davenport, 1997; Mrosovsky, 1980). Bioclimatic variables were constructed in R studio (version 4.0.0), using `ncdf4` (Pierce, 2019), `raster` (Hijmans & Eten, 2012) and `dismo` packages (Chambault et al., 2021). I used the nine bioclimatic variables relevant to temperature: Mean annual temperature, Mean diurnal range, Isothermality, Temperature seasonality, Max temperature of warmest month, Min temperature of coldest month, Temperature annual range, Mean temperature of warmest quarter and Mean temperature of coldest quarter. There are no previous studies that use climatic niche models for assessing sea turtle distribution suggesting the usage of specific ones (Chambault et al., 2021; Pikesley et al., 2015), therefore, I applied here a principal component analysis (PCA) to produce a number of new predictors, based on the `RStoolbox` package (Leutner et al., 2022), that allowed to capture the grand majority of the variance of the bioclimatic variables (Tourne et al., 2019). I chose the first three axes of the PCA (accounting for 99.4% of data variability, Fig. S1) and used them as predictor variables in the models, a choice which was based on the selection of principal components with an eigenvalue greater than the value one (Table S2) (Cliff, 1988).

Climatic suitability models

To determine the important foraging areas for juvenile and adult loggerhead sea turtles, a series of climatic niche models with an ensemble modeling approach, as to ensure the best predictability and mitigate the uncertainty associated with the selection of a single model (Hao et al., 2019). This approach combines different algorithms to consider both simple and complex models in the final output of climatic suitability (Le Heron, 2006). This method was developed using the sdm package in R (Naimi and Araujo, 2016). The algorithms used herein included Generalized Linear Models (GLM), Generalized Additive Models (GAM), machine-learning Random Forest (RF), and Multivariate Adaptive Regression Splines (MARS).

Since reliable data on the true absence of the species were unavailable, cells with no presence records were used to extract potential pseudoabsences. Pseudoabsences were randomly selected with a standard distance (buffer) away from the presence data. By applying alternative distances (3, 5, 8, and 10 cells away from presence data), it was observed that as the distance increased, the performance of the models improved, reaching a plateau at a distance of 8 cells (Table B.S1). Therefore, a buffer of 8 cells was used as the threshold above which pseudoabsences were sampled. A total of 3105 pseudoabsences were selected for juveniles, as an equal number of presence and absence points is suggested for large datasets (Barbet-Massin et al., 2012). For adults, a set of 1000 pseudoabsences was selected, as recommended for low prevalence datasets (Barbet-Massin et al., 2012). To avoid sampling bias, ten random sets of pseudoabsences were sampled for each of the two life stages.

To assess the predictive accuracy of the models, a ten-fold cross-validation was applied. For the evaluation of the models, we used the Area Under the Curve (AUC; (Fielding and Bell, 1997)) and the True Skill Statistics (TSS; (Allouche et al., 2006)). The final model was produced as the mean value of probabilities given by all cross-validated models and ten random sets. It should be noted that the final ensemble models exhibited a very good predictive accuracy for juveniles and adults, based on both metrics (AUC equal to 0.91 for juveniles and 0.82 for adults; TSS equal to 0.75 for juveniles and 0.62 for adults).

At last, I converted the final model outputs, which represented continuous distributions, to binary ones (presence-absence maps) based on the threshold of maximization of the True Skill Statistic (TSS), which is a method frequently recommended in the literature (Comte, 2013; Liu et al., 2016). I estimated changes between present and future distributions by comparing the differences in the number of cells with a projected sea turtle presence for each raster. Presence in neritic and oceanic grounds was determined using the 200m isobath adapted from the General Bathymetric Chart of the Oceans - GEBCO_2014, version 20150318 (https://www.gebco.net/data_and_products/gridded_bathymetry_data/). It is known that foraging grounds are often frequented by both juvenile and adult loggerhead sea turtles, especially when subadults begin approaching neritic grounds for feeding (Clusa et al., 2016). To identify possible common foraging grounds, overlapping surfaces between juvenile and adult potential distributions in the Mediterranean Sea were identified. Specifically, rasters of adult and juvenile present and future potential distributions were overlapped using the ArcGIS 10.1 environment.

Using the projections of climatically suitable habitats generated under present and future climate conditions, I spatially delineated the important foraging areas in the

region. In this context, important foraging areas were defined as sites capable of hosting climatically suitable foraging grounds for both juvenile and adult loggerhead sea turtles under both current and future conditions.

B.3 Results

Delineation of potential foraging areas under present-day conditions

The analysis revealed that foraging areas for juvenile loggerhead sea turtles were widespread, encompassing 56% of the entire Mediterranean basin. These areas predominantly spanned the central and western parts of the study area, with the majority (73%) located in oceanic waters. Additionally, they extended across the Ionian and Aegean Seas (Figure B.1a). Conversely, foraging areas for adult loggerheads were more spatially restricted, covering 16% of the entire basin, primarily in the eastern and central Mediterranean Sea. Over half (57%) of these areas were situated within the neritic zone (Figure B.1b).

Approximately 6.7% of the Mediterranean surface contains suitable areas for both juvenile and adult loggerhead sea turtles. Two-thirds of these areas were identified within the neritic zone, primarily in the central Mediterranean region (Figure B.3). In addition to sites located in the Tunisian plateau and the northwestern Adriatic Sea, suitable areas for both life stages were also identified along the western coasts of Turkey and the northern Aegean Sea in the eastern Mediterranean, as well as along the Spanish and French coasts in the western Mediterranean. The remaining one-third (33%) of common foraging grounds were found in the oceanic zone, predominantly in the Tyrrhenian Sea and the area near Sicily in the central Mediterranean.

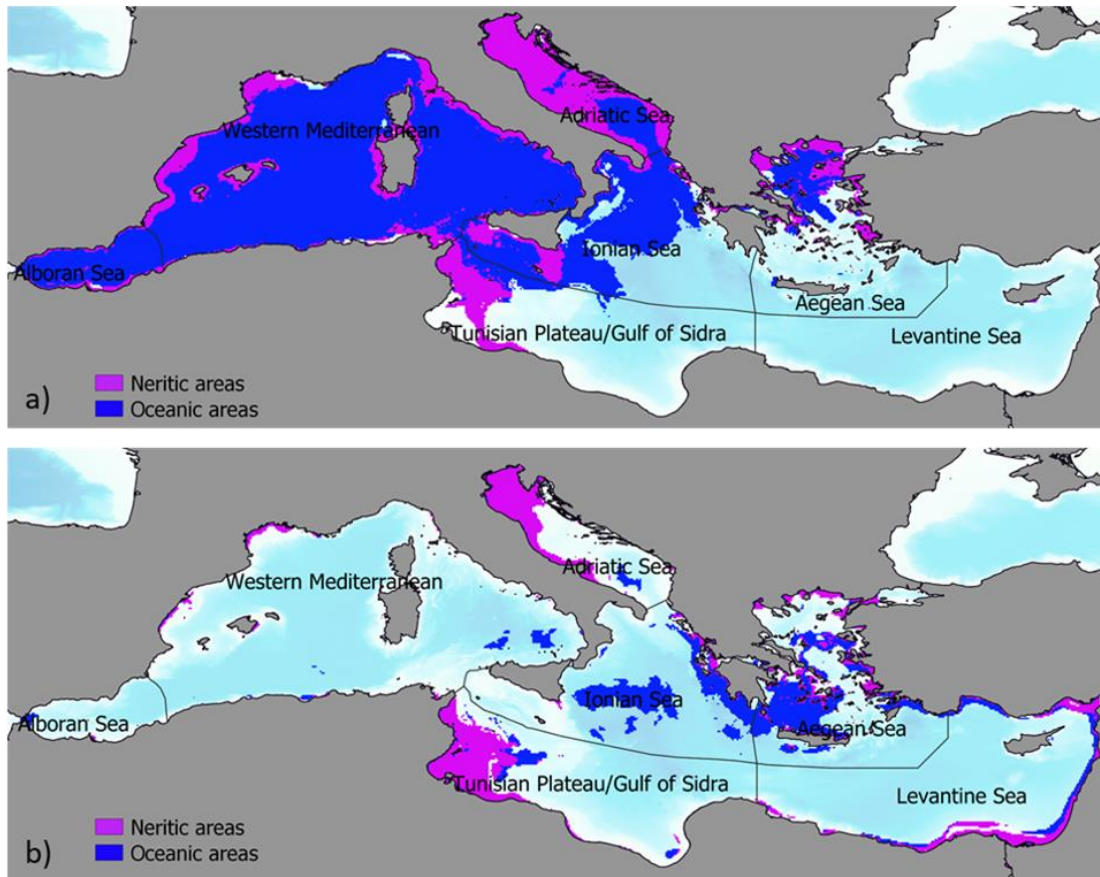


Figure B.1: The distribution of foraging grounds of (a) juvenile and (b) adult loggerhead sea turtles, *Caretta caretta*, under present (1991-2020) climatic conditions across the Mediterranean Sea. Neritic grounds are colored in purple, while oceanic ones are colored in

dark green. Marine ecoregions (sensu (Spalding et al., 2007)) comprising the Mediterranean Sea are delineated by black dashed lines.

Assessment of potential foraging areas under climate change

The models indicated a redistribution of juvenile foraging grounds, both within the neritic and oceanic zones, while the overall coverage remained relatively stable (Figure B.2a). By 2080, it is projected that new suitable habitats, covering a total of 5% of the Mediterranean, may emerge in the Aegean Sea, the Ionian Sea (eastern Mediterranean), and the Gulf of Gabes (central Mediterranean). These gains would offset the loss of sites currently identified as suitable, primarily in the Tunisian plateau and the area near Sicily in the central Mediterranean (resulting in a loss of 6% of the Mediterranean coverage) (Figure B.S2a).

The future climate is anticipated to favor the expansion of foraging grounds suitable for adult loggerhead sea turtles, increasing their coverage from 16% to 19% of the entire Mediterranean surface. This increase results from a notable redistribution of sites across the basin. While a significant portion of the projected suitable habitats is expected to remain stable, covering 11.8% of the Mediterranean, potential new suitable sites, encompassing an additional surface area of 6.8% of the Mediterranean, are likely to emerge in the future (Figure B2b). Some of these suitable areas are projected to be located in regions with limited previous coverage, such as the Balearic Islands, while others are expected to expand, such as suitable areas in the Tyrrhenian Sea (Figure B.2b). The analysis also revealed a potential shift in the distribution of foraging habitats towards the western Mediterranean Sea. However, approximately one-fourth of the current foraging sites may no longer support suitable conditions in the future; particularly critical oceanic sites currently located in the central Mediterranean and the southern Ionian Sea might experience contractions (Figure B.S2b).

In summary, the coverage of future neritic suitable sites is projected to remain stable across the entire Mediterranean basin (Figure B.2b). Conversely, oceanic areas suitable for adult loggerheads, currently covering 7% of the Mediterranean, are expected to increase their coverage to approximately 10% of the total marine surface of the Mediterranean, with more significant changes occurring in the western part of the basin (Figure B.S3).

For foraging areas capable of hosting both adult and juvenile loggerheads, their coverage is expected to increase in the future from 7% to 11% of the Mediterranean basin. These new areas are projected to be situated in both the western (Balearic Islands, Tyrrhenian Sea) and eastern Mediterranean (Ionian and Aegean Sea). This increase is primarily driven by the projected expansion of oceanic sites in the western Mediterranean (i.e., the Balearic Islands and the Tyrrhenian Sea) and the eastern part (i.e., the Ionian and Aegean Sea; Figure B.S3b). However, neritic areas in the Tunisian plateau and the Spanish coasts are likely to lose their current climatic suitability for hosting both life stages in the future.

In general, significant areas where both juvenile and adult loggerheads are predicted to coexist under both current and future conditions are sparsely distributed throughout the Mediterranean basin, covering 3% of the sea's surface. These areas are predominantly located in the neritic zone, accounting for 77% of the coverage. Our analysis highlights that the northwestern Adriatic Sea in the central Mediterranean hosts an extensive

important foraging area. Similarly, smaller important sites were identified along the coasts of the Aegean and Ionian Seas in the eastern Mediterranean, the coasts of the Tunisian shelf in the central Mediterranean, the Gulf of Lions in France, and the Tyrrhenian Sea in the western Mediterranean (Figure B.S3c).

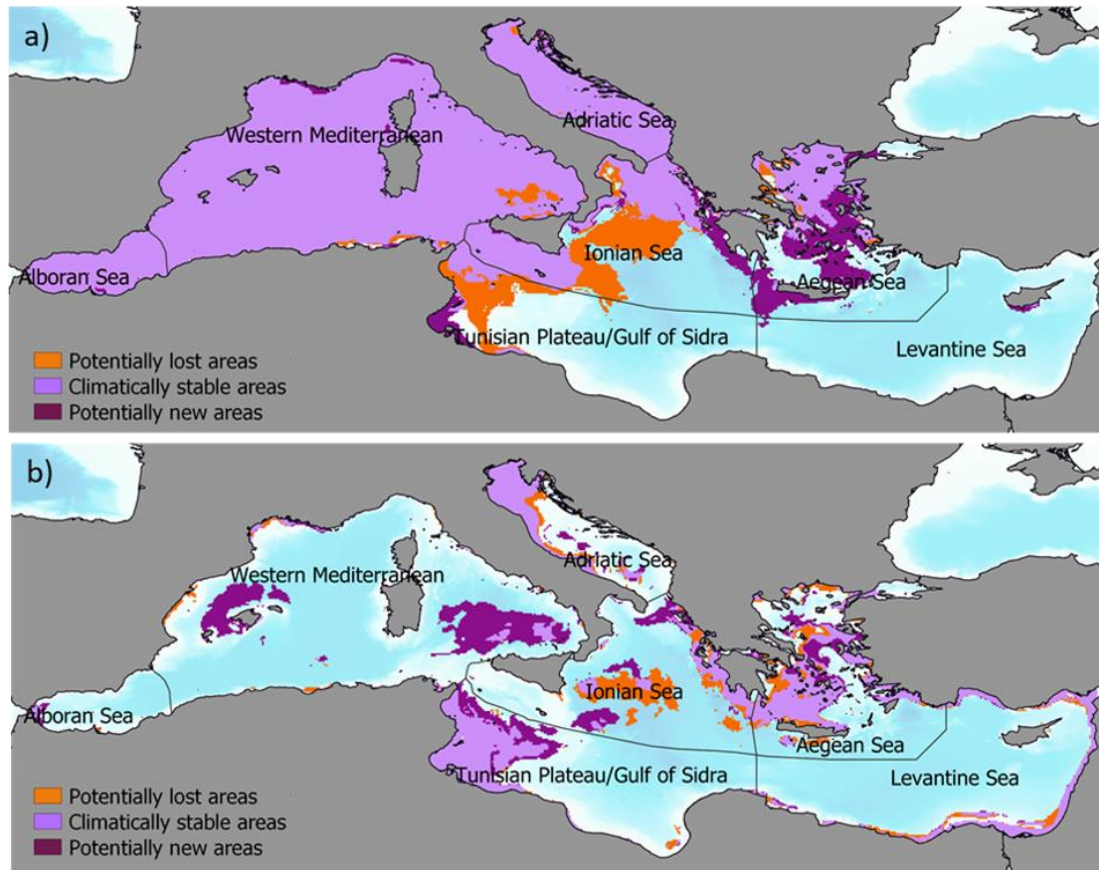


Figure B.2: The distribution of foraging grounds of (a) juvenile and (b) adult loggerhead sea turtles, *Caretta caretta*, under present (1991-2020) and future climatic conditions (2051-2080) across the Mediterranean Sea. Areas that will persist on supporting foraging both in the present and future conditions are delineated in pink color, while new potential foraging areas are in green. Present areas that might no longer support foraging in the future are colored in dark red. Marine ecoregions (sensu (Spalding et al., 2007)) comprising the Mediterranean Sea are delineated by black dashed lines.

The future climate is likely to favor the expansion of foraging grounds suitable for adult loggerheads, which were found to increase in cover from 16% to 19% of the entire Mediterranean basin. Actually, this increase was the result of a notable redistribution of sites located throughout the basin. While a large portion of the projected suitable habitats would remain stable (covering 11.8% of the Mediterranean), potential new suitable sites, covering an additional surface of 6.8% of the Mediterranean, would probably emerge in the future (Fig. B.2b). Some of these suitable areas were projected to be hosted in regions with limited previous cover such as the Balearic Islands while others were predicted to be expanded such as suitable areas in the Tyrrhenian sea (Fig. B.2b). This analysis further revealed a likely shift in the distribution of foraging habitats towards the western Mediterranean Sea. Still, approximately one fourth of the current

foraging sites may no longer support suitable conditions in the future; particularly critical oceanic sites currently found in the central Mediterranean and the southern Ionian Sea might experience contractions (Fig. B.S2b).

Overall, the coverage of future neritic suitable sites is expected to remain stable throughout the entire basin (Figure B.2b). Conversely, oceanic areas suitable for adult loggerheads, currently covering 7% of the Mediterranean, are projected to increase their coverage to approximately 10% of the total marine surface of the Mediterranean, with more notable changes occurring in the western part of the basin (Figure B.S3).

Regarding foraging areas capable of hosting both adults and juveniles, their coverage is expected to increase in the future from 7% to 11% of the Mediterranean basin. These new areas are predicted to be located in both the western (Balearic Islands, Tyrrhenian Sea) and eastern Mediterranean (Ionian and Aegean Sea). This increase is primarily driven by a projected expansion of oceanic sites in the western Mediterranean (i.e., the Balearic Islands and the Tyrrhenian Sea) and the eastern part (i.e., the Ionian and Aegean Sea; Fig. B.S3b). However, neritic areas in the Tunisian plateau and the Spanish coasts are expected to lose their current climatic suitability for hosting both life stages in the future.

Overall, significant areas where both juvenile and adult loggerheads are predicted to coexist under both current and future conditions are sparsely distributed throughout the Mediterranean basin, covering 3% of the sea's surface. These areas are mainly located in the neritic zone, accounting for 77% of the coverage. Analyses highlighted that the northwestern Adriatic Sea in the central Mediterranean hosts an extensive important foraging area. Similarly, smaller important sites were identified along the coasts of the Aegean and Ionian Seas in the eastern Mediterranean, the coasts of the Tunisian shelf in the central Mediterranean, the Gulf of Lions in France, and the Tyrrhenian Sea in the western Mediterranean (Fig. B.S3c).

B.4 Discussion

This analysis delineated critical foraging grounds for juvenile and adult loggerhead sea turtles under both present and future conditions in the Mediterranean Sea. While juveniles' habitats were primarily predicted in the central and western Mediterranean, adults' habitats dominated the central and eastern parts of the basin. An encouraging outcome of this study was the projected increase in suitability for adult foraging sites, with a projected shift of adult foraging grounds towards the western Mediterranean. For juveniles' foraging areas, a relative stability was observed with a potential redistribution of potential suitable habitats eastward. Overall, our analysis identified several important foraging areas for both life stages which are expected to maintain their climatic suitability.

Models revealed that the future distributions of adults and juveniles might change, in different directions, however. For juveniles, the overall cover of suitable areas would remain relatively stable, with some large areas however gaining and losing suitability in the central and eastern Mediterranean. On the other side, findings revealed new foraging areas at the western Mediterranean in the future for adults, suggesting a potential distribution shift. Their presence at the west Mediterranean has already been observed, however probably at lower abundances (Carreras et al., 2004; Luschi et al., 2018). Their highly motile behaviour could prove adaptive and help them search for more suitable habitats avoiding unfavorable climatic conditions (Luschi et al., 2003; Hawkes et al., 2009), mediated possibly by the degree of their fidelity to certain foraging (Casale et al., 2018; Casale et al., 2012). Still, evidence suggests species show flexibility and could relocate to new foraging sites (Shimada et al., 2020). The passive dispersal of post-hatchlings in new climatically suitable areas could influence the subsequent selection of foraging sites, possibly leading to new colonizations by future generations (Hays et al., 2010).

Keeping track of key neritic areas for the two life stages of loggerheads should be prioritized in order to set up long-term monitoring programs assessing population trends and movement patterns for loggerhead sea turtles (Davenport, 1997). The analysis revealed that adults' main foraging areas were inside the neritic zone, consistent with previous findings (Patel et al., 2015; Luschi & Casale, 2014). Warm neritic waters favor food availability helping mature and immature sea turtles increase their size and satisfy their energy needs (Bolten et al., 2003). In addition, mortality rate in the Mediterranean has been shown to be higher for adults foraging closer to the shore (Schofield et al., 2020). An indicative example consists the Adriatic Sea, a mainly neritic region, which is considered to be a hotspot of risk of fisheries interaction (Lucchetti et al., 2017). However, the northern Mediterranean is much more protected by the Nature 2000 sites, whereas the southern Mediterranean Sea, a neritic region inhabited by sea turtles from nesting rookeries throughout the entire basin (Casale et al., 2018) and predicted to host many foraging grounds shared by adults and juveniles (i.e., at Tunisian Plateau), is actually covered by a limited number of marine protected areas (MPAs) (Rodríguez-Rodríguez et al., 2020).

Apart from near-shore waters, the oceanic zone was highlighted as an additionally important zone for individuals' foraging activity. Immature individuals were predicted to use a vast oceanic foraging area, a finding in agreement with species' behavior mainly exhibited at this life stage, wandering over wide oceanic areas (Cardona & Hays, 2018). However, there is great complexity in different foraging strategies followed by

both smaller and larger juveniles (Peckham et al., 2011), and an absolute distinction seems to be rather ambiguous. Our analysis delineated oceanic areas previously identified by other studies, which used alternative type of data, i.e., bycatch incidents, aerial counts and stranding individuals (e.g., in the western Mediterranean; (Revelles et al., 2007), in the Ionian Sea; (Rees et al., 2017)). Presence of both life stages at oceanic foraging grounds (Schofield et al., 2010) emphasizes the need to better understand to what extent the oceanic environment contributes to their foraging activity and the potential contribution to serve as migratory corridors used by mature individuals in migrations between their breeding habitats and the neritic foraging sites. Protection of these distant foraging areas would need transboundary cooperation of neighboring countries, as some larger areas may be shared by the exclusive economic zones of two or even three states or areas could be hosted within the international waters (Petersen-Perlman et al., 2017).

Previous research has utilized distribution models based on various climate-related factors to determine sea turtle species ranges (Elith and Leathwick, 2009; Chambault et al., 2021; Pikesley et al., 2015), still, I have to acknowledge the existence of additional environmental factors (e.g., SST and ocean currents circulation patterns and/or primary productivity) and behavioral traits (e.g., site fidelity; (Schofield et al., 2010), species interactions; (Spotila, 2004)) that could also affect the distribution of foraging sea turtles in the future. Additionally, gaps in published information may limit our ability to identify other potential foraging areas. For instance, there's a shortage of satellite telemetry data for juveniles in the eastern Mediterranean, although other studies using different data types suggest this region may be utilized for foraging (Encalada et al., 1998). Future studies should aim to validate findings with additional telemetry data when available. Finally, in order to address the arising uncertainty, an integrated approach was employed, utilizing ensemble modeling, alternative sets of pseudo-absences, and different accuracy metrics (Elith and Leathwick, 2009).

Attempting to delineate the potential climatic impacts on marine ecosystems is crucial, no matter the level of uncertainty it embeds, it represents a useful tool for long-term conservation and management strategies (Learmonth et al., 2006). For sea turtles, a marine megafauna species with a greatly complex biology, whose persistence depends both on land and marine (neritic and oceanic) habitats, identification of climatically stable, life-stage specific habitats represents an important first step for present and future conservation planning (Corrigan et al., 2014), which could support the spatial dimension of systematic conservation planning of this species and its marine habitats. Along with that, anticipated shifts in habitat suitability for different life stages due to climate change can provide valuable insights to inform adaptive management strategies in a changing environment.

Chapter C. Diving into warming oceans: assessing 3D thermally suitable foraging areas of loggerhead sea turtles under climate change.

Publication:

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C.1 Introduction

As climatic conditions shift, the abiotic and biotic conditions at habitats across the current distribution of organisms may become partly or fully unsuitable. Consequently, a mounting body of evidence reveals distribution shifts for many marine species in response to climate change (Poloczanska et al., 2013; Pecl et al., 2017; Alabia et al., 2018). Range shifts represent a critical mechanism offering many species the ability to avoid extinction in front of climate change (Donelson et al., 2019). Scientists attempt to project future key habitats, however, with the vast majority of projections being based on present and future sea surface temperature (Robinson et al., 2017), ignoring the fact that many marine organisms move horizontally but also vertically in the marine space (Brierley, 2014).

Many organisms, such as marine megafauna, constantly move among different habitats of differentiated depth (Schaber et al., 2022; Derville et al., 2022), while others inhabit and forage in habitats of different bathymetry among distinct life stages, such as benthic fish with a pelagic larval phase (Leis & McCormick, 2002; Petitgas et al., 2013). In addition, crucial environmental factors for species persistence and habitat use vary with depth (Venegas-Li et al., 2018). As climate change is expected to occur disproportionately at different depths (Brito-Morales et al., 2020) and affect species vertical migration, three-dimensional habitats of marine organisms may be subjected to changes in the future (Jorda et al., 2020). Therefore, the delineation and protection of habitats promoting the vertical coherence across different depths, thereby minimizing species exposure to climate change, present a more holistic and viable conservation strategy (Brito-Morales et al., 2022). Still, identifying critical marine habitats by considering the three-dimensionality of the seascape remains a great conservation challenge and only a few publications attempt to identify vertically coherent conservation areas (Doxa et al., 2022; Brito-Morales et al., 2022).

As more historical data and scenario projections of changes in ocean climate are becoming available for various depths, new perspectives, opportunities and challenges arise in species distribution modelling and marine spatial planning (Levin et al., 2018). Currently, however, two-dimensional approaches are predominantly used, with marine scientists often constrained to select one bathymetric level to represent the habitats utilized by species, which most commonly is the sea surface (Zintzen et al., 2010; Costello et al., 2015; Chatzimentor et al., 2021). Although often unavoidable, this is an over-simplification for marine animals that exhibit movements along the water column across their life cycle, such as Chondrichthyes (Doherty et al., 2019), or that routinely use different depths for daily foraging, such as marine megafauna (Fortune et al., 2020). Considering the uneven warming of the sea across depths (Brito-Morales et al., 2020), temperature projections from multiple bathymetric levels in species distribution models could contribute to be enhancing our conservation potential (Queirós et al., 2016).

An ideal species to assess the importance of the vertical dimension in conservation planning are sea turtles. They use various and distinct habitats for breeding, development, and foraging, which span across various depths (Bolten et al., 2003), using habitats along a bathymetric gradient during a single day but also during different

phases of their lifecycle (Casale et al., 2018). Adults usually forage on benthic organisms and on prey found in the water column, while emerge very often on the sea surface to breathe, rest and bask (Iverson et al., 2017). Before reaching maturity, juvenile sea turtles usually forage in the water column of oceanic waters (Bolten et al., 2003). Both juvenile and adult life stages are expected to be subjected to range shifts, altered foraging activities or even phenological shifts (Poloczanska et al., 2009; Almpandou et al., 2019). Indeed, empirical evidence (Girard et al., 2021; Mancino et al., 2022; Santidrian Tomillo et al., 2022; Cardona et al., 2023) as well as projections (Dudley & Porter, 2014; Patel et al., 2021) suggest a poleward expansion of habitats used by sea turtles in the Atlantic Ocean and Mediterranean Sea and contraction of habitats used in the Eastern Pacific Ocean (Willis-Norton et al., 2015; Wallace et al., 2023). In the Mediterranean Sea, a climate-change hotspot, life cycle specific shifts were projected to include a westward expansion for adults and an eastward expansion for juveniles (Chatzimentor et al., 2021). Still, such modelling efforts have been based solely on sea surface warming scenarios (Chatzimentor et al., 2021), however habitats in deeper waters were also predicted to be warming in the region (Danovaro et al., 2018). As Mediterranean marine habitats are in risk due to increasing human pressures along the water column (Fanelli et al., 2021) and sea turtles take advantage of both shallow and deep waters to feed, it is important to identify hotspots of potential foraging which might be vertically cohesive.

To contribute to this conservation challenge, using the loggerhead sea turtles as a model species, I developed and applied a climate niche-based framework, both horizontally and vertically. This framework enabled me to: a) explore 3D habitat suitability for loggerhead sea turtles in the Mediterranean Sea incorporating knowledge on depth-dependent movements and strategies of the species, b) project the suitability of 3D marine habitats under future climate scenarios, and c) assess whether present-day and future suitable areas consistently host habitats spanning over different depths. As a first thing, I developed ensemble models for the two different life stages (i.e., juvenile and adult) of loggerheads by considering layers of 5m, 25m and bottom neritic waters (Kristiansen et al., 2024). Next, I explored the degree of consistency of the identified suitable marine habitats across different depths (i.e., near-surface, deep or water-column zones), and the potential future shifts of these sites due to climate change. This approach could offer an advanced and more holistic understanding over the spatial delineation of the species' habitats at the 3D marine space and useful insights for future conservation planning towards climate-smart conservation networks that would integrate the aspect of bathymetry.

C.2 Methodology

To spatially delineate important foraging areas in various bathymetric layers, I developed and applied a methodological framework that included six key steps: (i) extraction of presence data on juvenile and adult foraging loggerhead sea turtles (for details, please refer to Chatzimentor et al., 2021), (ii) compilation of sea temperature data based on present-day and future projections for 5m, 25m depth and sea bottom

depths layers, (iii) construction of bioclimatic variables for each depth layer, (iv) development of climatic niche models for the different life stages over different depth layers. Next, I (v) identified the overlap of thermally suitable marine habitats for different categories of depth (near-surface, deep and water-column habitats) under present-day and future thermal conditions and (vi) assessed potential changes in the distribution of these suitable, overlapping depth habitats under climate change.

Species presence data

I used presence data extracted from all available satellite track data for loggerhead sea turtles in the Mediterranean Sea as reported in an extensive (>1500 sources) literature review (Chatzimentor et al., 2021) in which collected tracks of juvenile and adult sea turtles were georeferenced and digitized. Based on this review, a digitalized database was compiled, containing a total of 3105 presence points derived from satellite tracks of 51 juveniles and 126 presence points derived from an equal number of adult sea turtles for which spatial information, in the form of a map or provided geographical coordinates, was available. For a post- or pre-nesting migrating adult, the end or start point of the route that it followed to arrive to its foraging area was identified as presence points. Kernel density estimations were also applied to define the centroids of broader surfaces associated with the final location of many tracks (for more details see Chatzimentor et al., 2021).

Climatic data

Climatic data for the Mediterranean region were obtained from statistically downscaled climate projections as part of the EU FutureMARES project (Kristiansen et al., 2024; Kristiansen & Butenschön 2022; doi:10.5281/zenodo.6523926). The dataset was created by bias-correcting and statistically downscaling Earth System and Climate Model simulations from a range (4-8) of CMIP6 model, prior to creating an ensemble dataset that contained the ensemble average along with information on the uncertainty across models. The downscaled dataset provided monthly averaged spatially resolved temperature data at three different depth layers 5m, 25m, and bottom depths, for the historical (1993-2022) and future (2023-2100) period, resolved at 1/12° degree longitude-latitude. This study focused on the Shared Socioeconomic and Representative Concentration Pathway (SSP, O'Neill et al. 2016) SSP5-8.5 (fossil fuel driven future), largely considered as unmitigated case scenario, to assess the risk of climate change. To define present-day climate conditions, I used sea temperature data for the period of 1993–2022 and for the future the period of 2051–2080.

Three depth layers were used to represent the vertical habitats used by juvenile and adult loggerheads. The first two layers (5 and 25m) represented the near-surface habitats while the third (bottom depth to 200 m) represented neritic bottom waters representative for the behavioural and biological attributes of the species. Both juvenile and adult loggerheads are capable of foraging throughout the water column but they only reach the seabed when found in the neritic zone (≤ 200 m depth) (Casale et al., 2018). Larger juveniles are able to reach deeper waters in order to feed (Chimienti et al., 2020). Individuals mainly feed on gelatinous zooplankton in oceanic habitats (water depths > 200 m) and switch to a diet of benthic invertebrates such as molluscs and crustaceans when they recruit to neritic habitats (depths < 200 m) (Hatase et al., 2007).

As large juvenile and adult sea turtles in neritic waters are known to forage at all depths on pelagic and benthic prey (Bolten et al., 2003), I defined ‘water-column’ habitat, as thermally suitable areas where all three depth layers (5m, 25m and neritic bottom layers) overlapped for each life stage (juvenile, adult). Both life stages frequent more surface waters in order to breathe, wander and also forage on pelagic species, so ‘near-surface habitats’ were defined as suitable areas where both 5 and 25m depths overlapped. Finally, ‘deep habitats’ were identified where thermally suitable depths of 25m and bottom neritic waters overlapped, as individuals also rest for extended periods on the seabed during overwintering (Hochscheid et al., 2005) or perform in-water behaviours such as burying themselves under the sand in the seabed (Papafitsoros, 2022).

Adults use foraging areas all year, except during reproduction and post- and pre-migration phases (Rees & Margaritoulis, 2013). So, to define the most representative foraging period, I used sea temperature data from September (i.e., after the completion of the nesting season) to March (i.e., before the beginning of pre-nesting migration). Juveniles exhibit year-round foraging (Bolten et al., 2003; Hawkes et al., 2009) so sea temperature throughout the year was used for habitat suitability modelling.

Based on sea temperature data, I constructed bioclimatic variables (sensu Hijmans et al., 2011) that have an ecological meaning for sea turtles, whose viability and activities are linked to temperature (Mrosovsky, 1980; Davenport, 1997; Pikesley et al., 2015). Bioclimatic variables were constructed in R (version 4.0.0), using `ncdf4` (Pierce, 2009), `raster` (Hijmans & Etten, 2012) and `dismo` packages (Chambault et al., 2021). We used the nine bioclimatic variables relevant to temperature: mean annual temperature, mean diurnal range, isothermality, temperature seasonality, max temperature of warmest month, min temperature of coldest month, temperature annual range, mean temperature of warmest quarter and mean temperature of coldest quarter. Furthermore, I applied a principal component analysis (PCA) to produce several new predictors to capture the grand majority of the variance of the bioclimatic variables (Tourne et al., 2019). The `RStoolbox` package (Leutner et al., 2022) was used to conduct the PCA. The first two axes of the PCA (accounting for greater than 99% of data variability) were chosen for our analysis and used as predictor variables in the models (Table C.S1).

Climatic suitability models

To determine the important foraging areas for juvenile and adult loggerhead sea turtles across each depth layer, I developed a series of climatic niche models, by using several alternative algorithms: Generalized Linear Models, Generalized Additive Models, machine-learning Random Forest and Multivariate Adaptive Regression Spline using the ``sdm`` package (Naimi & Araujo, 2016). For ensuring the best predictability, I applied an ensemble modelling approach, combining outputs of the different algorithms (Heron, 2006) as the mean to limit the uncertainty of the selection of a single model (Hao et al., 2019). This way, overfitting of a model is avoided and the ability of the model to be transferred in time and space is enhanced (Araujo & New, 2006).

Since reliable data on the true absence of the species were unavailable, the cells of no presence records served to extract potential pseudoabsences. Pseudoabsences were randomly selected with a standard distance (buffer) away from the presence data. A buffer of 8 cells was used as the threshold above which pseudoabsences were sampled. A total of 3105 pseudoabsences was selected for juveniles, as an equal number of

presence and absence points is suggested for large number of datasets (Barbet-Massin et al., 2012). A set of 1000 pseudoabsences was selected for adults, as suggested for low prevalence datasets (Barbet-Massin et al., 2012). In order to overcome sampling bias, ten random sets of pseudoabsences were sampled for the two life stages.

To assess the predictive accuracy of the models, a ten-fold cross-validation was applied. For the evaluation of the models, we used the Area Under the Curve (AUC; Fielding & Bell, 1997) and the True Skill Statistics (TSS; Allouche et al., 2006). The final model was produced as the mean value of probabilities given by all cross-validated models and ten random sets. Final ensemble models exhibited a good predictive accuracy for juveniles and adults, based on both metrics (AUC>0.72, TSS>0.53; Table S2). The conversion of the final model outputs that represented continuous distributions to binary, indicative of a presence-absence distribution, was based on the threshold of maximization of TSS, a method frequently used and suggested by the literature (Comte, 2013; Liu et al., 2016).

I identified potential present-day and future distributions of thermally suitable areas for the different layers of 5m, 25m and bottom neritic waters (Fig. C.1). In order to investigate whether thermal suitable areas span across different water depths, defining areas of 3D suitability, I identified overlaps among suitable habitats for the three depth levels, considering near-surface, deep and water column habitats (Fig. C.1). Next, I estimated the change between the potential present-day and future suitable habitats by comparing their spatial distributions and estimated thermal stable sites by calculating their overlapping distributions. I defined as losses, areas that appeared as thermally suitable in the present-day conditions but not under future conditions, whereas gains were areas that were not suitable in the present-day conditions but were projected to be suitable in the future. Thermally stable areas were areas that appeared suitable both for the present-day and the future conditions.

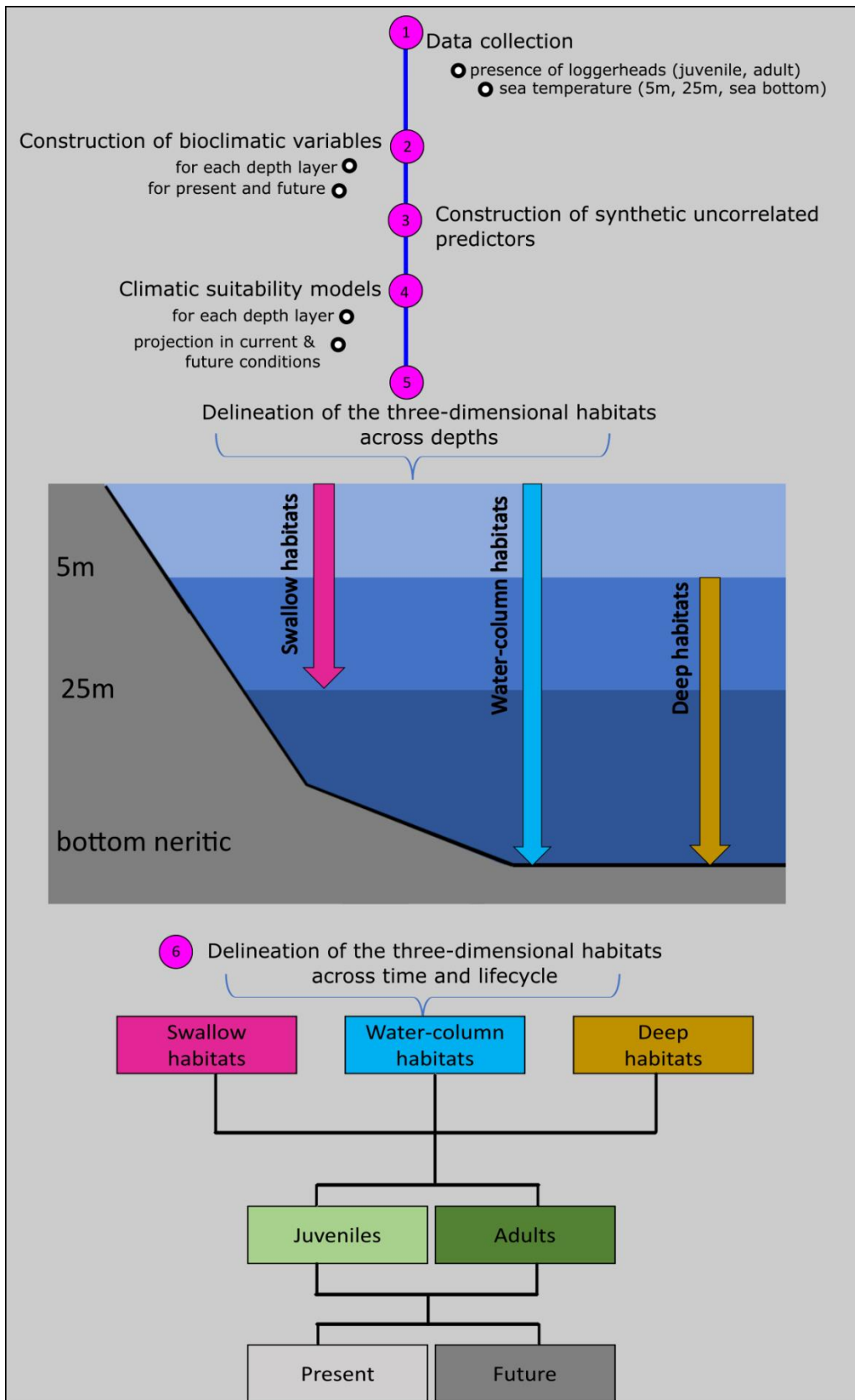


Figure C.1: Flowchart of the methodology followed in order to delineate present-day and future 3D thermally suitable habitats (near-surface, water-column, deep) for adult and juvenile loggerhead sea turtles.

C.3 Results

Distributions of potentially suitable habitats for adult loggerhead sea turtles were similar among single depth layers (i.e., for sea temperatures at 5m, 25m, or bottom) under both present-day and future climatic conditions (Fig. C.2a-c and Fig. C.2d-f). Most suitable areas were predicted to maintain their suitability in the future and were concentrated at the neritic zone both in the North Mediterranean, such as the Balearic Islands (west Med), the northern Adriatic Sea (central Med) and the Aegean Sea (east Med), as well as in the southern Mediterranean, in the coasts of Tunisian plateau (central Med) and the Levantine Sea (east Med) (Fig. C.2a-f).

In contrast, the distribution of suitable habitats for juvenile loggerhead sea turtles differed among the three depth layers (Fig. C.2g-l). When considering the 5m depth or the 25m depth layer, suitable foraging habitats covered the entire western and central Mediterranean Sea, whereas suitable bottom neritic waters were restricted to those of adult loggerheads (Fig. C.2g-k vs Fig. C.2i&l). Under future conditions, the bottom neritic habitats for juveniles were projected to expand from 8.8 to 13.6% of the Mediterranean Sea (Fig. C.2i&l).

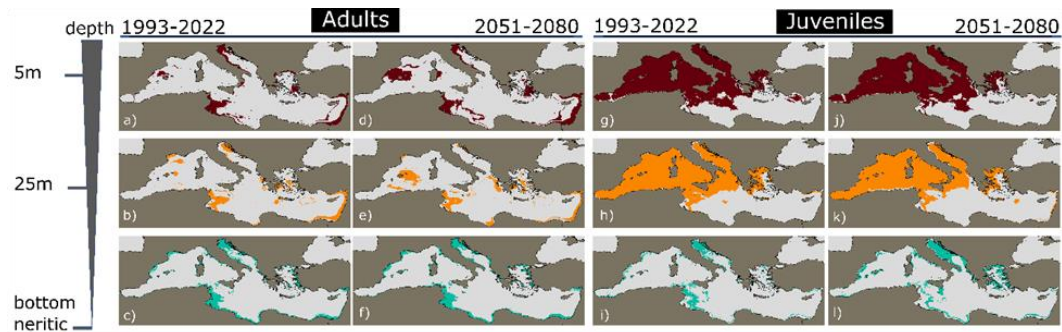


Figure C.2: Potential distribution of thermally suitable foraging areas for 5m, 25m and neritic bottom habitats for adult (a-f) and juvenile (g-l) loggerhead sea turtles under present-day and future conditions in the Mediterranean Sea.

Water-column habitats (i.e., overlap of the three single layer distributions) of adults mainly concentrated in the central and eastern Mediterranean Sea, were distributed at areas of well-known foraging sites such as the north Adriatic Sea, the Tunisian plateau and the coasts of the Levantine Sea (Fig. C.3a). These sites covered a 6.2% and a 6.1% of the Mediterranean surface under present-day and future conditions, respectively (Fig. C.4b). Within the sites of the north Adriatic Sea, the 3D habitats seemed to maintain their thermal suitability in the future (Fig. C.3a).

For juveniles, water-column habitats were concentrated in the north Mediterranean Sea coasts and the Tunisian plateau, covering 6% of the Mediterranean basin under present-day climatic conditions and 8.9% under future climatic conditions (Fig. C.4b). Potential new suitable habitats were projected to occur in the future in the Adriatic Sea, the coasts of North Aegean and sparse areas in the western coasts of west Mediterranean Sea (Fig. C.3b). However, the foraging ground of the Tunisian plateau was predicted to become thermally unsuitable in the future for juvenile loggerheads. The North Adriatic Sea was predicted to remain as thermal stable under future conditions (Fig. C.3b).

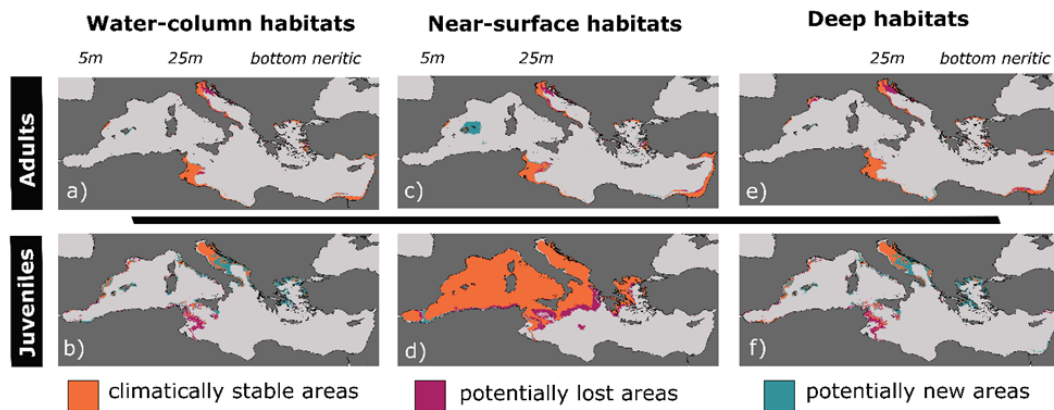


Figure C.3: Water-column habitats, near-surface habitats and deep habitats of juvenile and adult loggerhead sea turtles as a proportion of (a) the potential distribution of all thermally suitable areas and (b) the total percentage cover of the Mediterranean Sea.

For adults, near-surface and deep habitats were characterized by a similar distribution as water-column habitats (Fig. C.3a,c,e), with the exception of a potential future western expansion of near-surface habitats and, in particular, including coastal waters of the Balearic Islands (Fig. C.3c). Near-surface and deep habitats for adults covered 7.8% and 7.4% of the surface area of the Mediterranean Sea, respectively (Fig. C.4b).

For juveniles, near-surface habitats covered half of the Mediterranean Sea (52.6%; Fig. C.4b) spanning across the entire western and central Mediterranean Sea (Fig. C.3d). The vast majority of those near-surface habitats were projected to be suitable in the future, except areas in the southern-central limit of the present-day distribution (Fig. C.3d). Juveniles' deep foraging habitats covered 6.6% of the Mediterranean Sea (Fig. C.4b) and had a similar distribution as suitable water-column habitats (Fig. C.3b,f). Potentially new deep habitats for juveniles were projected to occur mainly in the Adriatic Sea and the North Aegean coasts while losses were projected for the foraging ground of the Tunisian plateau (Fig. C.3f).

Overall, I observed a large overlap of near-surface, deep and water-column habitats for adults over the whole Mediterranean Sea under both present-day and future conditions (Fig. C.3). The coverage of the three types of 3D habitats was comparatively similar, covering respectively 38%, 36% and 30% of the potential distribution of suitable habitats for adults at present-day (33%, 26% and 23% respectively in future distributions) (Fig. C.4a). Contrarily, near-surface habitats for juveniles prevailed in cover in comparison to deep and water-column habitats, with the first covering 82% of the potential present-day distribution (respectively 76% for future distribution), while

the latter sharing a percentage of 10% and 9% respectively (15% and 14% respectively in future distributions) (Fig. C.4a).

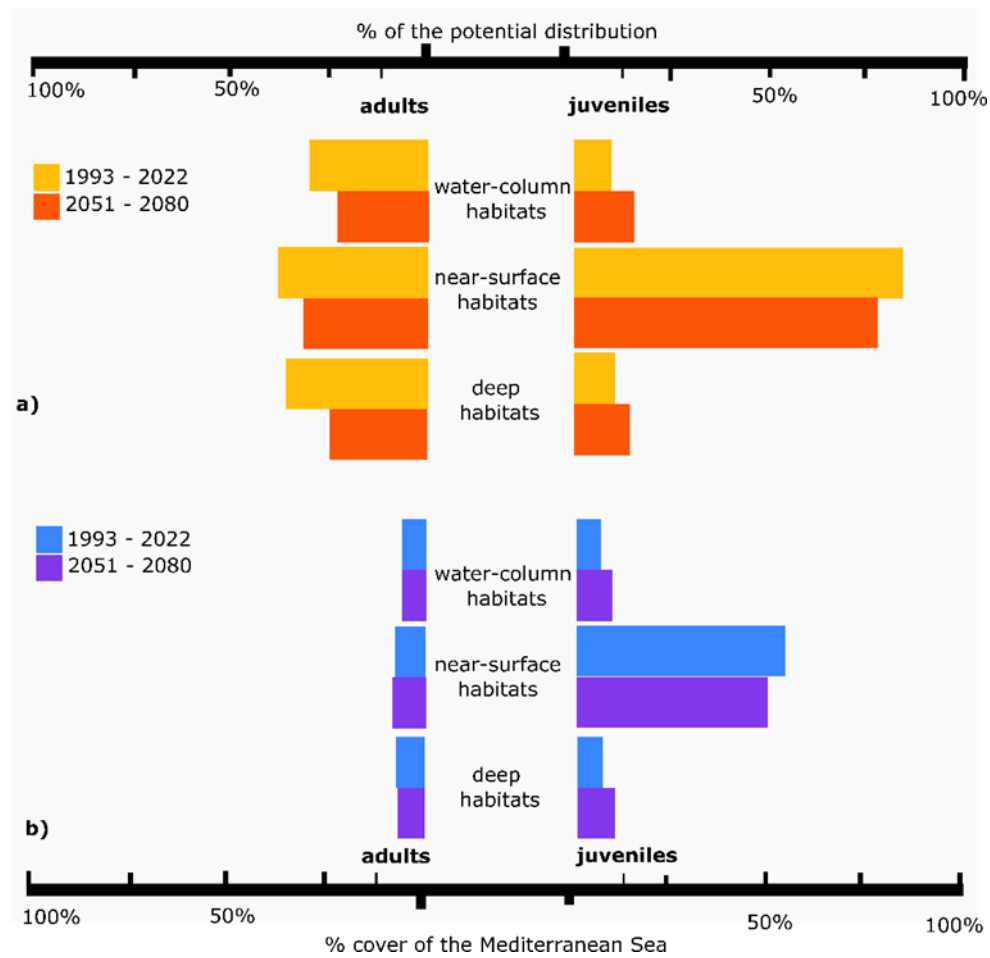


Figure C.4: Water-column habitats, near-surface habitats and deep habitats of juvenile and adult loggerhead sea turtles as a proportion of (a) the potential distribution of all thermally suitable areas and (b) the total percentage cover of the Mediterranean Sea.

C.4 Discussion

This study aimed to investigate potential thermal suitability of loggerhead sea turtles' habitats across various depths, and to explore whether suitability was distributed consistently at different depths. This analysis delineated a range of thermally suitable habitats near the surface, across the water column and in deeper waters, with potential suitability distributions being variant between juvenile and adult loggerheads for different depths. In front of the projected climate change, projected changes in thermal suitability of each depth layer produced altered patterns of thermal coherence, with gains and losses of favourable thermal conditions spanning across their distribution in the Mediterranean. Differences obtained suggest that the parameter of bathymetry should be incorporated in assessing the distribution of suitable habitats for marine species, using either the entire water-column or even part of it, however this task requires caution.

Similar to sea turtles, there are many marine organisms that utilize the whole water-column such as sharks (Coehlo et al., 2015; Doherty et al., 2019), while other animals exhibit much more restricted depth ranges in the water column, such as micronekton and zooplankton (Brierley, 2014). Ecology and behaviour of a species largely determine the selection of bathymetric layers. Here I illustrated how the selection of particular bathymetric zones, as opposed to others, can influence projections of suitable habitats or alternatively the combination of various depth-specific distributions might produce different results. For instance, combining 5m, 25m and bottom neritic temperature projections resulted in a distribution pattern of limited oceanic areas thermally suitable for adults, opposed to previous analyses utilizing the sea surface layer (Almpanidou et al., 2021; Chatzimentor et al., 2021). Moreover, juvenile sea turtles displayed distinct spatial patterns of near-surface 3D space compared to deep and water-column habitats, with the former covering broader areas in the western and central Mediterranean waters and the latter being spatially restricted.

Even though sea turtles frequently move around the seabed to feed, previous efforts have not yet considered deeper layers in spatial projections. Previous research findings have reported the use and suitability of coastal foraging areas, primarily in the central and eastern Mediterranean Sea for adults (Mazor et al., 2016; Casale et al., 2018; Haywood et al., 2020; Almpanidou et al., 2021) and mainly in the west and central Mediterranean for juveniles (Chimienti et al., 2020; Chatzimentor et al., 2021). The location and extent of the thermally suitable foraging areas identified here were consistent to a large extent with previous results obtained when only sea surface temperatures were considered (Almpanidou et al., 2021; Chatzimentor et al., 2022). The extent and distributions of depth-specific habitats depended on the life stage, reflecting the distinct foraging and life-history strategy adopted by juvenile and adult loggerheads. Despite possessing a range of foraging behaviors, adults use neritic habitats and mostly frequent them with increasing body size (Reich et al., 2007; Hatase et al., 2007). This model predicted that a variety of depth-specific habitats could be suitable for adults, with whole water-column prevailing over a mosaic of near-surface or deep habitats. On the other hand, juveniles have been reported in the oceanic zone but have been less

frequently observed in very deep waters (Freitas et al., 2018; Chimienti et al., 2020). This model predicted large areas of suitable habitat including not only shallow waters but also the deeper layers of the water column. Some restricted yet important habitats were identified that spanned the entire water-column, mainly in the northern Mediterranean basin, potentially reflecting coastal areas where larger-sized juveniles reach to forage on benthic and pelagic prey (Blasi et al., 2017).

Dissimilarities among different bathymetric habitats were observed in areas that will potentially gain or lose thermal suitability in the future. For instance, juveniles were predicted to expand their water-column habitats eastwards. However, the southeast edges of near-surface habitats would probably become unsuitable in the future. In general, populations of marine species at both polar and equatorial range margins are observed to be undergoing abundance changes, with decreased abundance towards the equatorial side of range (Hastings et al., 2020). Following these observations, it is possible that the potential loss of suitability on the southern edges of the juveniles' predicted distribution could drive a potential reduction in the abundance of loggerheads there (Mancino et al., 2022; Hochscheid et al., 2022). This is also the case with the predicted westward expansion of the thermally suitable habitats for adults, also supported by a growing number of observations of nesting events in western areas (Maffucci et al., 2016; Hochscheid et al., 2022; Mancino et al., 2022; Cardona et al., 2023;). Foraging areas in the west Mediterranean are much less frequented by adult sea turtles than by juveniles (Casale et al., 2018), however if thermal conditions improve in locations such as the Balearic Islands, this might enable adults to persist in the region supporting their reproductive potential (Hochscheid et al., 2022).

In the present study, I used a simplified approach to predict the potential distribution of sea turtle habitats based on a suite of climate variables. However, I acknowledge that there are additional factors affecting the selection and suitability of foraging habitats, as for example patterns of ocean current circulation and primary productivity, aspects of behaviour such as site fidelity (Schofield et al., 2010) and species interactions (Spotila, 2004). Loggerheads are known to forage mainly on benthic macroinvertebrates, on pelagic tunicates crustaceans and molluscs, and occasionally on fish. Key prey species may be affected by climate change, as has already been observed for the North Sea, where long-term changes in the abundance of jellyfish species have been linked to climatic signals (Thorpe et al., 2022). Strong associations between ocean productivity, the associated plankton landscapes and turtle distributions have been suggested (Pechham et al., 2011). Future alterations of open-ocean prey abundance may be a critical issue for marine turtles, but this topic has yet received very little attention. I, thus, encourage future studies on distribution modelling of marine turtles to integrate data on prey species. Furthermore, in order to reduce the uncertainty that is inherent to climatic suitability modeling (Elith & Leathwick, 2009), I applied statistical downscaling of an ensemble of estimates from global climate models to increase spatial resolution which is recommended as best practice for examining climate-driven changes in suitable habitats for both terrestrial and marine plants and animals (Storlie et al., 2014; Drenkard et al., 2021). To this direction, I also employed alternative sets of pseudo-absences and different accuracy metrics (such as AUC and TSS). Due to sea temperature projections been restricted to three depth layers, the estimation of habitat

suitability across a full depth continuum, from the surface to the seafloor, was not feasible. This limitation highlights the need for improved habitat projection models, for this and other species. Finally, I highlight the need to produce additional telemetry studies and data for sea turtle presence in the Mediterranean sea in order to corroborate these findings and gain insights for less sampled marine areas in the basin.

For organisms moving along the water-column, it is particularly important to identify the consistency of suitable habitats at different depths (Levin et al., 2018; Doxa et al. 2022; Brito-Morales et al., 2022). However, incorporating different bathymetric zones is not negligible, and uncertainty as well as differences in projected climate-driven changes among different bathymetric habitats, might render this task even more challenging, especially considering the various scenarios of climate change (Thuiller et al., 2019). Projections suggest that well-known foraging areas of sea turtles will preserve their thermal suitability in the future and often, but not always, among different depths. As scientists, managers and policy makers urgently seek for advanced adaptive ways for biodiversity protection, the identification of important areas for highly migratory marine species, like sea turtles, is an essential step to reach future conservation goals (Hays et al., 2019). However, as most marine organisms move along a bathymetric gradient in the open sea, the three-dimensionality of marine space should be incorporated in the designation of spatial management plans. Both existing and newly established marine protected areas hold potential as valuable tools for sea turtle conservation. Global evidence indicates that conservation measures could mediate in halting declines in sea turtle abundance (Mazaris et al., 2017). However, the broad distribution of sea turtles and their extensive movements across seas mean that individuals are unlikely to spend their entire life cycle, or even their adult lives, within these designated areas. While we acknowledge the significance of marine protected areas in enhancing sea turtle protection, safeguarding this highly mobile species requires a more comprehensive conservation approach. Recognizing limitations in protecting every part of their distribution range, prioritizing the delineation of crucial habitats and the establishment of key marine turtle areas becomes essential within this context. Moreover, the impact of climate change, leading to shifts in distribution and habitat loss, may pose additional challenges for efficient spatial management measures (Gissi et al., 2019). Conservation efforts should therefore adopt an adaptive approach, regularly revisiting and updating predictions based on the best available data, methodologies and projections.

Thermal stable habitats identified for loggerhead juveniles and/or adults across the shores of multiple Mediterranean countries highlight the need for transnational cooperation including increased knowledge exchange and common actions for sea turtle conservation (Mazaris et al., 2023). I highly recommend that future research focus on spatially delineating important depth-specific habitats for marine species that would effectively feed into marine spatial planning schemes enriching our insights on the three-dimensionality of ocean habitats. In this regard, depth-specific human activities should also be included, thus producing more robust estimates of spatial impacts of human pressures on marine life than when only surface waters are considered.

Chapter D. Are Mediterranean marine threatened species at high risk by climate change?

Publication:

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D.1 Introduction

As over 1,500 marine species face a serious risk of extinction (IUCN, 2021), conservation policies, such as the Convention on Biological Diversity (CBD), are urging efforts to prevent this and improve their conservation status (Secretariat of the Convention on Biological Diversity, 2010). On top of current local stressors faced by species, climate change will exacerbate the pressure faced by threatened species, pushing them closer to extinction (IPCC, 2014; Delach et al., 2019). Identifying species at high risk will prioritize our conservation efforts towards adapting to climate change (Foden et al., 2019).

The susceptibility of species to climate change is influenced by both their intrinsic vulnerability and the external threats they are exposed to (IPCC, 2014; Jones & Cheung, 2018). Vulnerability primarily stems from inherent biological or ecological traits of the species which determine their ability to cope with changing environmental conditions (Fortini & Schubert, 2017). For instance, ocean acidification would greatly impact particularly species relying on calcification processes (Pacifici et al., 2015). However, their sensitivity could be mitigated by their adaptive capacity, such as a highly mobile nature helping them to relocate away from unfavourable habitats (Lascelles et al., 2014). An additional factor that could elevate their risk to climate change is an increased exposure to altering conditions, for example, rising sea levels may lead to nest inundation for sea turtles, posing a threat to their reproductive success (Poloczanska et al., 2009).

Risk assessments using traits have become widely utilized across various organisms and associated human activities (Dawson et al., 2011; Pacifici et al., 2015). In marine ecosystems, climate vulnerability assessments sparse across several topics such as region-specific or species-specific assessments (Albouy et al., 2020; Hare et al., 2016; Stortini et al., 2015; Mamauag et al., 2013; Chin et al., 2010). Nevertheless, assessing climate risk across larger regions based on a diverse range of threatened species has been limited (but see, Gardali et al., 2012; Lee et al., 2015; Pacifici et al., 2017).

In one of the largest marine biodiversity hotspot such as the Mediterranean Sea (Coll et al., 2010), such climate risk evaluations are essential, as it is forecasted to experience significant climate change impacts (Marbà et al., 2015; Frihy & El-Sayed, 2013). Altering climatic conditions have already affected its marine biodiversity with distributions shifts and habitat degradation been observed (Garrahou et al., 2022; Chatzimentor et al., 2021; Chefaoui et al., 2018; Marbà et al., 2015; Albouy et al., 2013; Albouy et al., 2012). The combined impacts of anthropogenic threats have resulted in a concerning loss of biodiversity, with threatened species in the Mediterranean experiencing population declines (IUCN, 2021).

Herein, I aimed to conduct a climate change risk assessment for the critically endangered, endangered and vulnerable marine species of the Mediterranean Sea as defined by the IUCN Red List of Threatened species, based on the framework of the recent fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC). So, I considered risk to climate change as a function of a species' vulnerability traits (sensitivity and adaptive capacity) in interaction with the level of its exposure to a climate hazard. Most studies use convergent traits of vulnerability (Foden et al., 2019), however, there is limited evidence to identify which traits are most determinant (Pearson et al., 2014; Wheatley et al., 2017). Thus, I selected predominant traits of

previous climate risk assessments by reviewing the related literature. I focused on endangered marine species as a group of species already of high priority and interest to conservation (Bianchi & Morri, 2000; Coll et al., 2010). Currently endangered marine species are characterized by high vulnerability under present conditions, so they are a priori under high risk to any other pressure, like that of climate change. So, I aimed to identify species with the greatest vulnerability, exposure and risk to changes in ocean temperature in the Mediterranean Sea, as well as delineate high-risk areas which host most of them. Research findings could help steer our sight towards species and areas at highest risk in the Mediterranean and prioritize their monitoring and conservation.

D.2 Methodology

Collection of species data and traits

In order to identify the species' list, I collected information on all 104 critically endangered, endangered, and vulnerable species of the Mediterranean Sea (further referred to as 'threatened species') from the IUCN Red List of Threatened Species (IUCN, 2021), including a variety of taxa from benthic invertebrates to large marine mammals. Fourteen species were excluded from the dataset, such as three marine birds, two Lessepsian migrants (*Coryogalops ocheticus*, *Himantura uarnak*), the endemic *Paranemonia vouliagmeniensis* as it solely inhabits a brackish lake, and eight species with distribution ranges including the Mediterranean Sea according to the IUCN, but considered vagrants in the region (*Acipenser stellatus*, *Acipenser gueldenstaedtii*, *Acipenser nudiiventris*, *Entomacrodus solus*, *Eretmochelys imbricata*, *Pristis pristis*, *Pristis pectinata*, *Pomatoschistus tortonesei*). Thus, eventually 90 threatened species were collected at the end.

Building upon previous climate change vulnerability and risk assessments (Foden et al., 2013; Gaichas et al., 2014; Hare et al., 2016; Stortini et al., 2015), I gathered eleven ecological and life history characteristics, which depict the general susceptibility of the studied species. These traits encompass a variety of species-level attributes, such as ecological preferences and life history information (Foden et al., 2019). The initial three traits pertain to species' intrinsic sensitivity traits responding to the impacts of climate change: (1) Preference in narrow thermal conditions. I considered that species with narrow thermal ranges would have a greater probability of being impacted by temperature increase due to climate change (Foden et al., 2019). (2) Use of habitats likely to be impacted by sea level rise (e.g., marshes, sea grass beds, beaches, river deltas, and adjacent coastal areas) (Cazenave & Cozannet, 2014). (3) Dependence on calcification processes. I considered that species employing calcification processes, such as corals and mollusks, would be impacted the most by the reduction of the ocean pH. Fish were considered of medium sensitivity because of calcification processes for otolith formation and the impacts of ocean acidification on the survival of their larvae (Koenigstein et al., 2016; Poloczanska et al., 2016; Jones & Cheung, 2018).

The remaining eight traits referred to species' adaptive capacity: Specialized requirements on (4) habitat and (5) diet. We considered that species not tightly connected to specific conditions and requirements in habitat and diet might show greater resilience towards climate change impacts due to a broader niche (Foden et al., 2013). (6) Impact score of other non-climatic threats, reflecting the overall population

health and thus its ability to cope with added impacts and adapt to new conditions (Davies et al., 2004). Climate change impacts may interact with anthropogenic threats, such as overfishing or pollution, exacerbating the pressure on marine species. Therefore, I used the level of impact from anthropogenic threats of the IUCN Red List as a “trait” reflective of the added vulnerability due to additional pressures (Foden et al., 2013). (7) Conservation status, obtained from the IUCN Red List of Threatened species. (8) Dispersal ability, as species with low dispersal ability were assumed to have a lower ability for adaptation since they are less capable of shifting their ranges according to altering climatic conditions (Foden et al., 2019). (9) Vertical migration ability as an adaptive mechanism that species may use to avoid the warming marine surface (Jorda et al., 2020). (10) Generation length. We considered species with longer generations to have slower life histories and lower reproductive output. Long generation length and slow growth rate are often linked to an increased risk of extinction (Pearson et al., 2014). (11) Body size. The larger the body size of a given species, the higher its assumed position in the marine trophic guild, indicative of a K-strategy species (Gaichas et al., 2014; Hare et al., 2016). I considered species with larger body sizes more vulnerable to warming, as they have lower heat tolerance thresholds than smaller organisms (IPCC, 2014; Jones & Cheung, 2018).

I employed five databases, namely IUCN, Fishbase, SeaLifeBase, WORMS, and Aquamaps, to gather data on species traits. Information regarding habitat and dietary requirements was sourced from literature review and expert consultations. Vulnerability levels were categorized into three modalities (high/moderate/low) for all traits except diet specialization, which had two levels (low and high). For a comprehensive understanding of the acquisition of trait information and the assignment of ordered levels, please refer to Table D.S1 and the supplementary material.

Estimation of Climatic Vulnerability

To assess species vulnerability, I employed two distinct methods: a semi-quantitative and a quantitative approach. This dual-method approach was adopted to mitigate uncertainties stemming from relying solely on one vulnerability estimation method. The scores derived from both methods were subsequently combined into a single integrated vulnerability score.

According to the semi-quantitative approach, a species was classified as highly vulnerable if it exhibited a specified number of traits associated with a high level of vulnerability. To determine a minimum number of traits needed to assign high vulnerability at the species level, I followed a stepwise process; first, I assumed that if a species had at least one trait linked to a high level of vulnerability, then this species would be highly vulnerable. I repeated the process by gradually increasing the number of traits used as thresholds. Next, I plotted the number of species assigned as highly vulnerable against the corresponding thresholds; I observed that a certain plateau was reached for threshold ≥ 3 (Figure D.S1). According to this threshold, I considered highly vulnerable species with three or more highly vulnerable traits. Species with less than three highly vulnerable traits were characterized as having moderate or low vulnerability based on the prevailing vulnerability level of traits. If more traits of the species were of moderate level, then the species was characterized as moderately vulnerable, while it was characterized as having low vulnerability if more traits were of low level.

Following the quantitative approach, I assigned scores to the designated levels of vulnerability traits, where high, moderate, and low vulnerability received descending scores from 3 to 1, respectively. Subsequently, I calculated the sum score of all vulnerability traits for each species (Gaichas et al., 2014; Hare et al., 2016). Next, I divided the range of values into three equal intervals, corresponding to categories of high, moderate, and low vulnerability. In the final step, to generate an integrated vulnerability score for each species, I merged the scores obtained from both the semi-quantitative and quantitative approaches using a logical matrix (Jones & Cheung, 2018). This matrix facilitated assigning species into categories of high, moderate, or low overall vulnerability, as illustrated in Figure D.S2.

Estimation of exposure to increased sea temperature

To generate a comprehensive exposure assessment for each species, I integrated results from two metrics based on the characteristics of the species' existing distribution. The first metric analyzed maps illustrating the projected current distribution of each species alongside anticipated changes in ocean temperature within their projected habitat range. This metric quantified the percentage of the species' current thermal range that is expected to diminish in future scenarios. Species were deemed highly exposed if a significant portion or none of their current thermal range would be retained under future conditions. The second metric assessed the extent to which the current distribution of species might encounter elevated climatic conditions in the future compared to their present habitat. Species exhibiting a substantial portion of their distribution projected to experience heightened climatic conditions were considered highly exposed. For each studied species, I derived maps of current distribution from Aquamaps (Kaschner et al., 2019), a website providing predictions on marine species distribution based on ecological niche models built on environmental variables such as temperature, primary production, and salinity. Model outputs represent the probability of species occurrence (0–1) at a 0.5° spatial resolution. Cells with a probability equal to or greater than 0.5 were considered as cells where the species is present, whereas cells with a probability less than 0.5 were considered cells where the species is absent (Klein et al., 2015).

Before calculating the two metrics used to determine exposure scores for the species under study, I categorized each species based on depth. Utilizing data from Fishbase and SeaLifeBase, I compiled estimates of depth ranges for all species and classified them into one of three depth categories: a) sea surface, b) mean depth, or c) maximum depth. Species such as marine mammals and sea turtles, which primarily inhabit the water column but regularly surface for respiration, were assigned to the sea surface layer. Subsequently, I obtained current and projected sea surface, mean depth, and maximum depth temperature data from Bio-ORACLE (Tyberghein et al., 2012). Projected future temperatures for the period 2040-2050 were based on the "business as usual" climatic scenario RCP8.5 (Representative Concentration Pathway), derived from Atmospheric Ocean General Circulation Models (AOGCM). The first exposure metric was calculated as the proportion of the present thermal range that would be lost in the future. Exposure was estimated through equation (1):

$$(1) E_1 = 1 - \frac{\theta_{max,p} - \theta_{min,f}}{TR_p}$$

- $\theta_{max,p}$: maximum temperature of species' present thermal range

- $\theta_{\min,f}$: minimum temperature of species' future thermal range
- TR_p : present thermal range

To explore the exposure of the current species distribution to increased ocean temperature, I calculated the number of cells for which future temperature was projected to be higher than the species' upper thermal limit and estimated the percentage of current distribution for which future temperatures will exceed reported thermal range, based on equation (2):

$$(2) E_2 = \frac{\text{Nb of cells } \theta_f \geq \theta_{\max,p}}{\text{total Nb of cells}}$$

- total Nb of cells: the number of all cells of the present distribution of the species
- Nb of cells $\theta_f \geq \theta_{\max,p}$: Total number of cells (of the current distribution) where the future temperature will be higher than the species' upper thermal limit

Ultimately, I computed the average value of the two exposure metrics to generate an integrated exposure score for each species. The overall exposure scores ranged from 0 to 1, where a score of 1 indicated that a species' entire future distribution is projected to occur in regions with higher temperatures than the maximum temperature of their current distribution, while a score of 0 indicated that a species' entire future distribution is expected to remain below current maximum temperatures. Species were categorized into high, moderate, or low exposure based on equal intervals of the overall exposure score: [0, 0.33] for low exposure, [0.34, 0.66] for moderate exposure, and [0.67, 1] for high exposure levels.

Table D.1: The list of 11 vulnerability traits of the 90 threatened marine species along with their modalities (low, moderate, high), their source of extraction and the type of variable (continuous or categorical).

Traits of Vulnerability	Vulnerability ranking			Database	Type of variables
	low	moderate	high		
Preference in narrow thermal conditions	$Q2 < \Delta\theta < Q3$	$Q1 < \Delta\theta \leq Q2$	$\Delta\theta \leq Q1$	Fishbase, SeaLifeBase	continuous (extraction of quantiles)
Dependence on calcification processes	rest of the species (marine mammals, sea turtles)	species which possibly will be impacted by OA (fish)	species using calcification processes primarily for their survival (corals, molluscs, malacostraca, bivalvia)	Literature	categorical
Use of habitats likely to be impacted by SLR	absolute dependence on oceanic habitats	dependence on neritic habitats as well as oceanic ones	absolute dependence on coastal terrestrial and neritic habitats	IUCN	categorical
Specialized requirements on habitat	Habitat generalist, in common physical habitats	Strongly prefers a particular habitat but can survive in other habitats	Specialist on a restricted biological habitat	IUCN, Group of experts	categorical
Specialized requirements on diet	Prey generalist	-	Very specific requirements in prey selection	Group of experts	categorical
Impact score of non-climatic threats	low or unknown impact from human threats	medium impact from human threats	high impact from human threats	IUCN	categorical
IUCN status	Vulnerable	Endangered	Critically endangered	IUCN	categorical
Dispersal ability	migratory species	motile species, at least at one life stage	sessile species	Fishbase, SeaLifeBase	categorical
Vertical migration ability	species that occur in deeper waters (greater than 200m)	species occurring from 40m to 200m depth, with moderate ability to reach greater depths	species occurring only in shallow waters with low ability to reach deeper waters (up to 40m)	Aquamaps	categorical
Generation length	$yrs \leq Q1$	$Q1 < yrs \leq Q2$	$Q2 < yrs \leq Q3$	Fishbase, SeaLifeBase, WORMS, literature	continuous (extraction of quantiles)
Body size	$cm \leq Q1$	$Q1 < cm \leq Q2$	$Q2 < cm \leq Q3$	Fishbase, SeaLifeBase, WORMS, literature	continuous (extraction of quantiles)

Overall climatic risk score

The climate risk index was computed for each species by combining vulnerability and exposure scores, following the guidelines of a logical matrix (Jones & Cheung, 2018) as depicted in Figure D.1. Based on this index, each species was categorized into high, moderate, or low risk levels. Utilizing these risk levels alongside the current spatial distribution of species (obtained from Aquamaps distributions), I generated a regional map highlighting climate risk hotspots. These hotspots represent areas where a significant number of species with high climate risk are concentrated. Additionally, I investigated the coverage of marine protected areas (MPAs) in the Mediterranean Sea concerning these risk hotspots. MPA boundaries were obtained from the World Database on Protected Areas (UNEP-WCMC, 2019), focusing on sites identified as coastal or exclusively marine.

To identify traits that possibly relate to species' climate high-risk category, I performed a Joint Correspondence Analysis (JCA) using the “ca” package (Nenadic and Greenacre, 2007). JCA is an improved approach of Multiple Correspondence Analysis, that enables to explore the relationships among multiple categorical variables (Giusti et al., 2013). Specifically, it permits to reduce the dimensionality of a data matrix and visualize it in a low dimensionality subspace (Camiz & Gomes, 2013), while adjusting the overestimation of the total explained inertia (Greenacre, 2006).

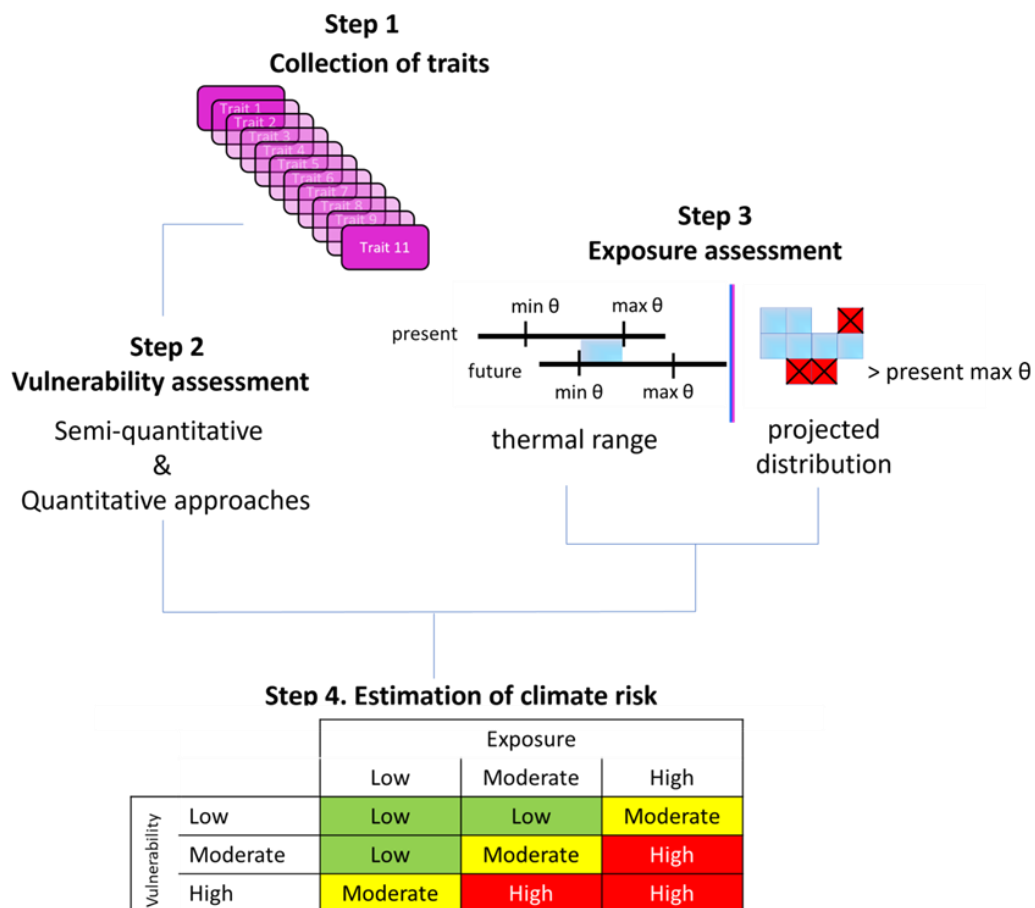


Figure D.1: Overview scheme of the estimation of climate risk. The estimation of the overall risk categories was based on the combination of vulnerability and exposure scores and categories. The table of risk estimation is adapted from (Jones & Cheung, 2018), for the three categories of risk and the estimation of the overall vulnerability.

D.3 Results

Nearly one-quarter (n=25) of the 90 threatened species inhabiting the Mediterranean Sea were predicted to be at high levels of climate risk (Table D.S2). Species of high climate risk belonged to Anthozoa (6 out of 16), Chondrichthyes (12 out of 45), sea turtles (3 out of 3), marine Mammals (3 out of 6) and Actinopterygii (1 out of 18; *Anguilla anguilla*) (Figure D.2). The risk to climate change and vulnerability significantly differed by taxonomic group ($\chi^2 = 26.381$, $p < 0.05$ and $\chi^2 = 31.735$, $p < 0.01$, respectively). Also, the risk to climate change for threatened species was significantly associated with climatic vulnerability ($\chi^2 = 66.534$, $p < 0.01$) and exposure to increased ocean temperature ($\chi^2 = 69.9$, $p < 0.01$).

Nearly two-thirds (n=55) of the 90 threatened species were characterized by high vulnerability to climate change, with species with high vulnerability spanning across diverse taxonomic groups, such as Anthozoa (n = 13 out of 16), Chondrichthyes (n = 30 out of 45), Actinopterygii (n = 6 out of 18), marine mammals (n = 2 out of 6), sea turtles (n = 2 out of 3), Bivalvia (n = 1) and Malacostraca (n = 1). Our findings demonstrated that a rather limited number of species (n = 12) exhibited high exposure to increased ocean temperature. Across the Mediterranean Sea, Chondrichthyes (n = 4), Actinopterygii (n = 1; *Balistes capriscus*), Anthozoa (n = 3), marine mammals (n = 2) and the two sea turtles reproducing in the Mediterranean Sea (n = 2; *Caretta caretta* and *Chelonia mydas*) showed the highest exposure under the projected ocean warming for the period of 2040 - 2050.

Two principal dimensions were retained by the JCA, explaining 62.5% of the total variance, while dimensions with inertias lower than 0.01 were discounted (Table D.S3). JCA results demonstrated that high-risk species were grouped together in the 3rd quadrant (Figure D.3a) and were associated (Figure D.3b). Other traits, such as low vertical migration ability, moderate thermal ranges and use of habitats likely to be impacted by SLR were also associated to high climate risk but to a lesser extent. Indeed, the traits situated close to the origin (0,0) of the JCA graph represent the ones that are close to the weighted mean of all traits for the analysed species, while those located away from the origin (0,0) are the more discriminated ones, representing those that contribute more to the high-risk trait profile (Khangar & Kamalja, 2017). Loadings of each trait modality on the selected dimensions are provided in the Appendix (Table D.S4).

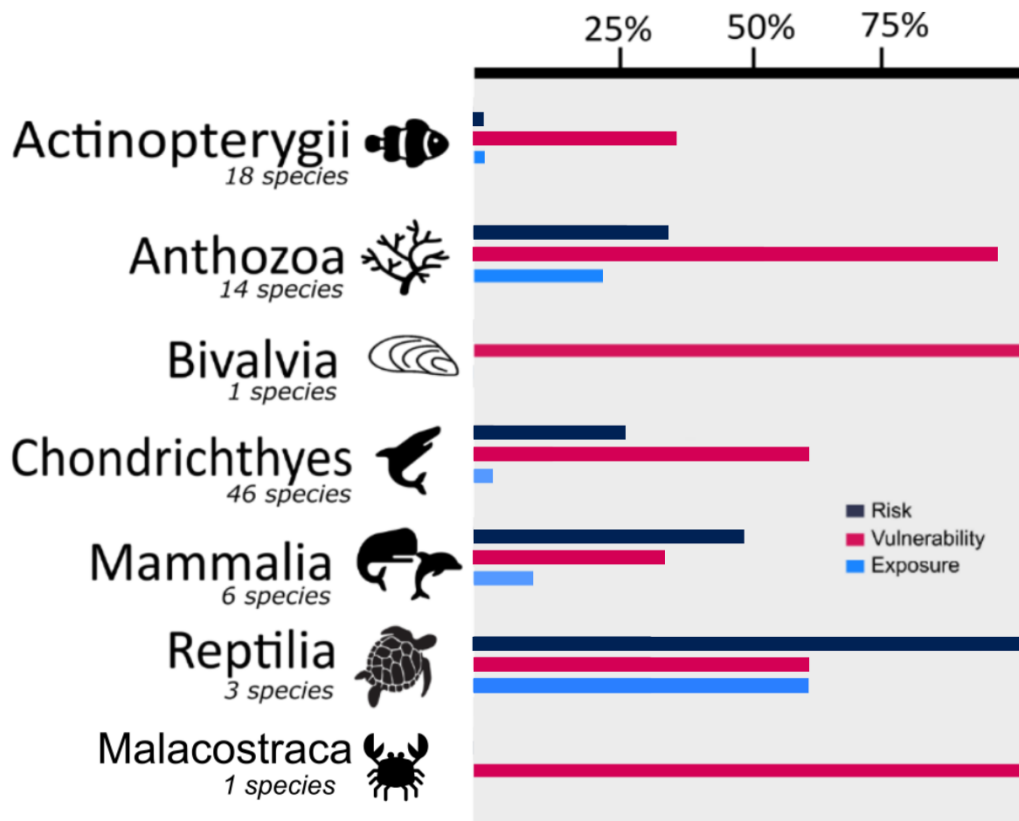


Figure D.2: Percentages of threatened marine species at high climate risk in the Mediterranean Sea. Risk is depicted with dark blue colour, vulnerability with magenta and exposure with light blue. Taxonomic group (and the corresponding total number of species considered) belong to high climate risk category, with the class of Cephalopoda (1 species) missing.

Across the Mediterranean Sea, a greater abundance of species at high climate risk was observed in neritic waters, with an average occurrence of eight species, compared to oceanic waters, where the average was 4.5 species. Among the marine ecoregions in the Mediterranean, the Alboran Sea and the Western Mediterranean exhibited the highest concentrations of high climate risk species, followed by the Adriatic and the Aegean Sea (see Figure D.4, Table D.S1). However, the percentage of high climate risk species relative to the total number of species varied from 21% to 31% across different ecoregions (see Figure 2, Table D.S1). These same regions were also identified as hosting significant concentrations of threatened species highly vulnerable and exposed to ocean warming (see Figure D.5). Given the distribution of threatened species at high climate risk throughout the basin, it was found that every Mediterranean Marine Protected Area (MPA) encompasses at least one of these species within its boundaries. Moreover, over 64% of MPAs, primarily situated in the Western Mediterranean (see Figure D.6), harbor more than ten species at high levels of climate risk. The highest concentrations of high climate risk species were documented in MPAs within the Alboran Sea, located in Spain's national waters. Notably, MPAs with extensive coverage are home to numerous high climate risk species, such as those along the Spanish coasts, the Ligurian Sea, and the Balearic Sea (comprising 14 species).

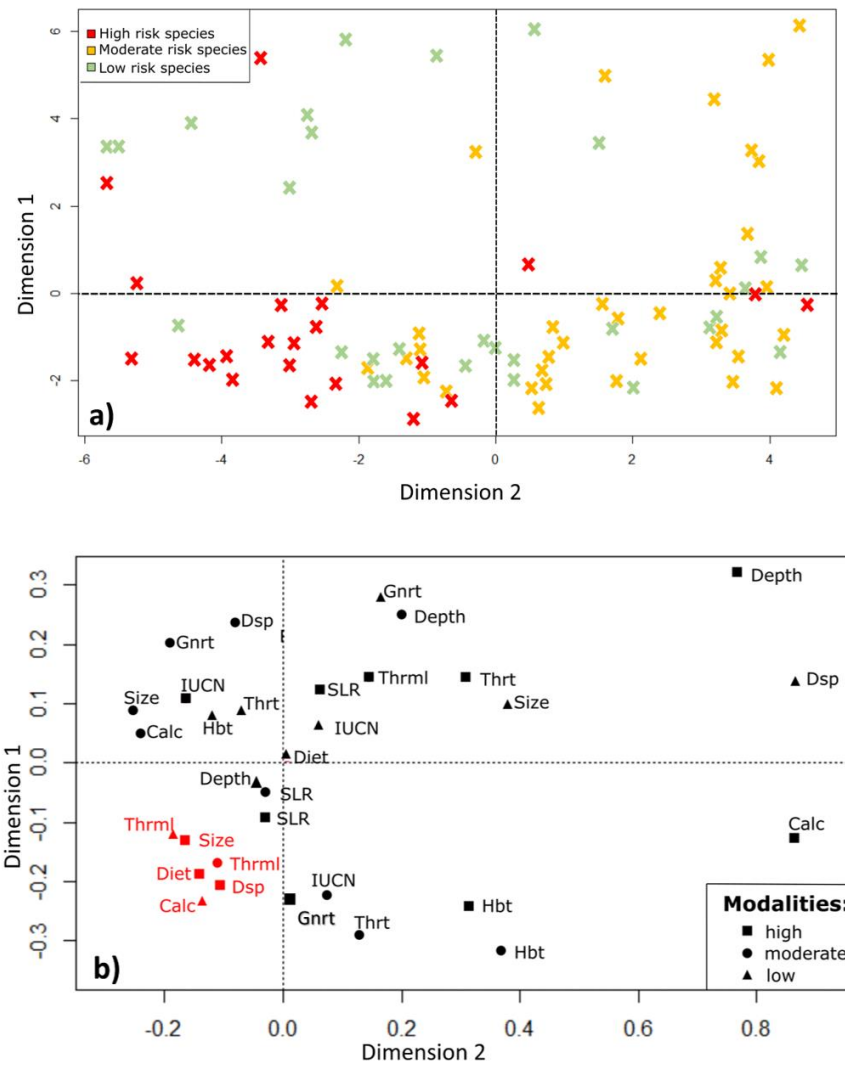


Figure D.3: a) Species inertias along the first and second dimension produced by the JCA, categorized according to their level of risk. b) Traits inertias along the first two dimensions produced by the JCA. Each trait modality is represented by a different shape (high; square, moderate; circle, low; triangle). Traits associated with high risk are depicted in red. The abbreviations of traits in the figure stand for: Gnrt: Generation length, Thrml: Preference in narrow thermal conditions, Depth: Vertical migration ability, Dsp: Dispersal ability, Calc: Dependence on calcification processes, IUCN: IUCN status, Size: Body size, SLR: Use of habitats likely to be impacted by SLR, Diet: Specialized requirements on diet, Hbt: Specialized requirements on habitat, Thrt: Impact score of other non-climatic threats.

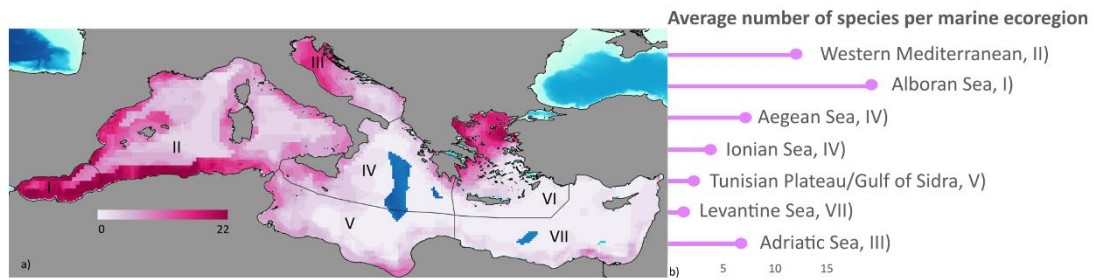


Figure D.4: Hotspot areas of threatened marine species at high climate risk in the Mediterranean Sea. In the right, the average number of threatened species at high and very high climate risk for each marine ecoregion of the Mediterranean Sea. Marine ecoregions (*sensu* Spalding et al., 2007) of the Mediterranean Sea are delineated by black lines.

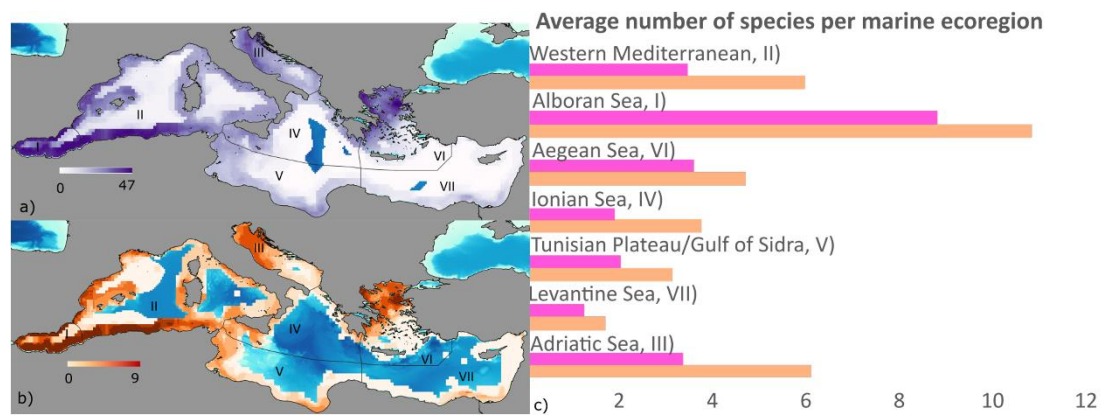


Figure D.5: Hotspot areas with high concentrations of threatened marine species at (a) high climatic vulnerability and (b) high exposure to ocean warming in the Mediterranean Sea. (c) the average number of threatened species at high vulnerability (purple) and high exposure (orange) for each marine ecoregion of the Mediterranean Sea. Marine ecoregions (*sensu* Spalding et al., 2007) of the Mediterranean Sea are delineated by black lines.

D.4 Discussion

This research underscored the likelihood that a substantial portion of endangered marine species in the Mediterranean Sea could face significant risks due to climate change. The effects of global warming are especially pronounced in regions where distribution shifts face physical limitations, such as the semi-enclosed Mediterranean Sea (Ben Rais Lasram et al., 2010). Coupled with the impacts of migrating thermophilic Indo-Pacific species, alterations in physicochemical conditions and ensuing shifts in biotic interactions are expected to intensify pressure on susceptible marine ecosystems (Ben Rais Lasram et al., 2010).

Given their diverse characteristics, species are affected by various aspects of climate change. Research indicates that Anthozoa are proportionally at higher climate risk compared to other threatened biodiversity in the Mediterranean Sea. Anthozoans, characterized by low dispersal capacity and a sessile nature, have been significantly impacted by past marine heatwaves, such as the substantial mortality events observed in 1999 and 2003 in the western Mediterranean (Rivetti et al., 2014). Furthermore, it is projected that a significant portion of Anthozoans' current distribution will encounter markedly different climatic conditions in the future, extending beyond their existing thermal range. This heightened risk to climate change poses a threat to the valuable ecosystem services provided by Anthozoans, as they form dense colonies that serve as crucial habitats for larval settlement and recruitment processes of various benthic species (Ponti et al., 2014; Angiolillo & Canese, 2018).

Risk to climate change may interact with pre-existing local stressors, as a lot of high-risk identified species undergo human-derived pressures. Charismatic marine megafauna, for instance, have been identified as facing moderate to high climate risk, with additional non-climatic threats potentially exacerbating the overall risk posed by climate change (Chatzimentor et al., 2021; Gissi et al., 2021). For instance, local stressors like eutrophication, which are likely to be intensified by climate change, could contribute to population declines (Rodgers, 2021). Several iconic marine mammal species in the Mediterranean Sea, such as the fin whale (*Balaenoptera physalus*), the sperm whale (*Physeter macrocephalus*), and the monk seal (*Monachus monachus*), were identified as highly vulnerable and at high climate risk in the current analysis. Their vulnerability and risk are further heightened by ongoing threats such as ship collisions and harmful fishing practices (Notarbartolo di Sciara, 2016). Additionally, sharks and rays face a serious risk of extinction in the Mediterranean, largely due to overfishing (Dulvy et al., 2014), which is likely to compound the impacts of climate change on species with narrow climatic ranges, such as the blacktip reef shark (*Carcharhinus melanopterus*) (Ben Rais Lasram et al., 2010; Chin et al., 2010). These findings underscore the importance of considering the combined effects of multiple stressors, as while highly commercial fish species like the Atlantic bluefin tuna (*Thunnus thynnus*), the common dentex (*Dentex dentex*), and the critically endangered common goby (*Pomatoschistus microps*) were predicted to face moderate climate risk, they were found to be highly vulnerable. Therefore, strategic and climate-smart spatial planning and management are crucial for addressing the interacting impacts of anthropogenic stressors and climate change (Almpanidou et al., 2021; Doxa et al., 2022; Bastardie et al., 2022).

This analysis has identified numerous climate risk hotspots scattered throughout the Mediterranean Sea. However, different regions within the Mediterranean basin face unique challenges due to the specific local pressures they encounter, thus requiring tailored management approaches. For instance, the Aegean Sea, projected to harbor a significant number of high-climate-risk species, is already grappling with the proliferation of invasive species, many of which are Lessepsian thermophilic migrants (Katsanevakis et al., 2020b). Nevertheless, a considerable portion of Mediterranean coastal environments still maintain relatively good ecological health (Bevilacqua et al., 2020), underscoring the imperative for integrated conservation planning. Such planning should encompass conflict resolution management strategies and species monitoring efforts tailored to the challenges posed by climate change.

The crucial role of protected areas in climate change adaptation is underscored by the discovery that Mediterranean Marine Protected Areas (MPAs) encompass overlapping habitats of a significant number of high-climate-risk species. Given that many MPAs in the region predominantly cover coastal and shallow waters, it is imperative that current management plans integrate climate-smart conservation strategies into systematic conservation planning (Katsanevakis et al., 2020a). These strategies should include robust monitoring of high-climate-risk species, bolstering population recovery capabilities, and implementing measures to control unsustainable anthropogenic practices that may exacerbate the impacts of climate change (e.g., marine litter; Soto-Navarro et al., 2021). Aligned with the EU biodiversity strategy for 2030, which aims to protect at least 30% of European seas, with 10% under strict protection, this study offers valuable insights for regional planning prioritization, as it offers an additional layer of spatially delineated hotspots of the most vulnerable species to climate risk.

Linking species' traits to climate change impacts and defining vulnerability thresholds can be challenging, however ecological, physiological, and life-history traits present a valuable approach for multispecies conservation planning, allowing for the functional grouping of species with similar characteristics (Gallagher et al., 2021). I aimed to address this challenge by employing a methodology based on well-established and widely used datasets, such as Fishbase, to gather species traits and exposure data, which were then combined with climate change model projections. To assess species vulnerability, I utilized an ensemble method and derived an integrated overall risk score to mitigate uncertainty associated with using a single estimation method (Araujo & New, 2007). While traits are often treated equally, it's important to acknowledge that certain characteristics may be more critical than others in determining vulnerability to climate change. Regarding the exposure of marine species to climate change, I attempted to address potential inaccuracies in distribution data used in this analysis by considering each species as present only for cells with a probability of occurrence of 0.5 or higher, a commonly used threshold for Aquamaps (e.g., see Brito-Morales et al., 2022; Doxa et al., 2022), improving the reliability of the data used in the assessment. Finally, I accounted for the three-dimensionality of the marine environment by calculating ocean temperatures within each species' distribution based on their respective depth range. This approach considers the possibility of species finding thermal refuges in deeper waters, instead of solely relying on estimations of sea surface temperature.

This study identified climate risk hotspots for threatened marine species in the Mediterranean Sea, along with prioritizing key species most at risk. It emphasizes the necessity for a systematic conservation planning approach to develop species-specific scenarios and management guidelines. Such an approach would build upon the ecological and life history traits of species and integrate current risk assessments, ensuring targeted and effective conservation efforts. The planet's oceans are undergoing global impacts of climate change and our efforts should focus on the deeper comprehension of the interaction of marine biodiversity and its natural coping mechanisms to pressures, but in parallel, on delineating the grounds of our interventions in the vast areas of oceans and seas. Therefore, there remains an ongoing imperative to direct our conservation efforts towards ecosystems and species that are particularly vulnerable and exposed to environmental change. However, it's also crucial to consider highly adaptive species, as they may serve as valuable stepping-stones in the effective management of environmental change. By focusing on both vulnerable and adaptive species, we can enhance our understanding of ecosystem dynamics and develop more robust conservation strategies that promote resilience and sustainability in the face of ongoing environmental challenges.

Chapter E. Climate change favours reef fish communities of reduced size and lifespan in the northeast Mediterranean Sea.

Δημοσίευση:

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E.1 Introduction

Warming oceans drive changes in marine physicochemical profile, with marine biodiversity following the redistribution of favourable conditions, performing range shifts, local population decline or increase and phenological shifts. Some species might expand their range, whereas other species are almost subjected to local population extinctions (Poloczanska et al., 2013). As species synthesis profile are expectedly changing inside marine communities, however functional changes might not follow. Despite the fact that distribution shifts and abundance changes might be more evident, changes in functional patterns might be not affected by the loss or abundance reduction of certain species due to functional redundancy and the migration or abundance increase of species with similar characteristics to those decreased or locally extinct (Fonseca & Ganade, 2001). However, if species-level shifts are accompanied by a change in traits synthesis, then this might indicate a possible change in ecosystem functioning, and consequences for the ecosystem services provided in human societies (Smith et al., 2021). Therefore, it is equally important also to monitor respective functional changes for marine communities in relation to the changing environmental conditions, by incorporating and processing information on species traits and functions along with observations and predictions performed.

Current research has revealed a lot about traits-environment relationships of the present marine communities in face of changing environmental conditions, although still limited for the marine realm in comparison to the terrestrial. Indicatively, many studies perform experiments exposing marine species in changing environmental conditions and identify consequent impacts on species functions, perform correlations among predicted range shifts and traits, observations on the community synthesis and functional changes along environmental gradients (Green et al., 2022). Research findings reveal useful implications for potential functional patterns and species synthesis profile on future marine communities. Evidence up until now suggests that marine communities among different marine regions might present common functional responses to the changing climatic conditions. Particularly it has been shown that in front of the increasing sea water temperatures during the past years, in regions like the North Sea and the Mediterranean Sea smaller sized fish have been observed to dominate population abundance (Baudron et al., 2014; Damalas et al., 2015a; Damalas et al., 2015b). Also, marine species traits have been identified as acting as mediators of additional sensitivity or adaptive capacity to environmental changes (Pearson et al., 2014; Pacifici et al., 2017). For instance, pelagic species have been observed to illustrate greater latitudinal shifts in response to warming, so use of pelagic habitat might infer a greater responsiveness to changing conditions compared to the demersal and benthic one (Poloczanska et al. 2016). Among all studies, a smaller branch of research is devoted to investigating future functional responses, with predictions for future functional patterns still being limited (Green et al., 2022).

Acknowledging such information offers us insights on species capacity to track changes related to the altered climate and what implications are supposed for marine and human coastal communities, as species response to climate-related stresses and changes could be linked to their characteristics and functions (Hadj-Hammou et al., 2021). For instance, fish are likely to follow a fast-slow continuum of life-history traits ranking species according to their life-history traits from early-maturing, short-living and fast-growing to late-maturing, long-living and slow-growing across environmental gradients at the sea (Beukhof et al., 2019). To this direction, accelerating ocean warming has been

assumed to lead to an increasing dominance and geographical expansion of fast-growing, early-maturing and short-lived species (Beukhof et al., 2019), with many studies supporting a shift to smaller-sized species. Organisms becoming smaller would have important effects as the size of animals mediates their contribution to how ecosystems function, and how human societies benefit from fisheries (Smith et al., 2021). Therefore, present conservation strategies would have the opportunity to incorporate more meaningful measures towards the monitoring of, among others, also trait-based indicators, functional changes in marine communities and be more prepared for human-related consequences of them.

Especially for a region like the Mediterranean Sea, this is highly important, as it constitutes a semi-enclosed basin with minimum potential on marine species performing northern migrations, as they are largely limited by the presence of land. Functional patterns might change dramatically with the predicted tropicalization of fish communities following the introduction of non-indigenous species (Ben Rais Lasram et al., 2010; Marbà et al., 2015). This indeed has caused chain-reactions in eastern marine communities of the Levantine and Aegean Sea, with the limitation of macroalgae canopy. However, many parts of the Mediterranean still serve as thermal refugia of colder conditions, like the Gulf of Lions, north Adriatic Sea and North Aegean Sea until the middle of the 21st century, offering a sanctuary for cold-water species, however by the end of the century, these areas are likely to become a trap for the whole coastal fish assemblage (Ben Rais Lasram et al., 2010).

Building on the aforementioned concerns, I tested the hypothesis that the changing environmental conditions will drive functional changes in swallow reef fish in a climate change hotspot like the Northeast Mediterranean Sea. For this, I modelled reef fish community mean weighted traits' variation as a function of reef fish predicted abundance levels, focusing on key functional traits associated with fish lifespan, growth and reproduction. I predicted the potential trait composition under future conditions of climate change as a function of predicted species abundance in the future and identified changes in the functional patterns of swallow reef fish. This work could offer a first insight on what functional patterns and changes might future environmental conditions favour in a climate change hotspot in the Mediterranean, such as the Northeast Mediterranean, and could support the identification of potential response traits in face the rapidly changing climate and subsequent impacts on provided ecosystem services.

E.2 Methodology

In order to predict potential shifts in the functional patterns of reef fish in the Northeast Mediterranean, I delineated present and future functional synthesis of reef fish communities. I collected information on the presence and abundance of reef fish species over the Northeast Mediterranean Sea and projected their present and future distributions based on abundance-based models. I then combined information on their traits, to estimate the present and future community mean-weighted traits, and identify changes in traits' values and distribution, testing for a middle-term (2030-2060) and a long-term scenario of climate change (2060-2090).

Study area and data collection

The study area encompasses all shallow territorial waters of the Aegean and Ionian Sea, situated in the north-eastern Mediterranean Sea. The Aegean Sea is divided into the North and the South Aegean basin, which are characterized by distinct oceanographic conditions, with the South Aegean Sea being more oligotrophic. The Ionian Sea is located in the west of the continental Greece and surrounds the southernmost Hellenic, hosting the deepest basins of the Mediterranean Sea. Abundance data were estimated for a total of 56 fish species, which were collected in 100 sampling stations, by means of underwater visual surveys performed by SCUBA divers at 5m depth (Sini et al., 2019). As abundance-based models are highly recommended for highly frequent and common species but might respond poorly on rare species (Waldock et al., 2022), we selected fish species for which we had abundance data from at least 20 sampling stations, resulting to a total of 26 species.

To run the species distribution abundance-based models, we selected important oceanographic parameters for fish, that are commonly used to predict potential fish species distributions. A total of 6 environmental variables were selected: (i) average sea temperature, (ii) min and max temperature of the coldest and warmest month, (iii) temperature seasonality, (iv) average salinity, (v) average oxygen concentration and (vi) average chlorophyll concentration. Sea temperature is largely documented to be correlated to marine species' richness and diversity in coastal and oceanic areas (e.g., sharks, tunas and billfishes; Tittensor et al., 2010). Temperature seasonality was selected, as it has been shown that fish assemblages vary over seasons, particularly in temperate coastal waters (Franco et al., 2006; Perry et al., 2018). We also selected min and max temperature of the coldest and warmest month as a proxy for the thermal extremes experienced in the area. Finally, salinity and chlorophyll-a represent important oceanographic parameters for fish, commonly used to predict potential fishing grounds (Tseng et al., 2011) and account for key processes in fish life history (Bœuf & Payan, 2001).

Environmental data for the Mediterranean region were obtained from statistically downscaled climate projections at different depth levels (Kristiansen et al., 2022; Kristiansen and Butenschön 2022; doi:10.5281/zenodo.6523926). The dataset was created by bias-correcting and statistically downscaling Earth System and Climate Model simulations from a range (4-8) of CMIP6 model, prior to creating an ensemble dataset that contained the ensemble average along with information on the uncertainty across models. The downscaled dataset provided monthly averaged spatially resolved temperature, chlorophyll, salinity and oxygen concentration data at three different depth layers 5m, 25m, and bottom depths, for the historical (1993-2022) and future (2022-2100) period, resolved at 1/12° degree longitude-latitude. Our study focused on the Shared Socioeconomic and Representative Concentration Pathway (SSP, O'Neill et al. 2016) SSP5-8.5 (fossil fuel driven future), largely considered as unmitigated case scenario, to assess the risk of climate change. To define present-day climate conditions for model predictions, I used environmental data for the period of 1993–2022. For middle-term future we considered the period of 2031–2060 and for long-term future the period of 2061-2090. All analyses were realized in R studio using R packages raster and ncd4 and ArcGIS 10.1.

Regarding the selection of traits, I considered five broadly used traits that represent aspects of growth, morphology and reproduction: (i) Longevity as the maximum years a species has been observed to live (years), (ii) maximum body size as the maximum

length reported (cm), (iii) age at maturity as the years that a species on average reaches maturity (years), (iv) fecundity as the log likelihood of maximum eggs produced annually by the species and (v) the growth performance index phi (GPI), as a growth index encompassing the K parameter and L_{∞} , under the equation: $\phi' = \log_{10}K + 2\log_{10}L_{\infty}$. GPI enables a comparison of growth rates among different species of fish and invertebrates reflecting the growth rate of a fish of unit length (Ragonese et al. 2012). Information on the traits of each fish species was derived from the database of Fishbase (Froese and Pauly, 2023) and in the case of absence of information from relevant publications (Tzanatos et al., 2020). When information on traits was not available at the species levels, I considered a phylogenetically relative species or estimated the mean trait values at the genus level, or even the family level when information at the genus level was unavailable.

Delineating observed trait-environment relationships.

In order to delineate the observed functional composition and relationships in the species pool, I performed descriptive statistics and Spearman correlation tests for the functional traits of swallow reef fish of the sampling stations in R studio, under package ‘corrplot’ (Wei & Simko, 2021). Using the information on species traits, their abundance in the sampling stations and environmental conditions there, I identified the observed trait – environmental relationships in the study area performing an RLQ analysis (Dray et al., 2014). RLQ allows for the investigation of the joint structure of three tables: sites x environmental variables (table R), species x functional traits (table Q), and species x sites (table L). Following the methodology of (Dray et al., 2014) we combined three separate analyses to maximize the cross-covariance between the environmental and trait ordinations. More specifically, a Correspondence Analysis (CA) was performed for the L table, a Principal Component Analysis (PCA) was used for the R and Q table using the CA site scores as row weights to couple R and L, and also using the CA species scores as column weights to couple Q and L, respectively. The three independent analyses were then combined in a single ordination, resulting in a co-structure between the three above-mentioned matrices, which is quantified through the so-called RLQ axes. The associations between species, traits and environmental variables along the RLQ axes represented the best compromise between traits and environmental variables through species abundances. Environmental variables were represented as the average tri-annual values for time periods of 2014-2016 and 2018-2020, as samplings were realized in years 2016, 2020-2021 (i.e., see Sini et al., 2019).

Assessing potential changes in functional composition under climate change.

In order to investigate the potential changes in traits’ distribution under climate change, I estimated present and future community mean weighted traits for reef fish. First, I used random forest models as recommended in the literature (Waldock et al., 2022), and projected the future abundance of reef fish by running abundance-based models based on the set of the four uncorrelated environmental variables (min temperature of the coldest month, max temperature of the warmest month, temperature seasonality, oxygen and chlorophyll concentration), for the middle-term (2030-2060) and long-term

scenario (2060-2090). Correlations were tested among the environmental variables using the Spearman correlation coefficient test in R, under the package ‘correl’. The performance of abundance-based random forest models was evaluated using three evaluation indicators suggested for species abundance models (Waldock et al., 2022). These were: (i) discrimination: spearman’s rank correlation, indicating how well model predictions discern low values from high values, (ii) precision: ratio of variation of predicted values to variation of observed values and (iii) accuracy: mean absolute error of predicted to observed values divided by mean observed abundance, indicating the degree of proximity to the observed value.

I calculated present and future community mean weighted traits composition, using the FD package (Lavorel et al., 2008; Laliberté et al., 2014). CWM was computed as the mean trait value of all species present in the community weighted by their relative abundances. I then mapped CMW traits per grid cell. In order to evaluate the consistency of the projected CWM traits over the observed ones, I used the three aforementioned evaluation indicators (Discrimination, Precision, Accuracy). Finally, I tracked potential changes in trait distributions among present, short-term and long-term future conditions, by graphically representing them with ridgeline plots using R package ggplot2 (Wickham, 2016). For each trait distribution, I calculated the median value, the minimum and maximum values and the standard deviation. Performing the Kolmogorov-Smirnov test (Massey, 1951) under R package ‘stats’ (R Core Team, 2020), I tested for any statistically significant differentiations among the present, middle-term and long-term distributions for each of the five fish functional traits, while performing Levene’s test for equality of variances (Levene, 1960) between present and future projections.

E.3 Results

Delineating observed trait-environment relationships and trait synthesis.

The observed functional composition of sampled swallow reef fish in the Northeast Mediterranean Sea is characterised mostly by reef fish species of short lifespan and size (Figure E.1). One third, that is 9 out of the 26 reef fish species have a lifespan longer than 10 years, with *Epinephelus spp.* having the maximum value of longevity (60 years), whereas the remaining two thirds of the reef species have a lifespan between 4 to 10 years. Also, 75% of reef fish reach an age of maturity of equal or lower than 2 years of their lifespan. Growth performance index phi ranges between values of 1.655 – 2.969, with *Scorpaena maderensis* and *Chromis chromis* owing the lowest values in the species pool (1.655 and 1.695 respectively). On what concerns maximum length, 75% of species reach a maximum length lower and equal to 42cm. Three reef fish of the *Symphodus* genus were characterized with the smallest sizes, namely *Symphodus ocellatus*, *Symphodus melanocercus* and *Symphodus rostratus*. At last, out of 27 reef fish, 15 species are characterized by a fecundity of lower than 5, while the highest values belong to *Thalassoma pavo*, *Epinephelus spp.*, *Diplodus sargus* and *Diplodus puntazzo* (7.11, 6.01, 5.9 and 5.9 respectively).

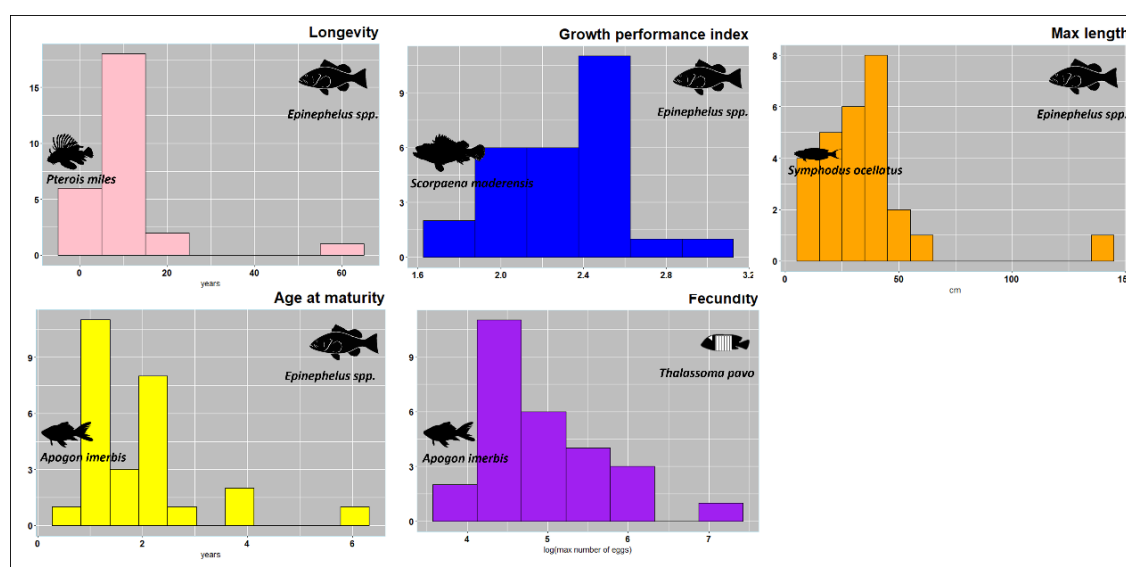


Figure E.1: Histograms of the five functional traits of swallow reef fish in the Northeast Mediterranean sea.

Main patterns of observed trait – environmental relationships were revealed by the first RLQ axis (representing approximately 97% of data variability). Environmental variables and traits that had the highest positive or negative score on the RLQ axes contribute the most to the observed patterns of trait-environment relationships, while variables with a score close to 0 contribute the least to the observed relationships. Lifespan, growth parameter phi and fecundity were among the most determinant traits, while temperature seasonality and minimum temperature of coldest month were among the most important environmental factors (Figure E.2).

The analysis revealed that reef fish with longer lifespan and age at maturity were predicted to be found in more seasonal waters, richer in chlorophyll and oxygen concentration. On the contrary, in warmer and more saline waters experiencing relatively warmer winter conditions, reef fish communities were mainly composed by species of higher growth and fecundity (Figure 2). Performing a Spearman correlation rank in order to test the magnitude of covariation among traits, I observed that longevity was also highly correlated to maximum length ($r_s=0.92$) and age at maturity ($r_s=0.72$) (Figure E.2).

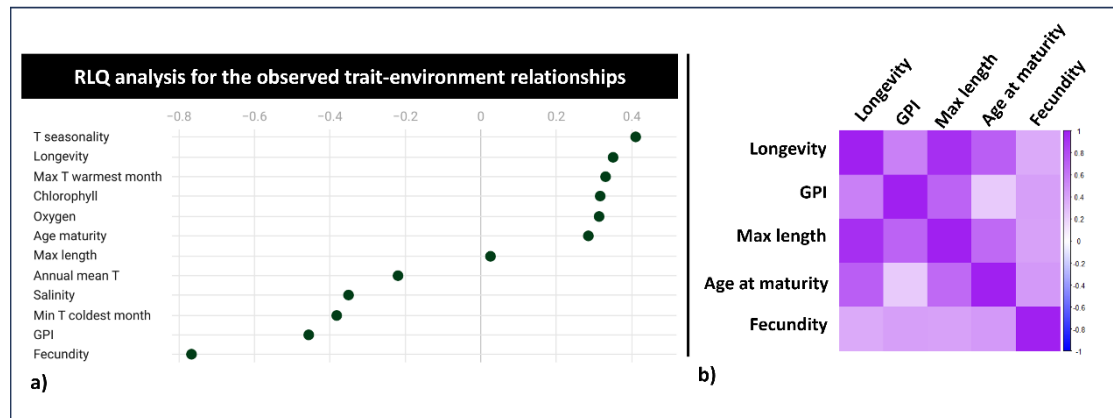


Figure E.2: a) Trait-environment relationships based on observed species abundances of swallow reef fish and environmental conditions from 100 sampling stations over the Northeast Mediterranean Sea, b) Spearman correlations among species traits.

Projected changes in community mean weighted traits

Models predicted that North-Eastern Mediterranean fish communities will shift towards species of lower longevity, lower maximum length and lower age at maturity, but also of higher growth and higher fecundity species (Figure E.3). Specifically, the median longevity is predicted to decrease significantly from present time to mid-century ($D(2) = 0.18742$, $p < .01$) and end-of-century periods ($D(2) = 0.25545$, $p < .01$). Similarly, long-term future max length and age at maturity were predicted to be significantly lower than present median traits ($D(2) = 0.3367$, $p < .01$ and $D(2) = 0.43661$, $p < .01$, respectively). The value of the estimated distance D between present to short-term future ($D=0.34$) is much higher than the one calculated for short-term future to long-term future ($D=0.1$), indicating the relatively faster transition to lower median values of maximum length. On the contrary, median growth performance index phi and median fecundity in the long-term future were predicted to have a significant shift towards higher values, in comparison to present and short-term future conditions ($D(2) = 0.34657$, $p > .01$ and $D(2) = 0.26037$, $p < .01$, respectively).

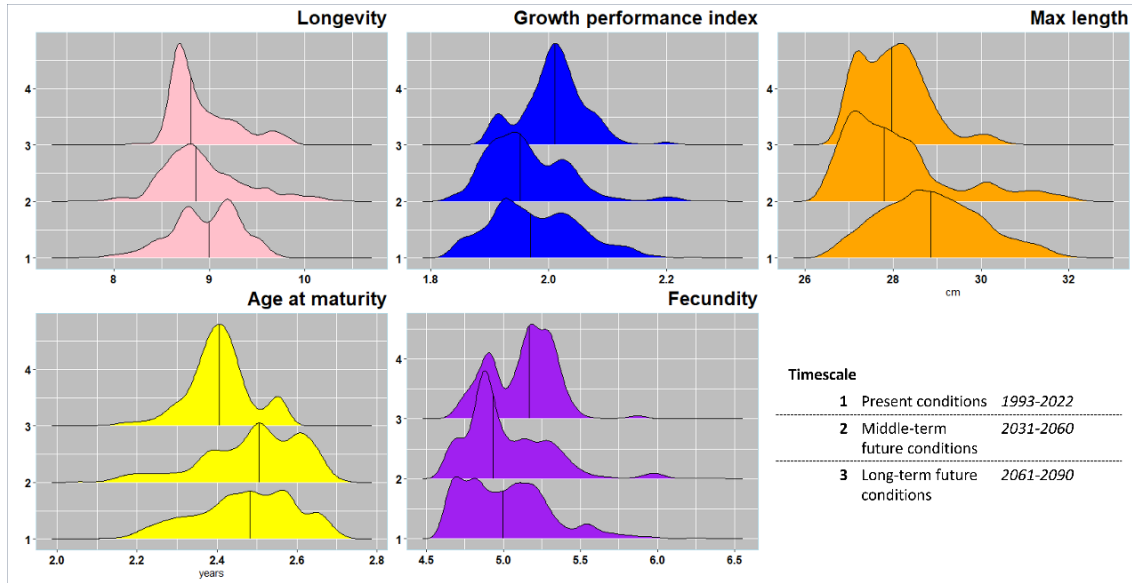


Figure E.3: Ridgeline plots of the distributions of CMW traits for present, middle-term future and long-term future conditions. Lines of median values are depicted in the distributions.

The projected variance of all community mean weighted trait values between present to long-term future conditions was predicted to be significantly reduced by the end-of-century. A significant decrease in the predicted long-term future distributions was revealed for longevity ($F(2) = 43.375$, $p < .01$), growth parameter phi ($F(2) = 371.67$, $p < .01$), max length ($F(2) = 363.31$, $p < .01$), age at maturity ($F(2) = 514.97$, $p < .01$) and fecundity ($F(2) = 210.58$, $p < .01$). However, for longevity from present to middle-term future scenario, variance was predicted to be significantly increased ($F(2) = 20.194$, $p < .01$).

	Kolmogorov – Smirnov test			Levene's test for Equality of Variances			
	present to short term future	short-term future to long-term future	present to long-term future		present to short-term future	short-term future to long-term future	present to long-term future
Longevity	0.18742**	0.19384**	0.25545**	Longevity	20.194***	95.819***	43.376***
Growth	0.09634**	0.41672**	0.34657**	Growth	40.457***	127.8***	371.67***
Max Length	0.34008**	0.0978**	0.3367**	Max Length	0.0425	241.95***	363.31***
Age at maturity	0.06919**	0.43353**	0.43661**	Age at maturity	0.9276	395.43***	514.97***
Fecundity	0.13506**	0.29314**	0.26037**	Fecundity	16.817***	72.656***	210.58***

Figure E.4: (a) Kolmogorov-Smirnov test for the test of the equality of the distributions of the five functional traits across present, short-term future and long-term future and (b) the Levene's test for Equality of Variances of the five functional traits across the three time slices.

E.5 Discussion

I investigated the potential changes in functional traits of shallow rocky reef fish communities in the Northeast Mediterranean, a climate change risk hotspot. Findings revealed a possible shift towards smaller size, shorter lived and with lower age at maturity fish species, as a response to changing environmental conditions. This trend seems to be detectable already from the mid-century period (2031-2060) but becomes even more pronounced at the end-of-century period (2061-2090), raising concerns about the possible changes at the ecosystem level.

Consistently with these findings, there have been recorded increasing population trends for species with shorter lifespan (Tzanatos et al., 2014; Damalas et al., 2021; Gómez-Gras et al., 2021) and decreasing trends for bigger-sized individuals in fish populations (Damalas et al., 2015a; Damalas et al., 2015b). This could also reflect a combined pressure deriving also from fisheries, as fishing impacts age, size and geographic diversity of populations (Brander, 2007). Disentangling the impacts of each one of these pressures is a challenging task, as there is still limited knowledge on the actual interactions of multiple stressors (Genner et al., 2010). Most importantly, climate change and fishing activity acting synergistically can cause a cascade of impacts in the provision of ecosystem services in the Mediterranean (Pita et al., 2021). Strong pressures, like changing environmental conditions, invasive species and overfishing, might drive the selection of certain trait categories, especially in distribution range edges where species are found close to their thermal limits, lowering even more the possible range of available traits in populations (Logan et al., 2014; Merilä & Hoffmann, 2016; Ehrlén & Valdés, 2020). These findings support this hypothesis bringing new evidence of a possible functional homogeneity for reef fish communities in the North-Eastern Mediterranean, one of the most prominent areas of ocean warming at the Mediterranean scale.

Shorter sized species represents one of the globally observed responses in front of increasing temperatures (Daufresne et al., 2009; Sheridan & Bickford, 2011). The very well-grounded rule between temperature and somatic size (Atkinson, 1994) predicts that in lower temperatures organisms increase with a lower rate. Size reduction has been observed for fish species of marine ecosystems (Daufresne et al., 2009; Cheung et al., 2013; Baudron et al., 2014) and freshwater ecosystems (Forster et al., 2012), for both cold-water and warm-water species (Daufresne et al., 2009; Cheung et al., 2013). For instance, two thirds of the commercially important species in the North Sea have been reduced in asymptotic length while sea water temperatures have significantly increased over the past decades (Baudron et al., 2014). However, avoiding a risky overgeneralization of size reductions, still opposite changes have been observed also (Ahti et al., 2020; Ohlberger, 2013). Particularly for the Mediterranean Sea, studies suggest a general reduction in species size (Genner et al., 2010; Audzijonyte et al., 2016; Rijn et al., 2017; Heneghan et al., 2019), while other studies suggest for the northern areas an increase in the mean size due to the migration of bigger-sized species (Albouy et al., 2013). Specifically the Aegean and Adriatic Seas are predicted to be colonized by species that will expand their distribution range (Moullec et al., 2016), particularly until the mid-century as conditions remain below the threshold of 12°-13°C (Clark et al., 2020).

Climate change impacts can be complex especially in semi-enclosed basins like the Mediterranean. Presently, the northern parts of the basin, like the Gulf of Lions, north Adriatic Sea and North Aegean Sea, serve as thermal refugia of colder conditions and

offer a sanctuary for cold-water species (Ben Rais Lasram et al., 2010). Minimum temperature of the coldest month was predicted to be an important condition for the swallow reef fish in the Northeast Mediterranean by this analysis confirming existing literature (Titelboim et al., 2019). However following ocean warming, these areas are likely to become a trap for the whole coastal fish assemblage due to the increasing temperatures (Ben Rais Lasram et al., 2010). Thermophilic and invasive species, that previously cold water temperatures acted as a natural barrier for their expansion, are expected to be now favored by increased sea temperatures and become more viable and abundant (Titelboim et al., 2019). Faster growth rates and low generation length, two of the most determinant traits revealed by our analysis, are key characteristics of most invasive species with high capacity to tolerate broad environmental conditions (Jungblut et al., 2018). Indeed, key physiological indicators have been augmented by changing environmental conditions, such as the metabolic and heart rate (Burraco et al., 2020), increasing their populations' persistence (Adloff et al., 2015).

Overall, trait-based approaches represent a useful tool for a climate smart conservation planning, as they allow incorporating information of ecological, physiological and life-history traits in future predictions and risk assessments. Considering marine functional groups with similar characteristics (Gallagher et al., 2021) might facilitate drawing conclusions regarding ecosystem functioning and ecosystem services in present and future communities. Few trait-based approaches investigated predictions for the functional patterns of the future conditions and particularly for the marine environment (Green et al., 2022). These approaches could contribute in the delineation of stress sensitivity characteristics, and the identification of vulnerable species and functions (Foden et al., 2019). Such approaches can provide guidelines so as to safeguard species with rare and significant functions for the ecosystem, irrespective of their abundance, as population reduction or local extinction would result in the creation of vacant functional niche (Koutsidi et al., 2020). I conclude that species occurrence and abundance future projections should be coupled with information on potential changes in the functional composition of marine communities, providing thus useful insights into potential ecosystem shifts.

In the present study, I selected five functional traits representing key dimensions of fish life history, growth and reproduction, in order to delineate future community mean weighted trait patterns and predicted the future abundance of fish based on a series of uncorrelated environmental variables. Still, the distribution and abundance of fish is dependent on additional factors and their interactions (e.g. temperature and sea currents circulation) and behavioral traits (e.g. biotic interactions (Hodge & Price, 2022) or dispersal capacity (Barber-O'Malley et al., 2022)). I acknowledge that fully identifying trait-environment relationships demands extensive data and the use and comparison of multiple methods. For instance, RLQ summarizes multivariate structures, but it does not provide significance tests, whereas the fourth corner only tests the significance of bivariate associations, not considering the covariation among traits or among environmental variables. Overall, the identification of trait-environment relationships is not trivial. Both the RLQ and fourth-corner analysis do not account for the evolutionary linkage of traits, and consider one trait at a time (Dray & Legendre 2008), which could explain why some traits are not significantly associated with environmental variables, as they could be responding to a combination of factors.

In conclusion, results present a general pattern of response traits and environmental drivers, with warmer areas hosting reef fish communities dominated by species of more

rapid growth, while in more seasonal environments communities are characterized by longer-lived fish species, following a k-strategy (Pianka, 1970). This conforms to large-scale differences in community structure, along a “fast-slow continuum” (Beukhof et al., 2019), previously shown for other terrestrial and marine communities, including fish (Juan-Jordá et al., 2013; Rochet et al., 2000). These findings could support and improve predictions on species responses to climate change, offering an additional dimension, linked to ecosystem functioning and ecosystem services of important marine communities, such as the reef fish. Appointed traits could contribute in the creation of novel and more sophisticated indices based on species traits, as well as on early warning signs according to responsiveness and sensitivity of functional groups to climate change. This could, in turn, assist the monitoring of current trends and responses to better prioritize future conservation actions and climate smart approaches.

Chapter F. Conclusions

F.1 Synopsis

The prediction of marine species responses to changing climatic conditions is a highly complex task subjected to a level of uncertainty, in every step of analysis. However, the continuous collection of high-quality data from field observations and the exploration of cause-and-effect relationships through experiments can validate and strengthen our knowledge and understanding of observed and predicted changes in environmental conditions, biodiversity patterns, and ecosystem functions. To this direction, previous decades of research have expanded our knowledge of the physiological functions, ecological requirements, and behaviour of species and their connection to their changing environments, with research continuing (Urban et al., 2016). Based on this information, we can observe species' responses to climate change from additional dimensions, enriching our predictions to identify vulnerable elements that require protection, as well as elements that contribute to adaptation. Prioritizing the monitoring of these elements can provide material for a cyclical feedback process between conducted predictions and their validation or rejection based on field data (Brown et al., 2022).

In this dissertation, I aimed to contribute to the current scientific discussion regarding predictions of changes in Mediterranean marine life due to climate change. I made an effort to enhance predictions of risk to climate change by considering biological and ecological characteristics, life cycle features, and three-dimensional habitats used by species. The first goal of the dissertation was to assess the different effects of temperature increase on various life stages of a highly migratory species, such as marine turtles, to holistically evaluate potential impacts on the spatial distribution of the species suitability throughout the Mediterranean basin. The second goal, assessed the potential suitability changes in front of the rising sea temperatures on both the life stages and bathymetric characteristics of habitats used by marine turtles in a three-dimensional Mediterranean Sea. Aiming to broaden the study of climate change risk from an individual species to a broader group of Mediterranean species, the third goal of the thesis was to evaluate the risk of climate change on a particularly vulnerable group of marine species in the Mediterranean, the threatened marine fauna according to the IUCN Red List. By selecting a variety of characteristics indicating sensitivity and adaptability to climate change impacts, as well as indicators of species distribution exposure to projected sea temperature increase, I attempted to estimate the risk levels faced by different threatened marine species in future climate change impacts, as well as to identify areas hosting species at the highest risk. With the aim of identifying characteristics expected to respond more to changing climatic conditions, the fourth and final goal of the dissertation was to assess changes in the functional composition of shallow-water fish communities in the northeastern Mediterranean due to upcoming environmental changes.

F.2 Discussion of results and potential applications

In this thesis (Chapter B), I identified the potential changes due to rising temperatures on the suitability of marine habitats for sea turtles, taking into account characteristics of their life cycle, such as their different distribution in the immature and adult life phases. Model predictions for the climatic suitability of habitats for the two stages differed geographically and topographically. The models predicted suitable areas for juveniles mainly in the central and western Mediterranean, in contrast to suitable areas for adults, which were predominantly forecasted for the central and eastern basin. An encouraging finding for future predictions was the possible increase in the extent of suitable habitats for adults and the relative stability predicted surface area for juveniles. The common foraging areas, primarily located in the neritic zone of the central and eastern Mediterranean, are likely to shift westward due to the redistribution of suitable areas for adults, as well as eastward due to the expansion of foraging areas for juveniles toward the eastern Mediterranean.

For an organism with a complex life cycle and behaviour (Casale et al., 2018), changes in the conditions it experiences can affect multiple life stages. If not considered in predictions, we are not able to undertake a comprehensive assessment of the range of climate change impacts on it. In management plans, it is important to identify the life stage that is more susceptible and vulnerable to environmental changes because smaller life stages are usually more vulnerable (Crozier et al., 2021). Predicting impacts only on the adult stage could make our predictions overly optimistic. Indeed, the characteristics of the predicted areas for immature and adult individuals differ, both in terms of their distribution pattern and depth range. The distribution of suitable areas for adults is much more scattered compared to the broader and more extensive distribution of suitable areas for immature individuals. Moreover, the majority of suitable areas for adults were predicted in the neritic zone, while most suitable areas for immature individuals were forecasted in the oceanic zone, farther from the coast. These findings highlight the value of including different life stages of marine species, as individuals may exhibit different behaviours, vulnerability, and adaptive capacity.

Climate-stable regions constitute a significant portion of the current distribution of the two life stages, predicting that the average temperature conditions will not change significantly, maintaining their suitability across a broad range. Nevertheless, when the thermal tolerance range of the species is considered in predictive models, estimates align more closely with reality, and changes are less radical (Gamliel et al., 2020). It is essential to protect the climatically stable areas identified, evaluate the status of their ecosystem structure and function, and assess their overlap with distributions of other significant species that may serve as prey or predators, as they often inhabit high-productivity areas. Changes indicating a reduction in suitability in known foraging areas were identified only in the Gulf of Gabès in Tunisia. Conditions there may change unfavourably for the species' climatic habitat, necessitating better monitoring of sea turtle populations and marine fauna in general, as this region may host the southern extremes of marine species distributions. Regarding juvenile individuals, further investigation is needed for their eastern expansion, as their presence is considered incomplete due to the lack of telemetry data for the eastern Mediterranean. Data exist for their presence in Cyprus, with key areas of their spread being the Southern Adriatic and the Ionian Sea, the Strait of Sicily, and the Tyrrhenian Sea, Algeria, and the western Mediterranean due to the upwellings formed, serving as abundant sources of

zooplanktonic prey for them (Casale et al., 2018).

On the other hand, the anticipated increase in favourability of conditions towards the western Mediterranean aligns with field observations (Mancino et al., 2022). Management should consider these findings as they could provide valuable insights for the design or expansion of future marine protected areas for sea turtles (Mazaris et al., 2023), given the apparent shift in their distribution westward. Additionally, nesting areas in the western Mediterranean, where sporadic events of egg-laying may occur, benefit from close monitoring of nesting trends, protection of adult females, nests, and hatchlings (Mancino et al., 2022). It is crucial to investigate the cumulative impact of anthropogenic pressures in these areas that may hinder successful future population establishment, such as high fishing efforts (Almpanidou et al., 2021). Systematic visits to the proposed new marine areas for adults in the western Mediterranean may lead to the establishment of more stable nesting areas. Thus, future enhanced and institutionalized protection for these previously occasional nesting areas is suggested (Mancino et al., 2022). Common areas for both life stages provide a fertile ground for spatially legislative measures that affect both stages, leading to greater overall effectiveness in their life cycle.

Assessing the bathymetric coherence of climatically suitable areas for marine turtles in the Mediterranean in the present and future (Chapter C), I identified suitable sea areas spanning different depths. I also highlighted cases of projections of future temperature increases that may affect the suitability of areas differently based on their depth. Deeper marine ecosystems have started to be recognized as ecosystems requiring attention for research and protection. Despite hosting particularly vulnerable ecosystems (cold-water corals, sponges), protection measures for these areas are currently insufficient (Morato et al., 2018; Visalli et al., 2020; Combes et al., 2021). Their exploration and protection are essential due to the exploitation of deeper oceans driven by the biotechnology industry, extraction of precious biochemicals, oil and gas, and mining activities (Dunn et al., 2018).

The integration of temperature predictions for 5m, 25m, and the seafloor led to a distribution pattern with fewer areas predicted as suitable for adult individuals in the oceanic zone compared to the previous analysis using surface sea temperature predictions only (Chapter B). Additionally, the distribution of immature individuals was more extensive in the surface layers compared to deeper ones and those extending throughout the water column that were spatially restricted. The distribution of suitable marine three-dimensional areas across different bathymetric zones varied for each life stage, reflecting the feeding strategy followed by immature and adult individuals. While adults exhibit a range of feeding behaviours, they primarily forage in the neritic zone, and their frequency of foraging increases with size (Hatase et al., 2007; Reich et al., 2007).

Regarding the extensive distribution of suitable areas near the sea surface for immature individuals, their presence in the oceanic zone is observed, but rarely at great depths (Freitas et al., 2018; Chimienti et al., 2020). This analysis predicted extensive suitability areas in the upper water column, with some significant areas extending throughout the water column, mainly in the northern Mediterranean. This reflects regions where immature individuals can reach coastal areas after reaching a larger size and migrate to

coastal areas to feed on benthic or pelagic prey species (Blasi & Mattei, 2017).

Temperature increase predictions on suitability differed for distinct bathymetric diets. For immature individuals, an expansion of their suitability distribution extending throughout the water column toward their northern and central suitable areas was predicted. In contrast, a contraction of their suitability near the sea surface in the southeast region was forecasted for the future. Concerning adult individuals, an expansion of climatically suitable areas toward the west was predicted, supported by an increasing number of observations of nesting events in the western Mediterranean (Hochscheid et al., 2022; Mancino et al., 2022; Cardona et al., 2023). Adults do not exhibit an increased frequency in foraging areas in the western Mediterranean as immature individuals do (Casale et al., 2018). Nevertheless, as climatic conditions in these areas become suitable for adult individuals, such as the coastal areas of the Balearic Islands, they may remain on western beaches and nest for consecutive years, maintaining a continuous presence (Hochscheid et al., 2022), as previously emphasized. The potential loss of suitability in the southern distribution and the gain of suitability in northern and western areas align with the broader pattern of species distribution changes in response to climate change, with species spreading towards the poles and contracting towards the Equator, and a decrease in abundance observed for areas near the southern extremes of distributions (Hastings et al., 2020; Hochscheid et al., 2022).

Previous research has generally shown that higher sea surface temperatures are associated with an increased frequency of daily dives, longer dive durations, and more dives to the seafloor by sea turtles (Iverson et al., 2019). On average, loggerhead sea turtles dive to depths of 5-15m, with less time spent diving below 50m. However, they spend over 70% of their time at depths of 0-30m, with an average dive duration ranging from 2 to 340 minutes. During winter, sea turtles engage in longer dives as reduced temperatures suppress their metabolic rates, leading to decreased oxygen consumption and prolonged aerobic capacity during their dives (Hochscheid, 2014). Nevertheless, loggerhead sea turtles have been found to perform deeper dives during higher temperatures. Elevated temperatures are linked to more frequent dives, suggesting that as temperatures rise, their dives may become more frequent (Iverson et al., 2019). Therefore, this could represent an adaptation mechanism to increasing temperatures or heatwaves, and their vertical movement should not be overlooked. These analyses can contribute to better understanding the increasingly competitive human activities in the sea, highlighting interactions between marine life and human pressures, especially in deeper bathymetric zones beyond the surface (Doxa et al., 2022).

By determining the exposure of bathymetric diets to increased sea temperatures and collecting a series of vulnerability and adaptive capacity characteristics (Chapter D), I attempted to assess the risk levels faced by threatened marine species in the Mediterranean. The findings of this study revealed that various taxonomic groups and threatened marine species face a high level of risk from climate change. Therefore, an ecosystem-based approach to ongoing and dynamically evolving management is necessary, with assessments of overall impacts on each marine community. Moreover, the examination should include not only individual species' vulnerabilities but also the combined vulnerability of interacting species to climate change, depending on the scale at which populations of each taxonomic and functional group are distributed in the Mediterranean (Ellis et al., 2011; Rilov et al., 2019).

In recent decades, researchers, conservationists, and policymakers have shifted their

focus from protecting a single species to preserving the structure and function of entire ecosystems. This shift allows us to move beyond understanding the potential responses of a species to a unique stress factor, to comprehend multiple factors affecting multiple organisms and their functioning in ecosystems. Similarly, there has been an increase in conducting experiments studying three or more organisms in response to changes in their conditions (Bass et al., 2021).

Most MPAs in the Mediterranean are predicted to host distributions of a significant number of species with a high level of climate risk. This underscores their crucial role in systematically monitoring these species, improving the potential for population recovery, and developing restrictive measures for unsustainable anthropogenic practices that may synergize with the impacts of climate change (Soto-Navarro et al., 2021). Marine protected areas in the Mediterranean need to explore the distributions of species they harbour, characterized by high climate risk. At least one species with a high-risk level is found in all MPAs, with over half of them hosting more than 10 species with high climate risk. MPAs alone cannot mitigate the impacts of climate change; their role lies in providing conditions that support species adaptation, reducing stress from other pressures, and monitoring the abundance and presence of these species (Rilov et al., 2019).

Marine protected areas, particularly those in the western Mediterranean, Adriatic, and Aegean, where the presence of species with high climate risk is more abundant, should incorporate the monitoring of climate-vulnerable species into their operational plans. They should identify which of these species they harbour, assess their conservation status, and propose management measures. Static spatial MPAs alone cannot fulfil their role in adapting to climate change; a management approach that encompasses the entire Mediterranean basin, regardless of MPA boundaries, is essential (Rilov et al., 2019).

MPAs themselves may not fulfil their role if the species they harbour shift their distributions beyond their boundaries. Unfortunately, the southern and eastern Mediterranean, where most populations are expected to decline, lack sufficient MPAs, and populations cannot benefit from management measures that would provide some adaptive capacity due to uncontrolled and regulated anthropogenic pressures (Rodríguez-Rodríguez et al., 2016). In the anticipated changes in the Mediterranean, it is crucial to collect data for the southern and eastern Mediterranean, where data are scarce. This region can provide information about ecosystems already undergoing transition due to the combined impact of temperature increase, fishing, pollution, and the introduction of new species from the tropics, as observed in the Levantine Sea (Rilov, 2016).

Finally, aiming to identify potential changes in key characteristics of fish communities in the northeastern Mediterranean due to changing environmental conditions (Chapter E), the results of the analysis indicated that future conditions may favour a shift in the functional composition towards smaller and short-lived fish in coastal areas, with the possibility of altering the functional patterns of the northeastern Mediterranean ecosystem, which, in turn, could impact the ecosystem services provided for human and non-human well-being. This pattern becomes evident for mid-term scenarios (2030-2060), but changes are even more pronounced for the long-term scenario (2060-2090). Indeed, Mediterranean fisheries landing data have shown an increasing trend in populations, primarily of species with shorter life spans, benefiting from the rise in water temperature (Tzanatos et al., 2014), as well as the absence of larger individuals

(Damalas et al., 2015a). In this scenario, both the impacts of climate change and fishing pressure may contribute to favourable age, size, and geographic diversity of species (Brander, 2007).

With the increase in sea temperature, formerly colder conditions acting as a natural barrier to the spread of warmer species may now become sustainable (Titelboim et al., 2019). Thus, species with shorter life spans, earlier maturation age, and smaller size are predicted to expand their range and abundance northward. The minimum temperature of the coldest month, representing a thermal extreme for fish, emerged as a crucial factor for fish community patterns in the northeastern Mediterranean. While temperature and size appear to have an inversely proportional relationship, exceptions to this rule exist (Ohlberger, 2013).

The anticipated connection of these characteristics with environmental variables may contribute to creating new and advanced indicators based on features and timely warning signs, allowing for better monitoring of current trends and responses and improved prioritization of management actions based on changing functional patterns. Further investigation is crucial to explore whether favourable conditions are predicted to extend to greater depths, such as 15m, as these species have three-dimensional distribution, and this choice could aid in their potential adaptation. This may involve the expected increase in abundance of smaller species and the decrease in the distribution of larger species in surface waters, with the possibility for these species to shift their distribution towards the Black Sea.

F.3 New research proposals and challenges

Management measures against climate change must be specific, with as many quantitative targets as possible and biologically informed about impacts on the flora and fauna of the region. As highlighted above, findings of this thesis can contribute to management proposals for climate change and marine biodiversity. Primarily, findings of the present thesis highlight areas in need of protection hosting multiple life stages of marine turtles, such as common foraging areas maintained under present and future conditions, considering anthropogenic pressures at both surface and deeper layers (Stelzenmüller et al., 2018). Findings on climate suitability in certain areas varied according to different life stage and different bathymetric zones. Life cycle and bathymetric behaviour of the species matter, so spatially determining three-dimensional management areas for marine turtles necessitates considering their inclusion. Acknowledging the bathymetric range a species possesses helps to select the most representative depths for environmental data in respect to species. However, further research for the environmental variables that organisms respond to along depth is essential, as alterations in the distribution patterns may be related to events and changes in bathymetric surfaces different from the one they frequent (Collie et al., 2008).

While temperature increase corresponds to a gradual change in climate conditions, researchers and managers can derive valuable insights for species responses from short-term events, such as extreme weather phenomena such as marine heatwaves (Rilov et al., 2019; Garrabou et al., 2022). The findings of this thesis provided an initial assessment of the climate risk for vulnerable marine animals, which could prioritize these species in face of climate change. Both extreme climate events and species responses to weather phenomena could provide useful insights as indicators for the potential species responses to average changes in their environmental conditions (Bates et al., 2018). Moderate-scale marine heatwaves could prove adaptive for some populations, as individuals with higher thermal tolerance survive and are selected (Smith et al., 2023), therefore extreme weather phenomena, and their frequency, intensity, and duration, should be incorporated in species distribution models for the future projections.

Findings of this thesis support that future conditions might favour a shift in the functional patterns of fish fauna of northeastern Mediterranean shallow waters towards smaller sizes and shorter lifespans. Since responses to climate change affect not only the species and their populations, but also biotic interactions and overall, marine communities, it is essential to analyze how potential changes might interact with the existing state of marine communities. A good monitoring by all possible means of the status of marine communities in the Mediterranean (Bevilacqua et al., 2020) could contribute to recording and understanding these changes that may lead to ecosystem-level transformations, such as the conversion of marine macrophyte ecosystems into barren areas (Rilov, 2016). Functional grouping of species within communities based on characteristics, such as their ability to migrate to greater depths (Thorpe et al., 2022), as identified in Chapter D, could shed light on marine communities that may be more susceptible to changes or, conversely, may have increased capacity for adaptation. Exploring alternative ways of perception and grouping could direct us in the creation of new monitoring indicators for species and community responses and predictions for ecosystem services.

Existing Marine Protected Areas (MPAs) can offer positive synergies for research, monitoring and further protection measures. While MPAs cannot directly mitigate the impacts of temperature increase, they can play a crucial role in securing conditions facilitating species adaptation. This includes safeguarding genetic diversity by ensuring an environment free from anthropogenic pressures such as pollution or maritime traffic, and by preventing the removal of individuals from the population from fishing (Rilov et al., 2019). As information accumulates regarding distribution shifts or abundance changes, collectively this information could contribute to identifying areas of change at sea. Thus, we should explore the level of possible protection of these areas by already existing protected areas, as some of these areas might be of great importance such as the well-known foraging area of sea turtles in the Gulf of Gabes, that was shown to be possible losing its thermal suitability in face of climate change.

The absence of protection and monitoring for such a significant marine area renders it exposed to multiple pressures beyond climate change and weakens populations' adaptive capacity. However, predictions could shed light on areas that are not expected to be impacted by climate-driven changes (Doxa et al., 2022). These areas also may spatially overlap with existing MPAs, so we would suggest future research to explore the possibility of it and assess future protection effectiveness. Moreover, future projections of distributions could help in designating potential new MPAs, as our findings revealed new areas for sea turtles in the western Mediterranean. Nevertheless, since the presence of MPAs in the southern and eastern Mediterranean is minimal (Rodríguez-Rodríguez et al., 2016), and conflicts may arise in respective countries, a more holistic understanding of the current situation for marine biotic communities and associated social groups is deemed necessary. This understanding should encompass ecological and socio-economic aspects, acknowledging that these areas may potentially host the most vulnerable southern distribution edges of marine species or even new species of tropical origin.

F.4 Conclusions

The general pattern of climate-induced changes includes poleward range expansions and equatorward contractions (Pinsky et al., 2020), with local hydrographic and microclimatic factors, however, causing a more spatially heterogeneous patterns of impacts (Helmuth et al., 2006). Within this context, projected changes in the climatic suitability for marine turtles showed a potential spread of adults towards the northwestern edge of their distribution in the Mediterranean. Nevertheless, increases and decreases in suitability were scattered across their distribution (Chapter B). Given observations supporting a potential westward shift in adults' nesting (Mancino et al., 2022), areas of increasing occurrence of foraging and nesting should be safeguarded against possible bycatch by intense incidental fishing or extended urbanization along nesting beaches, respectively.

The results of the analysis suggest that climate suitability changes varied according to sea turtle life cycle stage and thus, the corresponding foraging behaviour patterns of individuals. For instance, a reduction in climatic suitability was predicted for earlier life stages at the southeastern edge of their distribution in the Gulf of Gabes. Inclusion of different life stages emerged as a significant factor in a more comprehensive assessment of species suitability projections in face of climate change. The scattered and mainly neritic distribution of adults differed from the more extensive and oceanic distribution of immature individuals, differences primarily attributed to their foraging behaviour. At the depth level, an increase in suitability was projected for the deeper waters of the Adriatic and Aegean Seas for immature individuals (Chapter C). However, smaller immature individuals are less likely to approach these depths compared to larger, more mature individuals that exhibit better buoyancy, dive deeper, and some may begin to feed on benthic prey (Hays et al., 2004). Even for adults and larger immature individuals, pulmonary respiration restricts them to necessary surface visits, which may increase in frequency due to rising sea temperatures, representing a potential mechanism for acclimatization to higher temperatures.

While understanding the potential response of charismatic sea turtles to climate change is fundamental for comprehending broader impacts on marine biodiversity, high levels of climate risk are imminent for most marine taxonomic groups (Chapter D). Some species may have different responses due to their distinct characteristics mediating their reactions. However, certain species share common features and can be grouped into possible responses, such as species with high dispersal ability or pelagic species, mainly recorded to exhibit distribution shifts (Cheung et al., 2009; Walsh et al., 2015). Although the analysis has characterized some species as having a high risk due to climate change, the risk for each species and its populations may qualitatively differ based on the variety and significance of its interactions with other species. If the abundance of some species declines in response to climate change or other pressures, other species with similar niches, either already present in the biota or species colonizing it due to more favourable thermal conditions, may replace their ecological roles. Therefore, their functions could continue to be performed by different species (Fonseca & Ganade, 2001). This represents functional redundancy, and the ecosystem's function does not change significantly.

However, this thesis has demonstrated that in a region of interest for climate change, such as the northeastern Mediterranean, future conditions are expected to favour a shift

in the functional characteristics of shallow-water fish towards smaller sizes and shorter lifespans (Chapter E). The predicted increase in abundance and extent of smaller fish with shorter lifespans is likely to constitute a change for the functioning of the ecosystem in the northeastern Mediterranean, an ecosystem already impacted in the Southern Aegean by new herbivorous fish species (*Siganus luridus*, *Siganus rivulata*) originating from the Suez Canal, which exert pressure on marine macrophytes that have migrated to shallower waters (Rilov, 2016; Nikolaou et al., 2023).

In conclusion, the incorporation of our knowledge on species ecological requirements, habitats, physiology, behaviour and their lifecycle produced much more biologically informed results for our predictions on future distribution shifts, risk assessments to climate change and future functional patterns. This approach could enhance our modelling efforts and enrich methodological frameworks for future climate change assessments, with characteristics of marine species representing necessary parameters to be taken under consideration in current and future conservation plans.

G. References

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H. Appendix with supplementary methods and results

Supplementary material – Chapter B

List of sources used to compile a database of the available satellite tracked data and delineate the foraging areas of adult and juvenile loggerhead sea turtles in the Mediterranean region:

Adults' presences:

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Predictive capability of the model according to different buffers used

Pseudoabsences were randomly selected with a standard distance (buffer) away from the presence data. Applying buffers with alternative distances (3, 5, 8 and 10 cells away from presence data) it was observed that as distance increased, the performance of the models got better measured by indices of AUC.

Supplementary Table B.S1: Predictive performance of the model with application of different distances (buffer) away from the presence data.

Buffer	AUC			
	3 cells	5 cells	8 cells	10 cells
Juveniles	0.82	0.86	0.88	0.90
Adults	0.83	0.8485	0.85	0.8580

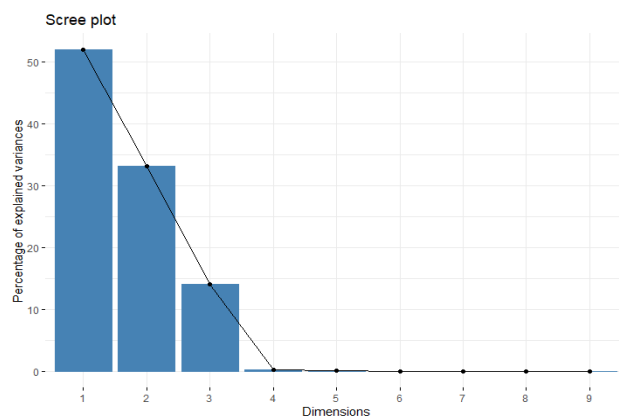
Principal Components Analysis (PCA)

PCA analysis constructs new uncorrelated variables (called eigenvectors or PCA axes), by using the nine bioclimatic variables. Each new variable interprets a certain percentage of data variability of the initial bioclimatic variables. The percentage of variability explained by the new synthetic variables is decreased moving from the first to the last variable.

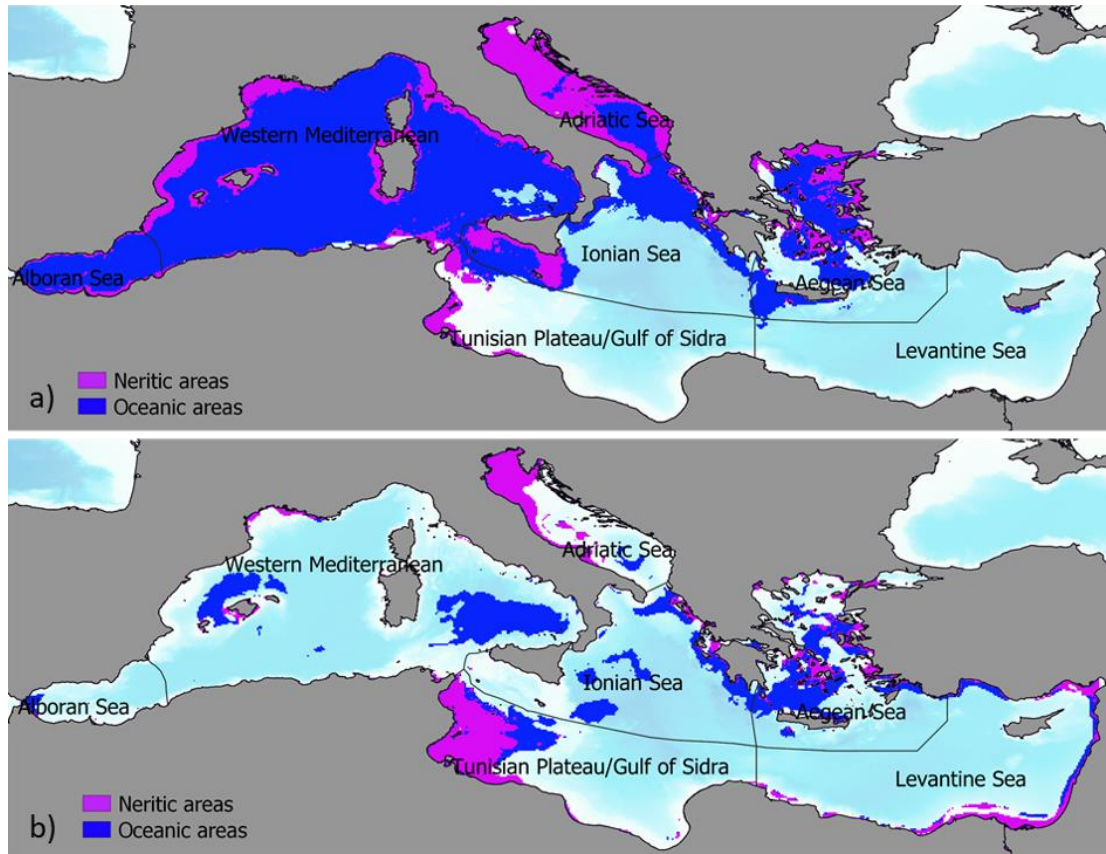
PCA processed the rasterbrick of 9 bioclimatic variables, both for the present and for the future conditions. It reconstructed new nine variables, the principal components, that are uncorrelated. Each one explains a certain percentage of variance of the previous data derived from the 9 bioclimatic variables. The selection of the suitable number of principal components to include in the analysis can be also drawn with the assistance of the scree plot (Fig. S1).

Supplementary Table B.S2: Eigenvalues of each one of the nine principal components of the PCA

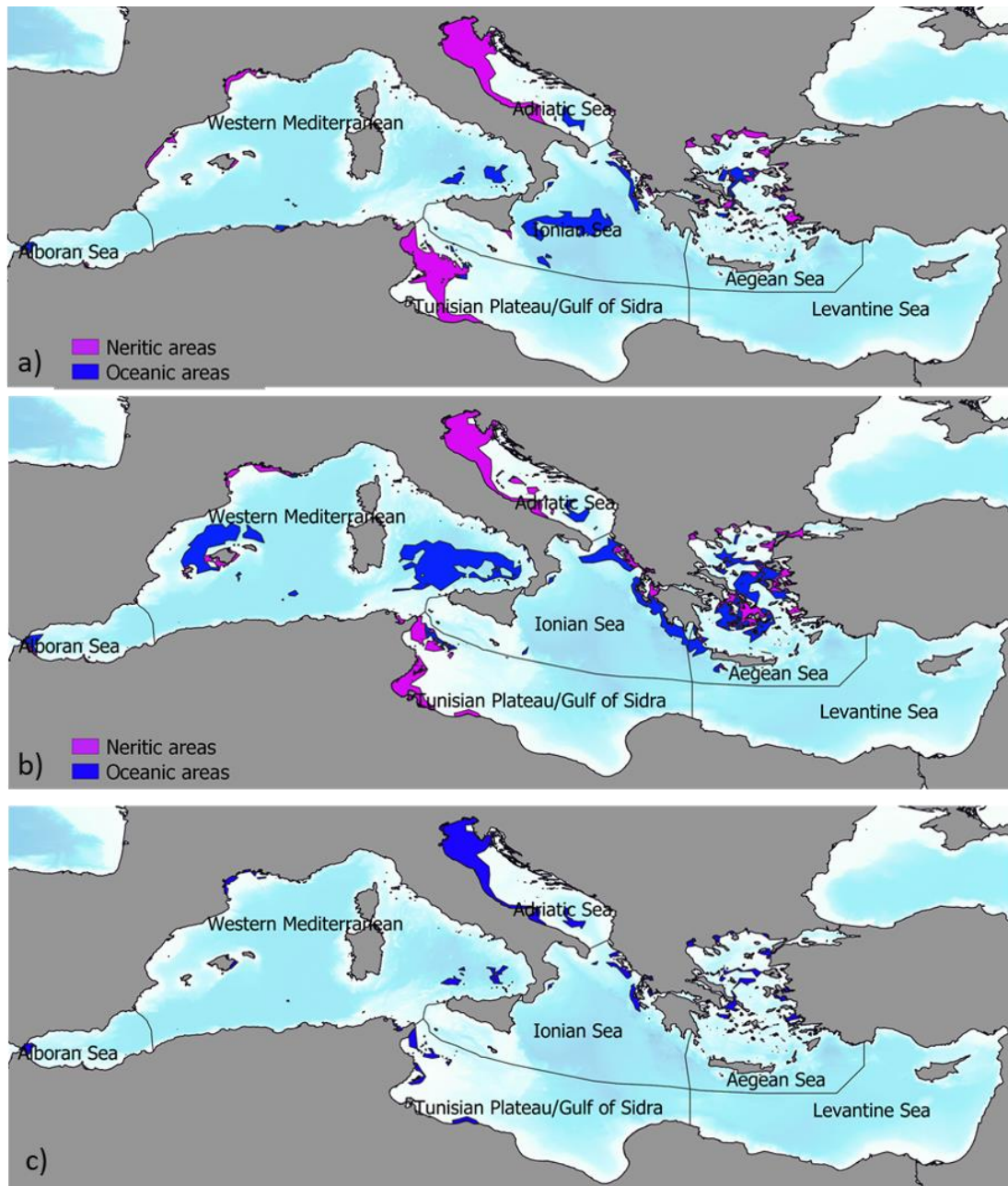
Principal Components	Eigenvalue
PC1	4.683096e+00
PC2	2.992103e+00
PC3	1.270969e+00
PC4	3.185494e-02
PC5	1.489704e-02
PC6	6.478261e-03
PC7	5.683383e-04
PC8	3.369513e-05
PC9	3.634985e-16



Supplementary Figure B.S1: Scree plot of the PCA of the nine bioclimatic variables showing the percentage of explained variance by its principal component. The first 3 principal components account for the 99.4% of the variance of the data.

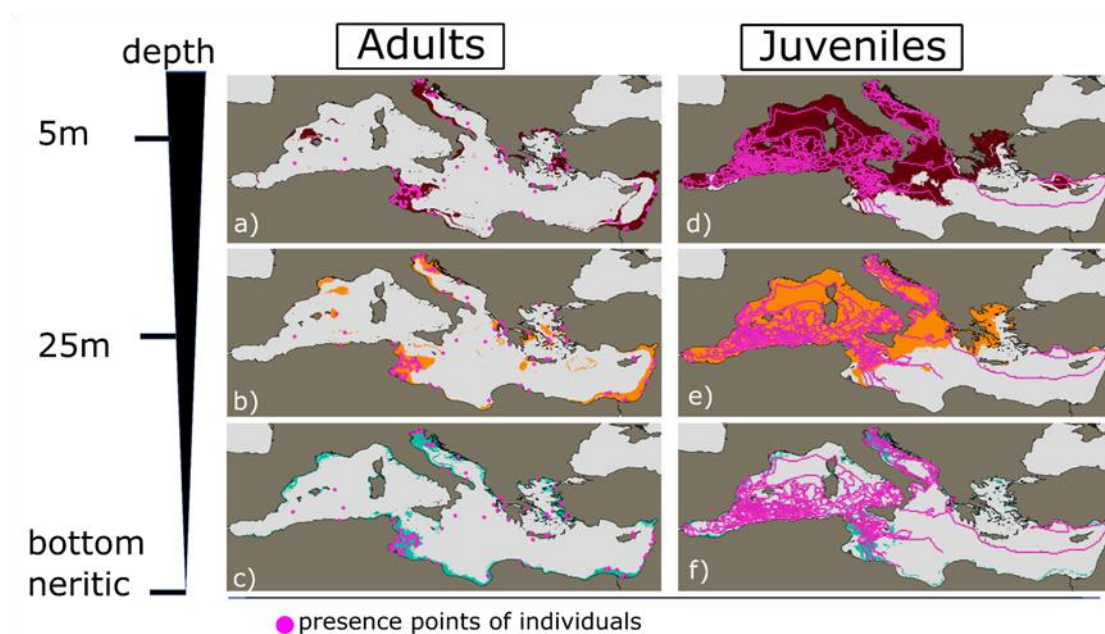


Supplementary Figure B.S2: The distribution of foraging grounds of (a) juvenile and (b) adult loggerhead sea turtles, *Caretta caretta*, under future (2051-2080) climatic conditions across the Mediterranean Sea. Neritic grounds are colored in purple, while oceanic ones are colored in dark green. Marine ecoregions (sensu Spalding et al., 2007) comprising the Mediterranean Sea are delineated by black dashed lines.



Supplementary Figure B.S3: The distribution of common foraging grounds of juvenile and adult loggerhead sea turtles, *Caretta caretta*, under (a) present (1991-2020) and (b) future climatic conditions (2051-2080) across the Mediterranean Sea. Neritic grounds are delineated in purple color, while oceanic ones are colored in dark green. In panel c) the distribution of important foraging grounds of juvenile and adult individuals, (i.e., areas that sustain their climatic suitability under present (1991-2020) and future climatic conditions (2051-2080)) across the Mediterranean Sea is depicted in red color. Marine ecoregions (sensu Spalding et al., 2007) comprising the Mediterranean Sea are delineated by black dashed lines.

Supplementary Material – Chapter C



Supplementary Figure C.S1: Potential distribution of climatically suitable foraging areas for 5m, 25m and neritic bottom habitats for adult (a-c) and juvenile (d-f) loggerhead sea turtles under present-day conditions in the Mediterranean Sea in combination with presence points of adult and juvenile sea turtles, respectively.

PCA analysis constructs new uncorrelated variables (called eigenvectors or PCA axes), by using the nine bioclimatic variables. Each new variable interprets a certain percentage of data variability of the initial bioclimatic variables. The percentage of variability explained by the new synthetic variables is decreased moving from the first to the last variable. PCA processed the rasterbrick of 9 bioclimatic variables, both for the present and for the future conditions. It reconstructed new nine variables, the principal components, that are uncorrelated. Each one explains a certain percentage of variance of the previous data derived from the 9 bioclimatic variables.

Supplementary Table C.S1: Proportion of variance explained for the first two out of nine produced principal components of the PCA analysis, for the nine bioclimatic variables of every depth layer considered (5m, 25m, bottom neritic) for the two lifecycle stages (juvenile, adult) considered.

Principal Components	Proportion of variance explained					
	Adults			Juveniles		
	5m	25m	Bottom neritic	5m	25m	Bottom neritic
PC1	0.9957	0.9905	0.9724	0.9679	0.9888	0.9978
PC2	0.0042	0.0094	0.0250	0.0294	0.0111	0.0020

Supplementary Table C.S2: Mean predictive performance (AUC and TSS indices) of each of the ensemble model for the two lifecycle stages (juvenile, adult) for every depth layer considered (5m, 25m, bottom neritic).

Lifecycle stage	Depth	Mean AUC	Mean TSS
Juveniles	5m	0.88	0.66
	25m	0.89	0.7
	Bottom neritic	0.73	0.38
Adults	5m	0.77	0.57
	25m	0.78	0.57
	Bottom neritic	0.91	0.79

Supplementary Material – Chapter D

Detailed description of information acquisition for traits and their ordered levels

1. Quantitative traits

I retrieved information concerning the species **preference in narrow thermal conditions** based on their preferred temperature range as noted in Fishbase for fish and sharks, SeaLifeBase for marine mammals, sea turtles and invertebrates, as well as WORMS which accounts for all marine taxa. Information on species **generation length** and **body size** were also retrieved from the abovementioned databases, considering an average generation length in case of various reported estimations per species and the maximum reported length per species for body size. To convert these quantitative traits into vulnerability ranks, I considered the 3 respective quantiles for each of the three traits, we assigned them into three levels of vulnerability (high, moderate, low).

2. Qualitative traits

Information on species **dispersal ability** was extracted from Fishbase and SeaLifeBase, considering two modalities, i.e., migratory (oceanodromous, anadromous, catadromous) or sessile species. Sessiles were considered as high climate change vulnerability species. Migratory species were considered as low vulnerability species to climate change, while motile species at least at one life stage were considered as moderate vulnerability species.

The **IUCN status** was retrieved from the IUCN RedList website (<https://www.iucnredlist.org/>), based on the Mediterranean regional assessment. Critically endangered species were considered in the high vulnerability rank category.

Information on the **impact score of other non-climatic threats** was also retrieved from the IUCN RedList website, from the “Threats in detail” section. I assigned species a high, moderate or low score according to the highest score received for a threat in the list. E.g., if for at least one threat the impact score was medium, then the species was considered of medium impact score of other non-climatic threats, whereas if at least one threat had a high impact score, the species was considered of high impact score.

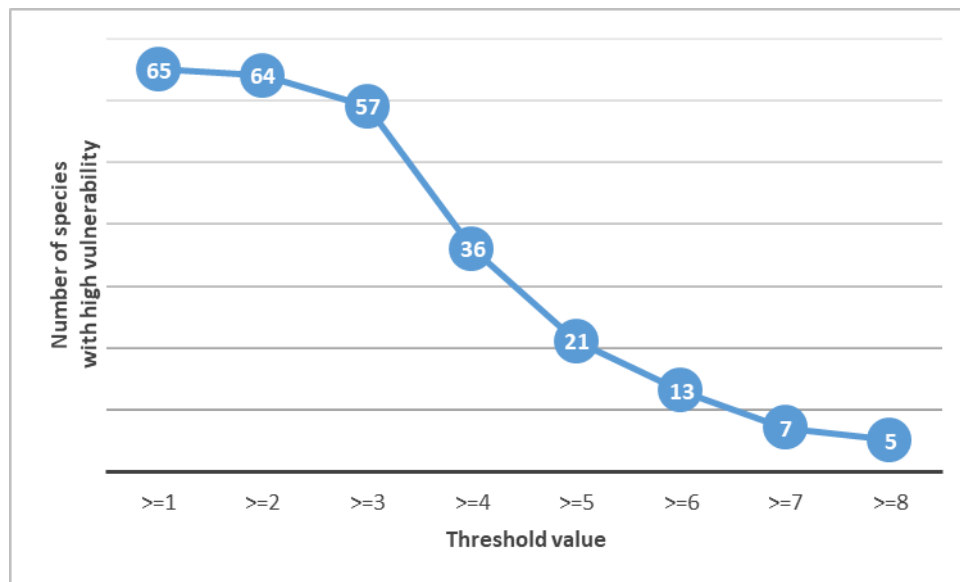
Information on **use of habitats likely to be impacted by sea level rise** was also retrieved from the IUCN RedList website, as reported in the “Habitat and Ecology” section. Considered habitats included: marine neritic, marine oceanic, marine deep benthic, marine intertidal, marine coastal/supratidal and artificial/aquatic & marine. For species assigned to solely oceanic habitats, vulnerability rank was considered low. For species assigned to coastal terrestrial and neritic habitats with no reference to an oceanic habitat, I assigned a high vulnerability rank. Moderate vulnerability referred to a combination of these habitats.

Regarding species’ **dependence on calcification processes**, I classified them according to their taxonomic group, which we retrieved from the IUCN RedList website. Highest

vulnerability was accounted for Anthozoa, Malacostraca and Bivalvia, which use calcification processes for their survival. Fish were accounted for medium sensitivity because of calcification processes in their ear and impacts of ocean acidification on lethality of larvae (Koenigstein et al., 2016). Rest of the groups, such as mammals and sea turtles, were accounted as of low vulnerability rank. Species that do not use calcification processes, like fish, but are vulnerable to ocean acidity levels during juvenile life stage, were categorized as moderate vulnerability rank species.

Information on species **vertical dispersal ability** as a possible response to climate change was retrieved from the Aquamaps database (personal communication). Based on species' depth ranges, we considered three categories: i) low vulnerability species, the ones occurring in depths greater than 200m, as they could be able to migrate deeper, ii) high vulnerability species, the ones occurring in the shallow waters up to 40m, as they would be more exposed to surface temperatures and iii) moderate vulnerability species those occurring within 40m to 200m of depth.

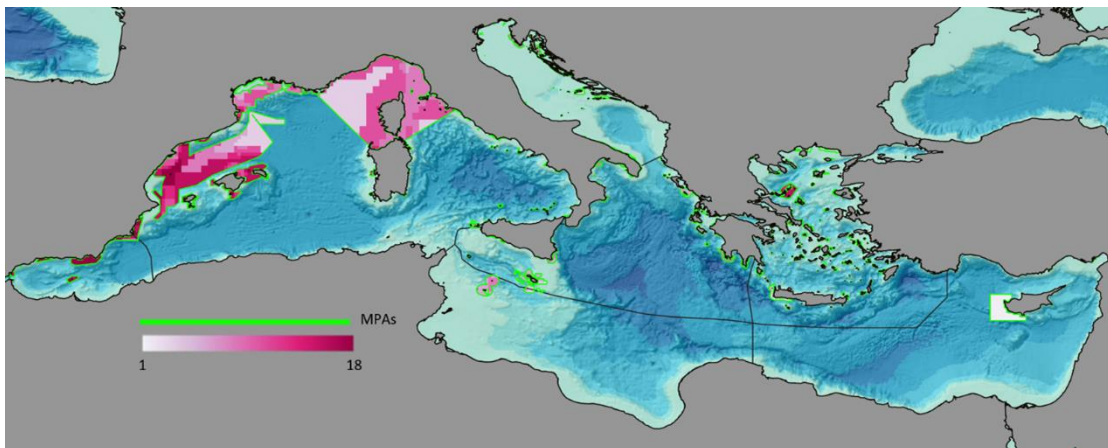
Finally, for the two traits of **specialized requirements on habitat and diet**, information was acquired from experts' judgement. Diet specialization was categorized in two large categories, of (i) diet generalists and (ii) species with very specific requirements in diet selection. Categories for specialized requirements on habitat were retrieved from the publication of NOAA Technical Memorandum on the Methodology for Assessing the Vulnerability of Marine Fish and Shellfish Species to a Changing Climate, based on experts' opinion (Morrison et al, 2015).



Supplementary Figure D.S1: Number of species considered as high vulnerable according to the selected threshold. The threshold values represent the number of traits of high vulnerability. The higher the threshold (more high vulnerability traits needed to define high vulnerability species) the lower the number of species with high overall vulnerability. In threshold ≥ 3 , the system seems to reach an overall plateau, as lower threshold values do not increase dramatically the number of highly vulnerable species.

		Vulnerability factor 1		
		Low	Moderate	High
Vulnerability factor 2	Low	Low	Low	Moderate
	Moderate	Low	Moderate	High
	High	Moderate	High	High

Supplementary Figure D.S2: Estimation of the overall vulnerability of a species based on a combination of semi-quantitative and quantitative approach (Vulnerability factor 1 & 2), according to the logical matrix adapted from (Jones & Cheung, 2018), for the three categories of vulnerability.



Supplementary Figure D.S3: Number of threatened species with high risk to climate change inside Mediterranean marine protected areas. Marine ecoregions (sensu Spalding et al., 2007) of the Mediterranean Sea are delineated by black lines. MPAs are highlighted in green color.

Supplementary Table D.S1: Number of high climate risk species in each marine ecoregion of the Mediterranean Sea. The last column includes mean number of all threatened species in each marine ecoregion.

Marine ecoregion	High climate risk species			All threatened species
	Mean number of species per cell	Minimum number of species per cell	Maximum number of species per cell	Mean number of species per cell
Adriatic Sea	7.9	1	16	34.9
Levantine Sea	1.7	1	11	6.5
Tunisian Plateau/Gulf of Sidra	3.28	1	11	15.3
Ionian Sea	3.4	1	15	12.9
Aegean Sea	6.05	1	20	22.6
Alboran Sea	18.6	10	22	60.1
Western Mediterranean	8.34	1	22	26.9

Supplementary Table D.S2: Threatened species of the Mediterranean Sea with high risk to climate change and their respective vulnerability and exposure scores. High risk is a combination of the species exposure and vulnerability rank. In order to be characterized with high risk, a species should have either a moderate exposure and a high vulnerability, or vice-versa, or both high ranks for vulnerability and exposure. Taxonomic group was selected based on the taxonomic organization of class, assigned by the IUCN RedList.

Species	IUCN status	Taxonomic group	Exposure	Vulnerability
<i>Aetomylaeus bovinus</i>	CR	Chondrichthyes	moderate	high
<i>Alopias superciliosus</i>	VU	Chondrichthyes	moderate	high
<i>Alopias vulpinus</i>	VU	Chondrichthyes	moderate	high
<i>Anguilla anguilla</i>	CR	Actinopterygii	moderate	high
<i>Balaenoptera physalus</i>	VU	Mammalia	high	moderate
<i>Carcharhinus brachyurus</i>	VU	Chondrichthyes	moderate	high
<i>Carcharhinus brevipinna</i>	VU	Chondrichthyes	moderate	high
<i>Carcharhinus melanopterus</i>	VU	Chondrichthyes	high	high
<i>Carcharhinus obscurus</i>	EN	Chondrichthyes	high	high
<i>Carcharhinus plumbeus</i>	EN	Chondrichthyes	moderate	high
<i>Carcharias taurus</i>	CR	Chondrichthyes	high	high
<i>Carcharodon carcharias</i>	CR	Chondrichthyes	moderate	high
<i>Caretta caretta</i>	VU	Reptilia	high	high
<i>Centrophorus granulosus</i>	CR	Chondrichthyes	moderate	high
<i>Cetorhinus maximus</i>	EN	Chondrichthyes	high	high
<i>Chelonia mydas</i>	EN	Reptilia	high	moderate
<i>Cladocora caespitosa</i>	EN	Anthozoa	high	high
<i>Corallium rubrum</i>	EN	Anthozoa	high	high
<i>Crassophyllum thessalonicae</i>	EN	Anthozoa	high	high
<i>Delphinus delphis</i>	VU	Mammalia	high	moderate
<i>Dermochelys coriacea</i>	VU	Reptilia	moderate	high
<i>Desmophyllum dianthus</i>	VU	Anthozoa	moderate	high
<i>Isidella elongata</i>	CR	Anthozoa	moderate	high
<i>Madrepora oculata</i>	VU	Anthozoa	moderate	high
<i>Physeter macrocephalus</i>	VU	Mammalia	moderate	high

Supplementary Table D.S3: Eigenvalues of each of the eight dimensions from the Joint Correspondence Analysis, with the percentage of the variance explained by each of them. Dimensions with darker colour were selected for the analysis (inertias lower than 0.013)

Dimension	Principal Inertias	% of inertia explained by JCA
1	0.041493	43.8%
2	0.025664	62.5%
3	0.012974	74.4%
4	0.006402	84%
5	0.004025	90.2%
6	0.001209	92.7%
7	0.000994	95%
8	0.000572	96.6%
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Total inertia:	0.100992	

Supplementary Table D.S4: Loadings of the vulnerability traits' modalities to the first two dimensions of the Joint Correspondence analysis. K=1 and K=2 represent the principal coordinate for each dimension K of the solution (x1000). Trait modalities grouped in the same graph quadrant are highlighted in bold.

Trait	Modality	K=1	K=2
Use of calcification processes	low	-130	-237
Dispersal ability	high	-107	-207
Specialized requirement on diet	high	-143	-186
Preference in narrow thermal conditions	low	-177	-125
Body size	high	-169	-131
Preference in narrow thermal conditions	moderate	-110	-168
Use of habitats likely to be impacted by SLR	low	-32	-91
Use of habitats likely to be impacted by SLR	moderate	-29	-50
Vertical migration ability	low	-46	-34
Specialized requirements on habitat	moderate	389	-317
Impact score of other non-climatic threats	moderate	125	-292
Specialized requirements on habitat	high	317	-240
Generation length	high	11	-229
IUCN status	moderate	74	-222
Use of calcification processes	high	865	-121
Specialized requirement on diet	low	7	9
IUCN status	low	57	64
Body size	low	376	101
Use of habitats likely to be impacted by SLR	high	62	126
Dispersal ability	low	862	135
Impact score of other non-climatic threats	high	305	145
Preference in narrow thermal conditions	high	144	146
Vertical migration ability	moderate	199	251
Generation length	low	169	277
Vertical migration ability	high	767	321

Use of calcification processes	moderate	-244	67
Generation length	moderate	-192	201
Dispersal ability	moderate	-81	237
IUCN status	high	-165	108
Body size	moderate	-252	99
Specialized requirements on habitat	low	-107	84
Impact score of other non-climatic threats	low	-68	90

Supplementary References

Morrison, W.E., M. W. Nelson, J. F. Howard, E. J. Teeters, J. A. Hare, R. B. Griffis, J.D. Scott, and M.A. Alexander. 2015. Methodology for Assessing the Vulnerability of Marine Fish and Shellfish Species to a Changing Climate. U.S. Dept. of Commer., NOAA. NOAA Technical Memorandum NMFS-OSF-3, 48 p.

I. Glossary of key terms

English term	Greek term	Explanation	Chapters	Literature
Climatic niche	Κλιματικός θώκος	<i>The range of climatic factors that a given species experiences, beyond which it cannot survive, grow or reproduce.</i>	B, C	Pearman, P. B., Guisan, A., Broennimann, O., & Randin, C. F. (2008). Niche dynamics in space and time. <i>Trends in ecology & evolution</i> , 23(3), 149–158. https://doi.org/10.1016/j.tree.2007.11.005
Climatic niche modelling	Μοντέλα κλιματικής καταλληλότητας	<i>These models explore the relationship between geographical occurrences of species and corresponding climatic variables.</i>	B, C	Adapted from Naimi, B. and Araújo, M.B. (2016), sdm: a reproducible and extensible R platform for species distribution modelling. <i>Ecography</i> , 39: 368-375. https://doi.org/10.1111/ecog.01881
Ensemble modelling	Συζευγμένα μοντέλα	<i>Or bioclimatic ‘envelope’ modelling approach: use of multiple models for range projections</i>	B, C	Araújo, M.B., & New, M.G. (2007). Ensemble forecasting of species distributions. <i>Trends in ecology & evolution</i> , 22, 42-7. https://doi.org/10.1016/j.tree.2006.09.010
Range shift	Μετατόπιση εύρους εξάπλωσης	<i>When the geographical limits within which a species survives and reproduces is altered.</i>	B, C	Bates, O. K., & Bertelsmeier, C. (2021). Climatic niche shifts in introduced species. <i>Current biology: CB</i> , 31(19), R1252–R1266. https://doi.org/10.1016/j.cub.2021.08.035
Climatically suitable areas	Κλιματικά κατάλληλες περιοχές	<i>Areas that are projected to host climatically suitable conditions for the species.</i>	B, C	Chatzimentor, A., Almpandou, V., Doxa, A., Dimitriadis, C., & Mazaris, A. D. (2021). Projected redistribution of sea turtle foraging areas reveals important sites for conservation. <i>Climate Change Ecology</i> , 2, 100038. https://doi.org/10.1016/j.ecochg.2021.100038
Three-dimensional suitable areas	Τρισδιάστατες κατάλληλες περιοχές	<i>Areas projected to host suitable conditions across consecutive depth layers.</i>	C	Chatzimentor A., Doxa A., Butenschon M., Kristiansen T., Peck M., Katsanevakis S., Mazaris A. D. (2024). Diving into warming oceans: assessing 3D climatically suitable foraging areas of loggerhead sea turtles under climate change. <i>Journal of Nature Conservation</i> – Under review
Marine megafauna	Θαλάσσια μεγαπανίδα	<i>All large-bodied organisms (body mass, ≥45 kg) inhabiting the</i>	B, C, D	Estes, J. A., Heithaus, M., McCauley, D. J., Rasher, D. B., & Worm, B. (2016). Megafaunal impacts on structure and function

		<i>coastal and open oceans, including bony fishes, elasmobranchs, mammals, reptiles, a species of sea bird (i.e., the emperor penguin), and a few species of mollusks (clams, squids, and octopuses).</i>		of ocean ecosystems. <i>Annual Review of Environment and Resources</i> , 41, 83-116.
Trait	Χαρακτηριστικό	<i>A broad range of species-level characteristics, including ecological preferences and life history information.</i>	D, E	Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M., & Huntley, B. (2019). Climate change vulnerability assessment of species. <i>WIREs Climate Change</i> , 10(1). https://doi.org/10.1002/wcc.551
Functional trait	Λειτουργικό χαρακτηριστικό	<i>Morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance.</i>	E	Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional. <i>Oikos</i> , 116(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x
Functional redundancy	Λειτουργικός πλεονασμός	<i>The concept of functional redundancy implies that species loss is compensated by other species contributing similarly to functioning.</i>	E	Fetzer, I., Johst, K., Schäwe, R., Banitz, T., Harms, H., & Chatzinotas, A. (2015). The extent of functional redundancy changes as species' roles shift in different environments. <i>Proceedings of the National Academy of Sciences of the United States of America</i> , 112(48), 14888–14893. https://doi.org/10.1073/pnas.1505587112
Community-mean-weighted trait	Μέσο σταθμισμένο χαρακτηριστικό κοινότητας	<i>Mean of trait values present in the community weighted by the relative abundance of taxa bearing each value.</i>	E	Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quéfier, F., Thébault, A. and Bonis, A. (2008), Assessing functional diversity in the field – methodology matters!. <i>Functional Ecology</i> , 22: 134-147. https://doi.org/10.1111/j.1365-2435.2007.01339.x

Vulnerability	Τρωτότητα	<i>The propensity or predisposition to be adversely affected.</i>	D	IPCC. (2014). <i>Summary for policymakers</i> (Climate Change 2014: Impacts, Adaptation, and Vulnerability, pp. 1–32). Cambridge University Press.
Exposure	Έκθεση	<i>The presence of people, livelihoods, species or ecosystems, environmental functions, services, and resources, infrastructure, or economic, social, or cultural assets in places that could be adversely affected.</i>	D	IPCC. (2014). <i>Summary for policymakers</i> (Climate Change 2014: Impacts, Adaptation, and Vulnerability, pp. 1–32). Cambridge University Press.
Risk	Κίνδυνος	<i>The probability of harmful consequences resulting from climate change. Risk results from the interaction of vulnerability, exposure, and hazard.</i>	D	IPCC. (2014). <i>Summary for policymakers</i> (Climate Change 2014: Impacts, Adaptation, and Vulnerability, pp. 1–32). Cambridge University Press.

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