Species interactions, ecosystem functioning and the resilience of marine vegetated ecosystems in a global change era

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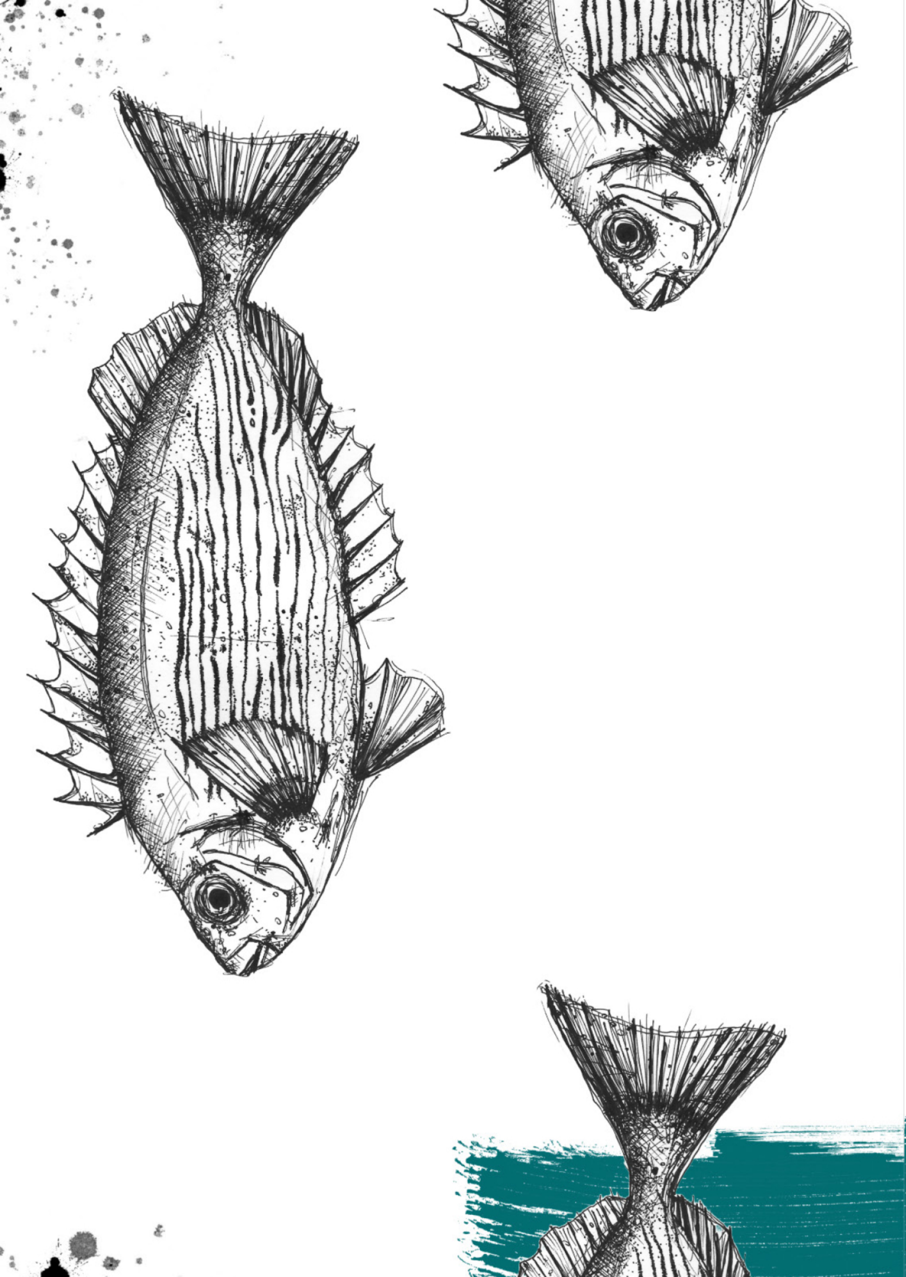

Doctoral
Thesis

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AND THE RESILIENCE OF MARINE VEGETATED
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DEPARTAMENTO DE BIOLOGÍA EVOLUTIVA, ECOLOGÍA y CIENCIAS AMBIENTALES
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Species interactions, ecosystem functioning and the resilience of marine vegetated ecosystems in a global change era

Memoria presentada por Mario Minguito Frutos para optar al Grado de Doctor por la Universitat de Barcelona

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A mi Madre,

a mi Padre,

a mi Hermana,

a Laura.

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Félix tenía razón, debería haber empezado mucho antes. Me gustaría agradecer a muchas personas, las que han compartido tiempo y espacio en los últimos 1718 días, pero también a aquellos con los que llevo compartiendo momentos toda una vida. Soy un afortunado. En casi 32 años, he podido hacer grandes amistades en diferentes contextos y es probable que con algunos sea más injusto en términos de espacio que con otros, espero que me sepáis disculpar. Así, sin mucha más introducción (lo cual les sonará impropio de mí a aquellos que verdaderamente me conocen), me gustaría comenzar por mis supervisores.

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Matthew, If I'm honest with you, when I read the offer and applied for this position, I only could think of visiting Australia. It was like a childhood dream to me. Although it has been a real pleasure to work with you all this time, I was also terrified in our very first online meetings. I was not only talking about models to a mathematician but, moreover, in English! Is this one of the fundamental reasons that I am grateful to you. I have never felt insecure or questioned after our meetings, but all the opposite. From you I have learnt to be more structured, organized, to solve one problem at a time. I really hope that science or life gives us the opportunity to meet again here or there.

En 1718 días la gente viene y va, pero algunas se quedan y permanecerán para siempre. Gracias Candela por ser una de ellas. El Gloria fue solo el principio, luego vinieron otras muchas campañas, Creta, Brest. Pero si por algo te estoy agradecido es por el día a día. Sin enterarme pasaste de compañera a amiga, haciendo los días siempre mejores dentro y fuera de las cuatro paredes del CEAB. Gracias por tener siempre tiempo para escucharme, en lo profesional y en lo personal. Aunque a veces pienses que no, te escucho y aprendo. Félix, el unicornio. Ha sido fantástico encontrarte, no solo por el dolor de cabeza que me han quitado tus diseños y tu ayuda con la maquetación, sino por las tardes de Esteve, los días de buceo (nunca suficientes) o los fines de semana de juegos y fuego valyrio. Gracias a los dos por Mero, Trufa y ahora Ura, por dejarnos cuidarles y por traerles siempre.

Rohan, thanks for all your help over these years. I am still fascinated after reading or listening to any of your stories, ecological or historical - who could ever forget the best tour guide of the Knossos Temple. I hope at some point we can meet in your natural habitat, the Lakshadweep archipelago! Xavi, sin aquella pregunta muy al principio de todo, probablemente nunca hubiéramos disfrutado de las aguas cristalinas del sur de Creta. Tu generosidad para ayudarme en mis inicios es algo que no olvidaré fácilmente, cómo me gustaría haber coincidido más. Jordi, gràcies per comportar-te amb mi com un company més, per venir cada dia a dir bon dia transmetent aquesta bondat que tant et caracteritza i per escoltar-me cada vegada que envaeixo el teu despatx amb dubtes o pensaments. Hoy el despacho vuelve a rebosar energía tras un tiempo solitario durante la pandemia, un lujo hoy en día en el CEAB para un mero "predoc". Lucía, Aina, Pol y Marta, es fantástico volver a tener con quien hablar entre horas, el olor a café en el despacho, pero, sobre todo, poder recordaros constantemente lo mayor que soy. Me hace muy feliz haber sido vuestro compañero y estoy seguro que con vosotros, tanto el grupo, como la ciencia, tienen el futuro asegurado.

No podrían existir unos agradecimientos sin incluir el “Piso Power”. Allí encontré a Mateu. Gracias por acogerme rápidamente y facilitar mi inmersión en la cultura blanenç y ceabina, siempre te estaré agradecido por eso. Es cierto que pronto me abandonaste para irte a los EEUU y luego también en el inicio de la pandemia, pero esas partidas de tenis de mesa (nunca mejor dicho), los momentos bricomaníacos y todos lo que vinieron después son ya historia. Y de pronto, Elena fue una más. Gracias por formar parte de nuestras vidas, por enseñarnos la combinación de “diavola y carbonara” e inculcarnos la cultura del Akuma, el Sa Lola y, por supuesto, del buen vino. Estoy seguro de que seréis muy felices allí donde vayáis. Marta, si no existieras tendrían que inventarte, eres única y especial (aunque no tan única, “¡no flipes!”). Menos de un año juntos en el piso fue tiempo más que suficiente para dejar una inmensa huella en nosotros, “obvio”. Gracias por escuchar (no tanto por interrumpir mis historias, a veces, interminables), por tu empatía y comprensión, por nuestras discusiones (aunque nunca las he considerado tal), pero, sobre todo, gracias por permanecer a nuestro lado. ¡Ah! Y también por Lola. Carmen y Sergio, parece que fue ayer cuando os mudabais a Dinamarca. Gracias por las mañanas, por las rutas, las comidas y las tardes de juegos durante los fines de semana post-pandémicos. Giulia, Stefano y Alejandro, la vida nos tenía preparado un suceso que nos uniría para siempre. Pero por suerte todo salió bien, no ahondemos demasiado en aquello. Grazie mille ai nostri amici italiani, per averci accolto nella loro casa, per averci fatto sentire autentici italiani per un paio di giorni e per averci aiutato a preparare un viaggio indimenticabile. Alejandro, la decimocuarta es y siempre será nuestra, que glorioso momento para que vinieses (introduce aquí tu característica onomatopeya). Tras otro miércoles surrealista, permíteme no decir nada más. Julia, aunque no estuvieses en el piso power, se sintió como tal. Gracias por estar siempre al principio de todo esto. Mucha fuerza en esta etapa final también para ti.

En el CEAB he encontrado a muchísima gente buena con la que he convivido durante este tiempo en los cafés y las comidas, pero con los que también he podido vivir las siempre sorprendentes fiestas de navidad, celebraciones de tesis, comidas en la cala, jueves de cine o de sa capça, y de Mediterrani. Gracias por acogerme realmente bien y formar una maravillosa comunidad. La mayoría ya os habéis ido: Roger, Jana, Ibor, Hector, Nerea, Adrià, Jose, María, Dani; os echamos en falta. Por suerte, muchos seguís aquí: Joan, Xevi, Celia, Jongmo, Jenni, Mar, Marta, Andrea, Laia, Laia, Xavi, Caro, Anna, David; habéis vuelto como Marta y Vicente (¡referentes!); o habéis llegado más recientemente como Uxue, Esther, Francesco, Raül, Nerina, Nina, Agus; y así hemos podido seguir echando risas y haciendo que el teletrabajo no merezca la pena. Luego están mis otros compañeros de departamento, Pol, Jesús, Catuxa, María (ya me entendéis), gracias por no matarme cuando vengo a dar la turra. Cris, dentro de poco estarás escribiendo unas líneas como estas (probablemente más emotivas). Mientras tanto, yo me alegro de haber empezado tan próximos en el tiempo y de haber podido coincidir, excepto por tus innumerables campañas y estancias, ¡cómo te envidio! La vida te tiene preparada aventuras extraordinarias. ¡Jorge! El otro madridista, qué bueno verte al final más de lo que te vi cuando éramos compañeros de despacho. Espero que algún día me contrates (esto es serio). ¡Fer! ¿Qué pensabas que me había olvidado de ti o que guaje? Cómo me voy a olvidar con esas fabes que nos preparaste. Qué manera de ganarte a todo el mundo en tan poco tiempo y que combinación tan perfecta formáis tu y Clara, y ahora Jara. Qué pena que os fueseis, pero con vosotros tengo claro donde nos encontraremos. Y por último Anaïs. Gracias por ser una compañera de equipo más, por tu alegría cada vez que voy o vienes a saludar, por tu fe en mí, por convertirte en amiga y por presentarnos al ¡teu marit! Xavi, más Champions llegarán, sólo dos partidos han hecho falta para saber de qué madera estás hecho; qué ejemplo de *seny* y *valors* (no es broma). Gracias a todas las personas que conforman el CEAB, que consiguen que el trabajo y la investigación sean una tarea agradable y enriquecedora y que han hecho de mi etapa allí un tiempo feliz.

Mis queridos mallorquines, el recibimiento fue inmediato. El día dos ya estaba cenando con vosotros y al poco tiempo, buceos, tardeos, excursiones y panades. Gracias, Merit, Xisca, Carlota por aquellos maravillosos días que añoro con nostalgia. Gracias a Carlos y Guille, de quienes pude aprender mucho en aquel tiempo entre IMEDEA y el Limia. Que alegría encontrarnos en Sevilla, aunque Guillermo ya no estuviese para fiestas, ni *sabotages*. Roc, todo este tiempo y la sensación de que no nos hemos visto lo suficiente es obvia. Le echaremos la culpa a la pandemia (y también a la tesis). Gracias Bárbara por hacer feliz a mi amigo, pero por supuesto, por tu bondad y tu cercanía, por tu manera de expresarnos tu cariño y por entre los dos (aunque todos tenemos claro que Roc aportó poco en este sentido) habernos traído a Eneko. ¡Cómo olvidar a mis compañeros galleguiños! Qué año tan inolvidable con Guadalupe, Lutxy, Marcos, Manuel, Joana, Sandra, Sofía, Cecilia y Antonio, qué bueno poder disfrutar de Galicia con vosotros. Me gustaría hacer mención especial a Iñigo y Sara. Cómo me entristeció que aquel año acabase. Iñigo, gracias por ser la punta de lanza, por enseñarnos el camino y por hacernos estar siempre "a gusto". Qué hubiese sido de mí sin tu valentía. No te vayas de NZ sin avisarme, sigo soñando con ese viaje. Sara, gracias por tu bondad y tu cariño, por tener siempre una palabra amable y por lo más importante, por reírte de mis chistes malos. Tú sí que debes de ser gallega a estas alturas y por eso también te envidio. Con suerte nos veremos dentro de poco en algún congreso. Moviéndome hacia la otra esquina, me gustaría agradecer al equipo de Rivemar, por vuestra manera de enseñar el buceo, qué manera de descubrir un mundo nuevo. Aunque sobre todo gracias a Martín, ¡menudo verano! Y antes de cerrar, no me puedo olvidar de mi familia granaína de Camino de Ronda, 208. Qué bonitos meses con Noli, Noel, Ana y Laura, gracias!

La universidad trajo viajes de ecuador y fin de carrera, fines de semana en Ávila, muchas fiestas post-examenes, pero también mucho mus y café. Gracias por todo ese tiempo Olga, María, Carlos, Capo, Elisa, Irina. Alba, Borja, Marta, Luís, por suerte también vivisteis muchos de aquellos momentos (aunque Luís tú no tanto [aquí insertaría un sticker]) y aún nos tenemos los unos a los otros. El amor trajo nuevas incorporaciones, las pequeñas Valeria y Carmen y también Mar. Cómo me alegro de veros evolucionar, casaros, de que os vaya tan bien en vuestras nuevas casas y palacios (esto obviamente va por Alba y Borja), pero, sobre todo, de veros felices cada vez que vuelvo. Gracias por todos estos años. Ylenia, qué orgullo. Durante años te he admirado sabiendo de tu prometedor futuro. Siempre has sido un ejemplo a seguir. Gracias por ayudarme a crecer en tantos aspectos. Hoy, el futuro es presente, y todo lo que pensaba de ti se ha hecho realidad. Espero que sólo nos separe el Atlántico, que pronto puedas tener en tu tierra el terreno que te mereces y, por supuesto, que me invites.

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Los señores de la noche, anteriormente conocidos por su apetencia por el rile, nunca faltan a su cita. Eso sí, seguro que llegan tarde. Ortega, Christian, Juan, Ugarrio, Javi, Chino y Diego, con algunos son ya casi dos décadas… y con otros casi tres! Da igual que unos llegaseis antes y otros después, lo importante es cómo resistís y habéis llenado todo este tiempo de anécdotas, únicamente superadas por los momentos de risas (y los días de play). Cómo hemos madurado, aunque quizás haya sido gracias a ellas, Ainhoa, Georgi, Irene, Laura, Irene y Sara, que felices los veo a vuestro lado. Pero ahora ya, ni vosotras, ni nosotros somos los protagonistas, ahora todos los focos se los llevan Luca y Martina. Gracias Sara y Diego por concederme el honor de hablar en vuestra boda, junto a mi inseparable Chino. Obviamente, no pude superar al concejal de festejos del Ayuntamiento de Tomelloso, Conrado Jiménez, ni a mi buen amigo Javier, pero Sara se sabe mi discurso de memoria, así que ¡Joróbate Flanders! Gracias por ser únicos y no separaros de mí a pesar de mis idas y venidas. Os quiero amig@s.

Como todos sabéis hay alguien que sobresale por encima del resto. Mi hermano de otros padres, Toñi y Arteche, a los que también tengo que agradecer todos los valores que me han transmitido durante años y cómo me han cuidado. A pesar de que Toñi me hiciese los bocadillos de mortadela mientras que a su hijo se los hacía de jamón, "¡qué rarito es el niño!". Toño, pocos son los recuerdos que se me vienen a la memoria en los que no apareces. Gracias por tu lealtad, tu amistad pura todos estos años, por estar siempre pendiente y llamar cuando todavía estoy por la m-50, por tu capacidad de adaptarte a todo y por presentarme a mi primer amor, la pelota. Creo que no me equivoco al pensar que nuestra vida hubiese sido mucho peor si no nos hubiésemos tenido el uno al otro. Por suerte, tú encontraste rápidamente a alguien, y qué bien elegiste. Yohara, que rápido comprendí lo que Toño vio en ti. Gracias por entrar en nuestras vidas y adaptarte a todo, sin peros, sin preguntas. Gracias por hacerle feliz y por no separarte de él, por estar siempre dispuesta a todo, excepto a renunciar a unos buenos spaghetti carbonara. Gracias a los dos por quererme como soy y por seguir preguntando que cuando me vuelvo a Fuenlabrada.

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Marisol, Juan, vaya mujer habéis criado. Qué orgullosos estaríais si oyeseis lo que oigo yo a diario de boca de sus compañeros y amigos. ¡Buena maña! En lo que a mí respecta, muchas gracias por acogerme tan bien desde el primer día, demostrarme vuestra preocupación y cariño y, por supuesto, por llenar el congelador de longanizas de Graus.

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Silvia, no sabes cuánto te quiero hermana. Quizás en nuestra familia no lo decimos demasiado. Pero así es y así ha sido siempre. Tengo el recuerdo imborrable (aunque tú y la ciencia digáis que no), de la primera vez que te vi entre los brazos de mamá. Aquel día cambió todo, ya no estaba yo solo, y menos mal. Hoy estoy feliz de ver la mujer en que te has convertido, de cómo nos has enseñado a demostrarnos el amor que nos tenemos, de tu generosidad y de tu risa sonando al ritmo de la de mamá. Pero también me enorgullezco de tu capacidad de trabajo, de tu esfuerzo y perseverancia, si vieras con qué orgullo le hablo de ti a la gente. Tu también estás terminando una etapa vital, y por suerte podemos estar tranquilos, sabemos que todo te irá bien.

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Blanes, 15 de mayo de 2024

List of publications derived from this thesis

Chapter 3

Minguito-Frutos, M.[1*], Adams, M. P.[2,3,4], Alcoverro, T.[1], Vilas, M. P.[5], Alonso, D.[1], Mayol, E.[6,7], Bernardeu-Esteller, J.[8], Marín-Guirao, L.[8], Ruiz, J. M.[8], & Boada, J.[1,9] (2023). Quantifying the role of photoacclimation and self-facilitation for seagrass resilience to light deprivation. *Frontiers in Plant Science*, *14*, 1186538. https://doi.org/10.3389/fpls.2023.1186538. Impact factor (IF) (2022): 5.6, Quartile = Q1, Decile = D2 (Plant Science).

Chapter 4

Minguito-Frutos, M.[1*], Boada, J.[9], Pagès, J. F.[1], Marco-Méndez, C.[1], Arthur, R.[1,10], Adams, M. P.[2,3,4], & Alcoverro, T.[1] (2023). Species-specific acclimatization capacity of key traits explains global vertical distribution of seagrass species. *Global Ecology and Biogeography*, *32*(6), 976-986. https://doi.org/10.1111/geb.13673. IF (2022): 6.4, Quartile = Q1, Decile = D1 (Ecology).

Chapter 5

Minguito-Frutos, M.[1*], Arthur, R.[1,10], Boada, J.[1], Marco-Méndez, C.[1], Adams, M. P.[2,3,4], Pagès, J. F.[1], Buñuel, X.[1], Pessarrodona, A.[11], Turon, X.[1], Ballesteros, E.[1], Tamburello, L.[12], Farina, S.[13,14], Skouradakis, G.[15,16], Kletou, D.[17], Cebrián, E.[1], Santamaría, J.[1], Verdura, J.[18], & Alcoverro, T.[1] Grazing halos reveal differential ecosystem vulnerabilities in vegetated habitats. Under review in *Ecology*. IF (2022): 4.8, Quartile = Q1, Decile D3 (Ecology).

Chapter 6

Minguito-Frutos, M.[1*], Buñuel, X.[1], Marco-Méndez, C.[1], Sanmartí, N.[6], Skouradakis, G.[15], Boada, J.[9], Pagès, J. F.[1], Alcoverro, T.[1], & Arthur, R.[1,10] Tropical range-extending herbivorous fishes shoal with native temperate species to gain foraging benefits. Under review in *Biological Invasions*. IF (2022): 2.9, Quartile = Q2, Decile = D3 (Biodiversity Conservation).

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Contents

Summary

Human domination of Earth's Systems is transforming life at a planetary scale. A plethora of anthropogenic pressures disrupt environmental conditions, degrading ecosystem functioning and posing unprecedented threats to global biodiversity and human life support systems. In this context of global anthropogenic change, acquiring accurate ecological knowledge is crucial for identifying warning indicators and ecosystem tolerance limits. Such knowledge can inform ecosystem managers and aid in mitigating stressors at local and/or regional scales that further fuel this global change.

Marine vegetated ecosystems, including seagrass meadows and macroalgal forests, rank among the most productive habitats on Earth. They support a significant portion of the world's biodiversity and fisheries while contributing to carbon sequestration. However, these ecosystems face severe threats from global change, which vary according to their tolerance limits and eventually shape their vulnerability against human pressures. In addition, macrophyte ecosystems often exhibit nonlinear responses to stress, including abrupt and catastrophic shifts. These inherent ecosystem properties further complicate predictions about their resistance and resilience (and, therefore, their management), making these systems excellent models for assessing the effects of global change in nature.

In this thesis, I focus on key ecological mechanisms that shape the functioning and resilience of marine macrophytes and explore their interactions with herbivores under various global-change-related stressors, such as eutrophication, overfishing, or tropicalization. Specifically, I investigate (i) seagrass responses to cope with light limitation, (ii) how species-specific attributes allow seagrasses to colonize distinct depth ranges on a global scale, (iii) the influence of abiotic and biotic factors in shaping ecological contexts and thus macrophytes vulnerability to herbivory, and (iv) how mixed-shoaling behaviours between range-extending and native herbivorous fishes influence their specific foraging activity and efficiency in the tropicalized environments of the eastern Mediterranean Sea.

The first results in this thesis emphasize the importance of physiological photo-acclimatization for macrophyte resistance and recovery (i.e., resilience) against light limitation. While such acclimatization can reduce minimum light requirements, only self-facilitation mechanisms alleviating mortality rates lead to bistability in seagrass meadows. Secondly, the species-specific ability of seagrasses to persist across depth ranges depends on their acclimatization potential in key physiological, morphological, and structural traits, regardless of species size or functional group. Third, plant-herbivore interactions in marine macrophyte ecosystems are mediated by an array of endogenous and exogenous factors of biotic and abiotic nature. These factors include the identity of both biotic interactors, herbivore size, or the fear imposed by predators, and the nutrients, temperature, and depth conditions. Lastly, the global redistribution of tropical and warm-adapted species results in novel species interactions in temperate environments. In the eastern Mediterranean, range-extending herbivorous fish species engaged more in mixed-species shoaling behaviours, forming larger groups and increasing their foraging activity and efficiency. In contrast, native Mediterranean herbivores do not exhibit that ability to shoal in mixed-species groups nor obtain such foraging benefits.

Overall, this thesis focuses on species features and ecological contexts to understand how species and marine vegetated ecosystems cope and respond to stressors of human origin. This thesis highlights (i) the role of species-specific acclimatization capacities of marine macrophytes in shaping their vulnerability to anthropogenic impacts degrading water quality, especially at their deep limits, (ii) the highly species-specific and context-specific vulnerability of macrophyte communities to herbivory, and (iii) that the mixed-species shoaling behaviour of range-extending species with temperate species results in a mechanism that partially explains the enormous herbivory pressures experienced by macrophytes in tropicalized reefs. Consequently, management at local scales is critical for maintaining healthy and resilient macrophyte ecosystems in the face of global anthropogenic pressures.

Resumen

La dominación humana sobre los Sistemas Terrestres está transformando la vida a escala planetaria. Un sinfín de presiones antropogénicas perturban las condiciones ambientales, degradando el funcionamiento de los ecosistemas, poniendo bajo seria amenaza la biodiversidad global y los sistemas que soportan la vida humana. En este contexto de cambio global antropogénico, adquirir conocimientos ecológicos precisos resulta imprescindible para identificar indicadores de alarma y límites de tolerancia de los ecosistemas. Este conocimiento puede informar a gestores ambientales y ecosistémicos, ayudando a mitigar impactos a escala local y/o regional que retroalimentan el cambio global.

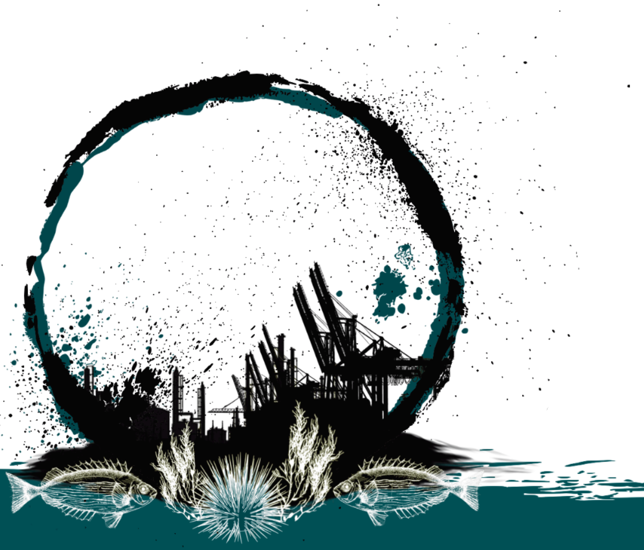
Los ecosistemas marinos dominados por vegetación, incluyendo praderas de fanerógamas y bosques de macroalgas, se sitúan entre los hábitats más productivos del planeta. Estos sistemas sustentan una proporción significativa de la biodiversidad y las pesquerías globales a la vez que contribuyen al secuestro de carbono. No obstante, también sufren amenazas severas derivadas del cambio global que varían de acuerdo a sus límites de tolerancia y dan lugar a diferentes vulnerabilidades ante dichas presiones. Además, los sistemas de macrófitos marinos exhiben habitualmente respuestas no lineales al estrés, incluyendo transiciones abruptas y catastróficas hacia estados alternativos. Estas dinámicas dificultan aún más las predicciones acerca de su resistencia y resiliencia (y, por tanto, su gestión), convirtiendo estos sistemas en modelos excelentes para evaluar los efectos del cambio global en la naturaleza.

En esta tesis estudio mecanismos ecológicos clave que dan forma al funcionamiento y la resiliencia de los ecosistemas de macrófitos marinos, a la vez que exploro sus interacciones con herbívoros, ante factores de estrés relacionado con el cambio global que incluyen, la eutrofización, la sobrepesca, el calentamiento de las aguas marinas o la tropicalización. Específicamente, aquí investigo (i) las respuestas de las plantas marinas para hacer frente a la limitación lumínica, (ii) cómo los atributos específicos de las fanerógamas les permiten colonizar distintos rangos de

profundidad a escala global, (iii) la influencia de factores abióticos y bióticos sobre los contextos ecológicos que moldean la vulnerabilidad de los macrófitos al herbivorismo, y (iv) cómo los comportamientos de formación de bancos mixtos entre especies de peces herbívoros tropicales y nativos influencian su actividad y eficiencia de forrajeo en los ambientes tropicalizados del este del Mar Mediterráneo.

En primer lugar, esta tesis enfatiza la relevancia de la foto-aclimatación fisiológica para la resistencia y recuperación (i.e., resiliencia) de los macrófitos marinos ante la limitación lumínica. Mientras la capacidad fotoaclimatativa puede reducir los requerimientos específicos mínimos de luz, sólo los mecanismos de facilitación densodependientes dan lugar a biestabilidad de las praderas marinas. En segundo lugar, la habilidad específica de cada especie de fanerógamas para persistir a través de los rangos de profundidad depende de su potencial de aclimatación en rasgos fisiológicos, morfológicos y estructurales clave, con independencia de su talla o grupo funcional. En tercer lugar, una amplia gama de factores endógenos y exógenos de naturaleza abiótica y biótica median las interacciones planta-herbívoro en los ecosistemas de macrófitos marinos. Estos factores incluyen la identidad de ambos interactores bióticos, el tamaño del herbívoro o el miedo impuesto por los depredadores, así como las condiciones de nutrientes, temperatura y profundidad. Por último, la redistribución global de especies tropicales y adaptadas a ambientes cálidos resulta en nuevas interacciones entre especies en ambientes otrora templados. En la cuenca este del Mediterráneo, las especies de peces herbívoros tropicales que están extendiendo su rango se asociaron más activamente en bancos mixtos, formando bancos más grandes e incrementando su actividad y eficiencia de forrajeo. En cambio, las especies nativas mediterráneas no exhibieron tales habilidades para agregarse en bancos mixtos ni obtuvieron dichos beneficios de forrajeo.

Esta tesis se centra en los atributos de las especies y las características de los contextos ecológicos para entender cómo las especies y los ecosistemas marinos vegetados lidian y responden ante diversas presiones antropogénicas. Esta tesis ensalza (i) el rol de las capacidades de aclimatación específica de las especies de macrófitos marinos en moldear su vulnerabilidad ante los impactos antropogénicos que degradan la calidad del agua, especialmente en sus límites profundos, (ii) la vulnerabilidad altamente específica y dependiente del contexto de las comunidades de macrófitos marinos al herbivorismo, y (iii) que los comportamientos de agregación en bancos mixtos de las especies de peces conejo tropicales resultaron en un mecanismo que explica, parcialmente, la enorme presión de herbivorismo experimentada por los macrófitos marinos en los arrecifes tropicalizados del Mediterráneo oriental. En consecuencia, la gestión a escala local es crítica para mantener la salud y la resiliencia de los ecosistemas dominados por vegetación marina frente al avance del cambio global.



1. General introduction

1.1. The ecology of global change: A collapsing world?

“Human beings are now carrying out a large-scale geophysical experiment of a kind that could not have happened in the past (…). This experiment, if adequately documented, may yield a far-reaching insight into the processes determining weather and climate” (Revelle & Suess, 1957).

Roger Revelle and Hans Suess wrote these words more than 65 years ago, just as the Great Acceleration was underway, and the realisation was just beginning to dawn that the unbridled fossil-fuel burning by industrialised societies was having an earth-wide impact. There has been a mounting torrent of scientific evidence since these early years, starting with Keeling’s pioneering CO_2 measurements (Keeling, 1960), making now an unassailable fact that greenhouse gas emissions are the primary cause of *global warming* (Broecker, 1975). Indeed, human economic activities are pushing the Earth System into an entirely new anthropogenic geological era, the Anthropocene (Crutzen, 2002; Steffen et al., 2015; Steffen et al., 2020). However, while most of the focus had been on greenhouse gas emissions, global warming, and climate change, the Anthropocene is characterised by a host of additional anthropogenic stressors that together comprise the multi-faceted environmental crisis of our time. Hence, instead of *climate change* Lubchenco and co-authors (1991) proposed the broader term *global change* to refer to: “large-scale alterations in patterns of land and water use and anthropogenic changes in environmental chemistry, in addition to climate change”.

Global change is a civilisational crisis unlike any we have experienced before. Today, anthropogenic pressures on the world’s ecosystems are greater than ever, as the unprecedented velocity and magnitude of human interventions leaves virtually no habitat or region free from stress (Halpern et al., 2008; Halpern et al., 2019; Jaureguiberry et al., 2022). There is a growing recognition that global climate change is bringing the Earth System dangerously close to crucial tipping points (Armstrong McKay et al., 2022; Ditlevsen & Ditlevsen, 2023; van Westen et al., 2024). Thus, the holistic discipline of global change ecology attempts to respond to the challenge of describing the impacts of human life and activities on the world's ecosystems (Lubchenco et al., 1991; Vitousek, 1994; Schlesinger, 2006). The exponentially expanding human footprint on land, water, and air, which misuses Earth's resources to fuel unceasing economic development, has made obvious that the intervention of humans and our societies on the world's natural resources has resulted in a "human domination of Earth's ecosystems" (Vitousek et al., 1997; Steffen et al., 2015). These anthropogenic pressures, in addition, do not act in isolation. Local stressors including the direct modification and destruction of habitats, pollution and eutrophication of water bodies or resource over-exploitation (to list just a few) act additively, antagonistically, or synergistically, leading to far-reaching implications for ecological communities (Crain et al., 2008; Levin et al., 2009; Fig. 1.1). The challenge for science is to understand these processes of change on world's species and ecosystems so that we can remedy the losses, manage for resilience or learn to adapt to a world of decreasing functionality (Bellard et al., 2012; Dirzo et al., 2014; Ceballos et al., 2015; Ceballos & Ehrlich, 2018). Hence, an urgent imperative for science is to characterise how species and ecosystems respond before an imminent collapse (Scheffer, 2009). This is the best hope of preventing ecosystem collapses and securing ecological resilience (Rockström et al., 2009).

Beyond the ethical considerations for preserving biodiversity, there are urgent, existential reasons to address this crisis, as the Earth's basic life support systems are increasingly under threat (Lubchenco et al., 1991). Apart from such a simple self-interest and strong moral imperative, understanding how Earth's ecosystems are responding to global change is perhaps the most pressing intellectual problem of our times. Addressing this ecological crisis in its entirety would, of course, be an impossible task (Fig. 1.1). Instead, this thesis addresses three aspects of global change that are particularly acute in marine benthic ecosystems: (i) understanding mechanisms influencing species tolerance to human-induced light reduction in water bodies (**Chapters 3** and **4**), (ii) exploring the influence of abiotic and biotic factors in plant-herbivore interactions shaping the differential ecosystem vulnerability to herbivory (**Chapter 5**), and (iii) understanding species interactions in novel species assemblages resulting from tropicalization of temperate ecosystems (**Chapter 6**). In the rest of this introduction, I will:

i. Briefly outline the three main challenges of global change I addressed within this thesis.

ii. Introduce the main biological actors – seagrass- and macroalgal-dominated ecosystems – and provide a broad overview of their basic ecology and functioning.

iii. Discuss what we know of how global change is modifying these ecosystems.

iv. Discuss the vulnerability and potential threats to the resilience of marine vegetation under global change.

v. Introduce my principal study area, the Mediterranean Sea, arguing why it is a perfect laboratory to study the impacts of global change.

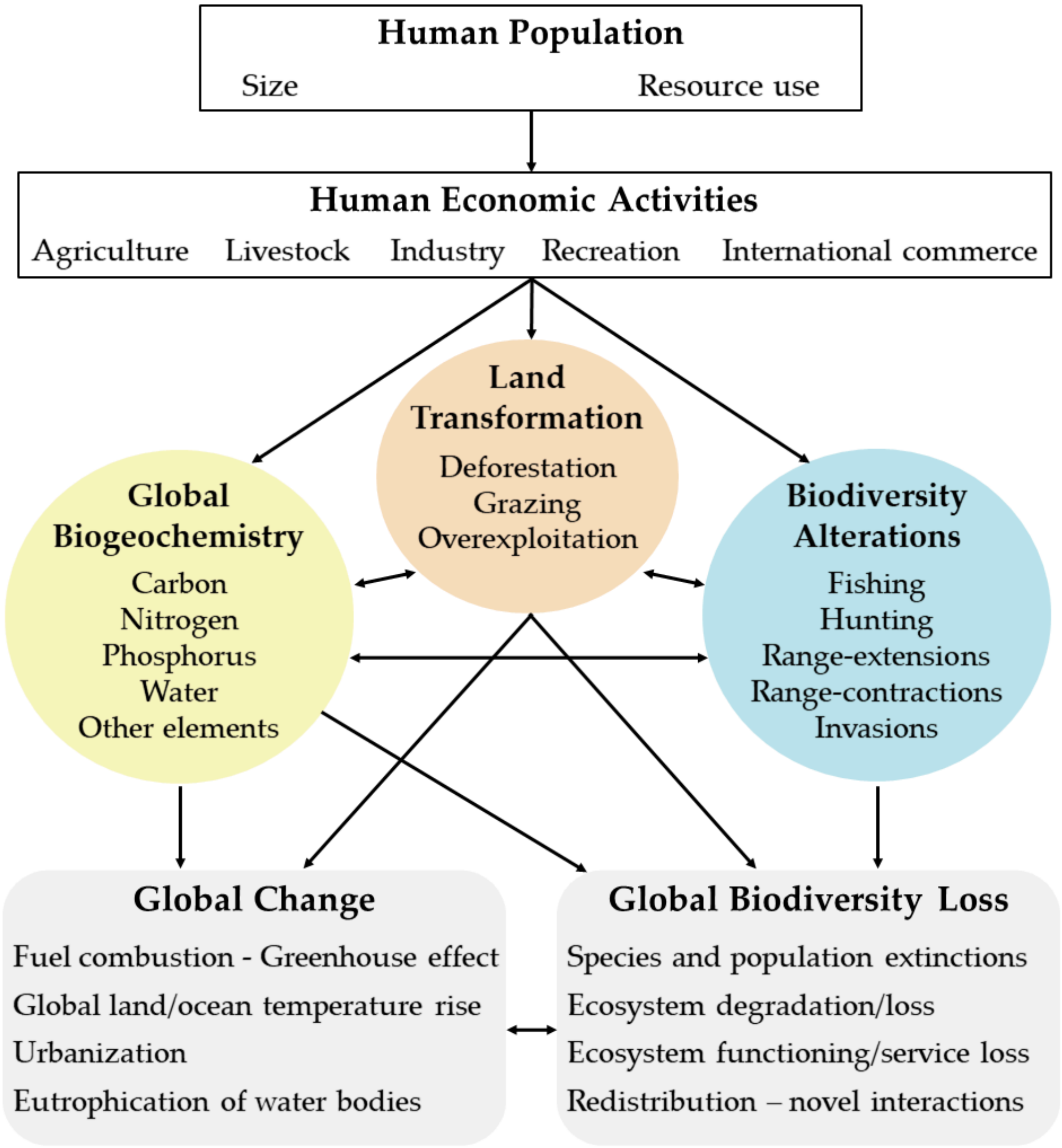


Figure 1.1. Diagram summarizing the main components of global change (adapted from Vitousek et al. (1997)). Human economic activities have led to an uncontrolled use of Earth's natural resources, giving rise to a myriad of interconnected processes related to (i) global biogeochemistry changes, (ii) land transformation, and (iii) biodiversity alterations. These alterations in the abiotic and biotic contexts of the world's ecosystems set the pace of global change and global biodiversity loss.

1.2. Ecological challenges imposed by global change

Anthropogenic climate change, pollution of water bodies, overfishing, and species invasions are ranked among the most severe drivers of global change currently threatening the world's ecosystems and their biodiversity (Vitousek et al., 1994; Sala et al., 2000; Fig. 1.1). At lower levels of human-mediated stress, species may respond with an initial tolerance and show some acclimatization capacity of response. However, as global change impacts intensify, species unable to show locally adaptive responses are forced to move to more conducive environments and create novel species configurations or die (Pecl et al., 2017; Vergés et al., 2019; Smale, 2020; Garrabou et al., 2022). Understanding the limits to species acclimatization and ecosystem resistance is particularly important in foundation species since their response has far-reaching consequences for the rest of the habitat (Heck et al., 2003; Thomsen et al., 2010). Moreover, ecosystem responses are unlikely to be linear. Beyond a point or threshold, species and ecosystem dynamics could change disproportionately in the face of stress (May, 1977; Scheffer et al., 2001). For systems that respond in this way, it becomes urgent to identify the minimum ecological conditions required to keep ecosystems healthy and resilient. In the following sections, I introduce some of the subjects addressed in this thesis, including species tolerance/acclimatization to impacts resulting from global change, linear and nonlinear ecosystem resistance mechanisms, the influence of abiotic and biotic factors on shaping trophic interactions, and the novel interactions and ecosystem consequences as species move fuelled by anthropogenic heating.

1.2.1. Species tolerance to anthropogenic stress under global change

Some species are better able than others to acclimatize to the rapid transformations imposed by global change. While the vulnerability of a species depends on how close it is to its intrinsic tolerance limit (Assis et al., 2018), it is also strongly related to its specific adaptive capacity. This capacity is determined by its ability to resist and recover to changing conditions (together referred to as resilience;

see Section 1.5. for further details) (Levin & Lubchenco, 2008). Such adaptive capacity is additionally constrained by species-specific traits that, even within the same phylogenetic groups, give rise to large variability in species vulnerability (Kilminster et al., 2015; Mauffrey et al., 2020; Fong et al., 2023). The influence of traits on species' performances under stress (i.e., any individually measurable physiological, morphological, structural, or growth traits responding to stress; Violle et al., 2007) is particularly relevant for habitat-forming species, as it can have flow-on consequences for the overall ecosystem (Gillis et al., 2023). To safeguard ecosystem structure, functioning, and services, it is critical to understand how species-specific strategies help predict context-specific vulnerability to anthropogenic (interacting and cumulative) stressors affecting habitat-forming species (Crain et al., 2008; O'Brien et al., 2018; Mauffrey et al., 2020). Knowing which attributes or traits contribute to such ecosystem vulnerability could help inform policies for a resilient future (Levin et al., 2009; Chichorro et al., 2019).

1.2.2. Tolerance to a limit: Understanding nonlinear ecosystem responses

Few ecosystems show simple linear responses to stress, making it challenging to predict their often nonlinear dynamics in the face of global anthropogenic change (Scheffer & Carpenter, 2003; Scheffer et al., 2009). Ecosystems are capable of resisting disturbances to a certain extent and may have a host of state-stabilizing mechanisms that help maintain systems relatively unchanged when exposed to moderate stress (Nyström et al., 2012). The strength of these stabilizing feedbacks is usually linked to species composition, diversity, species performance, and acclimatization capacity, as well as to the nature of species-environment interactions (Conversi et al., 2015; Maxwell et al., 2017). However, when these mechanisms are disrupted, ecosystems lose stability and start showing a series of responses that indicate an approaching threshold (May, 1977). Crossing these tolerance thresholds makes ecosystems suddenly shift to alternative organizational states, which are generally less structured, diverse, and productive (Holling, 1973; Scheffer et al., 2001). The resulting alternative state is also highly stable, characterised by a completely different suite of reinforcing feedbacks that make the recovery of the original state very challenging (van der Heide et al., 2007; Ling et al., 2015). Altogether, the best option for maintaining ecosystem stability and avoiding these abrupt and catastrophic collapses is to understand and monitor the gradual anthropogenic pressures that trigger them (Scheffer et al., 2001).

1.2.3. Species on the move: Pole-ward range-shifts set novel species interactions

Global change is causing the redistribution of Earth's biota as species alter their ranges in response to changing conditions (Pecl et al., 2017). Changes in biodiversity and community composition are occurring in most habitats as a result of variations in species performances, introduced species, range shifts, or species functional extinctions, among others (Poloczanska et al., 2013; Dirzo et al., 2014; Sunday et al., 2015; Valiente-Banuet et al., 2015). Thus, global warming and human-induced biological invasions conspire to create a series of novel interactions involving species that have not encountered each other in the past. These interactions are of particular concern at temperate latitudes where species from warmer environments find new hospitable ecosystems (Vergés et al., 2014a; Zarzyczny et al., 2023). At leading edges, social animals with more generalist behavioural traits and similar functions to those found in recipient ecosystems could be favoured in their pole-ward colonization (Holway & Suarez, 1999; Smith et al., 2018; Stuart-Smith et al., 2021; Miller et al., 2023). Understanding how these novel appearances can alter ecosystem functioning is vital in forecasting the fate of vegetated habitats, helping to identify conservation bright spots, and informing management actions to secure the continuity of ecosystem services (Vergés et al., 2019).

1.3. Marine vegetation: Biology, ecology and functioning

Marine vegetation, often referred to as marine macrophytes (e.g., Krause-Jensen et al., 2020), is a heterogeneous group of species formed by marine flowering plants and seaweeds (hereafter referred to as seagrasses and marine macroalgae, respectively). Although the term *marine macrophytes* encompasses both seagrasses and marine macroalgae (Christie et al., 2009; Olafsson, 2017), they form very different ecosystems on soft sandy bottoms (i.e., seagrass meadows or beds) and rocky reefs (i.e., marine or macroalgal forests). However, as a group, they play a crucial role in benthic coastal ecosystems worldwide. Marine macrophytes, as habitat-forming or foundation species (Thomson et al., 2015), form extensive and highly productive habitats, sustaining the complex structure, functioning and biodiversity of coastal environments across tropical, temperate and subpolar regions (Green & Short, 2003; Christie et al., 2009; Bennet et al., 2016; Krause-Jensen et al., 2020). In addition, marine vegetation provides essential services for human societies, such as the support of artisanal and industrial fisheries, natural coastal protection, nutrient filtration that improves water quality, and carbon sequestration that helps buffer some of the current impacts of global change (Fourqurean et al., 2012; Duarte et al., 2013; Unsworth et al., 2019a; Pessarrodona et al., 2023).

Seagrasses are a functional group of marine vascular plants composed of 72 species belonging to 12 genera, all within the order Alismatales (Short et al., 2011) with a relatively similar growth form but essential differences in their traits (Marbà & Duarte, 1998; Kilminster et al., 2015). Marine macroalgae, in contrast, involve a broader phylogenetically and functionally diverse group that forms very distinct habitats. Macroalgal forests create complex three-dimensional habitats ranging from canopy-forming algae such as *Cystoseira*, *Durvillaea*, *Fucus*, *Saccorhiza*, and *Sargassum* to giant kelps; all within the orders of Fucales, Laminariales, Tylopteridales, and Desmarestiales (Wernberg & Filbee-Dexter, 2019). At the other end, the so-called algal turfs form habitats with little to no three-dimensional structure, composed of a diverse group of algae, including species of filamentous, fast-growing, and opportunistic algae (Filbee-Dexter & Wernberg, 2018).

Both seagrass meadows and macroalgal forests are undergoing dramatic reconfigurations globally as they are particularly vulnerable to light deprivation (Ralph et al., 2007; Krause-Jensen et al., 2007) and overgrazing by herbivores (Eklöf et al., 2008; Ling et al., 2015), among other essential sources of anthropogenic stress (Smale, 2020; Nguyen et al., 2021). As a result, they serve as excellent models to test the impacts of global change on ecological communities (Short et al., 2011; Strain et al., 2014; Krumhansl et al., 2016). However, it is now broadly recognized that their responses and relative tolerance to each particular stressor and the cumulative anthropogenic pressures imposed by global change are strongly mediated by species-specific attributes and traits (Kilminster et al., 2015; Mauffrey et al., 2020).

1.3.1. Life history traits and functional groups of seagrasses and macroalgae characterise their responses to stress

Seagrasses and marine macroalgae exhibit a plethora of life history strategies and adaptive mechanisms that determine their relative vulnerability to anthropogenic stressors. The specific set of strategies of each macrophyte confers it with a characteristic resistance to cope with different stressors, such as light reduction, rising seawater temperatures, or increased herbivory (O'Brien et al., 2018; Mauffrey et al., 2020). However, even species belonging to the same phylogenetic groups can exhibit high variability in their traits, making it difficult to generalize responses between species or when responding to completely distinct or interacting stressors (Kilminster et al., 2015; Gillis et al., 2023). Apart from resistance, post-disturbance recovery will likely differ as well as a function of species-specific life history traits. Thus, the use of species-specific attributes and traits has been suggested as a useful functional comparative approach that helps to provide more accurate information when assessing seagrass meadows or macroalgal forests dynamics under different sources of anthropogenic stress (Kilminster et al., 2015; Mauffrey et al., 2020).

Seagrass species have been classified based on life history traits that mainly relate to their growth and reproductive strategies (i.e., colonizing, opportunistic, and persistent species) (Kilminster et al., 2015). In general, this functional classification has helped to describe how seagrasses respond to disturbances. For instance, persistent species (i.e., those with larger sizes, biomass, and physiological resistance) typically form extensive long-lived meadows that are remarkably resistant to stress but can take decades to recover once disturbed (Roca et al., 2016). Hence, when managing ecosystems dominated by persistent species, it is critical to prevent their collapse rather than restore them (van Katwijk et al., 2016). Unlike persistent seagrasses, colonizing (i.e., shorter turnovers, investment in dormant seeds, and low physiological resistance) or opportunistic species (mixed strategy) form enduring or transitory meadows that exhibit low resistance but fast post-disturbance recovery rates. While the transitory nature of meadows might be triggered by anthropogenic stress, recovery times in these meadows will be more intrinsically affected by their reproductive strategies (at least in some species), calling for ensuring seed set, viability, germination, and survival (Kilminster et al., 2015). However, examples of meadow degradation or collapse highlight the species-specific dissimilarities in seagrass resilience within functional groups and even within the same genera. For instance, *Cymodocea nodosa* and *Zostera marina*, similar species according to the functional classification of Kilminster et al. (2015), exhibit quite different ecophysiological strategies, which confer them specific acclimatization capacities in the face of transient light deprivation and shape their resilience (Silva et al., 2013). Recovery trajectories have also shown species-specific patterns. While *Zostera noltii* showed initial signs of recovery after 15 years of absence resulting from a eutrophication process in Mondego Bay (Portugal), *Zostera muelleri* in Moreton Bay (Australia) took only three years to recover from a flood-related loss that increased turbidity, nutrient concentrations, and reduced light availability (Campbell & McKenzie, 2004; Cardoso et al., 2010).

Forest-forming (i.e., canopy-forming algae and kelps) and turf-forming species comprise some of the main macroalgae subgroups targeted in this thesis. These groups possess inherently distinct strategies that mediate their responses to anthropogenic impacts (Krumhansl et al., 2016; Mauffrey et al., 2020). Although kelp species rank among the fastest-growing primary producers on the planet (Mann, 1973; Smale et al., 2013), turfs are rising nowadays leading to a global homogenization of benthic ecosystems on coastal rocky reefs (Filbee-Dexter & Wernberg, 2018; Pessarrodona et al., 2021). This substitution of kelps for turfs seems to be driven by a higher competitive ability of turf-forming species in the face of anthropogenic pressures. However, while turfs might be favoured by increases in nutrient enrichment and reductions in top-down control that lead to detrimental effects on the establishment of foundation species, whether this is promoting the rise of turfs or just limiting the abundance of forest-forming species remains to be clarified yet (O'Brien & Scheibling, 2018). Moreover, understanding macroalgal dynamics to human pressures poses other difficulties given, for example, that trajectories of change are determined by a broad range of context-dependent processes and simultaneous stressors that impact with varying intensity at local or regional scales (Strain et al., 2014; Krumhansl et al., 2016; Duarte et al., 2022).

1.3.2. Functioning of seagrass and macroalgal habitats

The high productivity of macroalgal forests and seagrass meadows stems from their ability to thrive under restricted light, nutrient, and temperature regimes (Dayton, 1985; Lee et al., 2007), coupled with their effective defence mechanisms against herbivores (Vergés, 2007; Hernan, 2017). The occurrence and timing of these critical drivers determine whether habitats are primarily limited by nutrients and/or light availability (bottom-up control) or herbivore consumption (top-down control) (Burkepile & Hay, 2006; Borer et al., 2006). Seagrass and macroalgal primary production have often been directly associated with light or nutrients limitation around the world (Lotze & Worm, 2001; Lee et al., 2007); however, these habitats have also shown clear signs of vulnerability to herbivore-mediated collapses globally (Eklöf et al., 2008; Filbee-Dexter & Scheibling, 2014). In fact, in marine systems, where trophic effects and herbivory rates are often greater than in land (Shurin et al., 2002; Wood et al., 2017), the virtual elimination of predators by overfishing have usually led to herbivore outbreaks that amplify the intensity of herbivore control over primary producers (Steneck, 2002; Myers & Worm, 2003; Estes et al., 2011).

Whether top-down or bottom-up processes control ecosystem dynamics remains a long-lasting and (likely) unresolved debate in ecology (Conversi et al., 2015; Wood et al., 2017). Both processes interact distinctly, regulating ecosystems via influence on primary production and/or herbivore-mediated mortality (Burkepile & Hay, 2006). In macrophyte ecosystems, several factors such as nutrient enrichments, light limitation, anthropogenic heating, or predator presence shape herbivory top-down control by altering plant-herbivore interactions, often aggravating the expected damage from the changing conditions themselves (Boada et al., 2017; Pagès et al., 2018; Pessarrodona et al., 2019). Vulnerability to ecosystem collapses can be explained by the strength of species interactions across trophic levels (i.e., plant-herbivore-predator), which are highly context-dependent as several factors influence them (Borer et al., 2006; Ling et al., 2015). The classic *top-down – bottom-up control* debate must, therefore, include the understanding of *biotic/abiotic – endogenous/exogenous* factors that determine the strength of these interactions and substantially influence ecosystem vulnerability (Conversi et al., 2015). Challenging as it is, ecology needs integrative methods and metrics that incorporate sources of environmental complexity into the understanding of trophic relationships fundamental for ecosystem dynamics, thus providing more accurate information for the management of natural systems (Wood et al., 2017). In ecosystems prone to catastrophic transitions, such as those dominated by marine vegetation, understanding the extent to which specific stressors modulate their trophic relationships, and in particular, the interactions between macrophytes and herbivores, will help explain differential vulnerabilities across ecological contexts.

1.4. Marine vegetation in the era of global change

Global change is causing dramatic shifts in the distribution and ecological function of macrophytes (Waycott et al., 2009; Wernberg et al., 2023). For example, with increasing anthropogenic pressures, turfs are emerging as prevalent habitats where luxuriant macroalgal forests used to thrive (Filbee-Dexter & Wernberg, 2018; O'Brien & Scheibling, 2018; Pessarrodona et al., 2021); and seagrasses will continue their decline unless effectively protected (Unsworth et al., 2018; de los Santos et al., 2019). These undesired trends are leading to decreased productivity of such coastal benthic ecosystems around the world, as well as the loss of their structural complexity, functioning, and services (Cullen-Unsworth et al., 2014; Unsworth et al., 2022; Duarte et al., 2022). However, marine vegetation responses to global change do not always follow similar trajectories or respond with the same patterns across regions (Krumhansl et al., 2016; de los Santos et al., 2019; Dunic et al., 2021; Duarte et al., 2022). While the high heterogeneity between (and within) these groups of species undermines our capacity to understand their relative vulnerability to drivers of anthropogenic stress; in each local context, the intensity of anthropogenic pressures will be largely determined by the identity of the stressor and its potential interaction with others (Crain et al., 2008; Strain et al., 2014). Hence, basic ecological research on specific stressors affecting macrophyte species is crucial for gaining precise insights into the impacts associated with global change and the potential responses of species and ecosystems. This knowledge contributes significantly to improving predictions, thereby enabling the essential downscaling from global to regional and local models that facilitate the development of effective management and conservation policies (Lubchenco et al., 1991; Levin et al., 2009).

In this thesis, I will focus on four primary drivers of global change affecting marine macrophyte ecosystems, namely eutrophication, overfishing, anthropogenic heating, and the arrival of range-extending species (Fig. 1.2). While it is acknowledged that these may not encompass all factors influencing seagrass and macroalgal communities, they are particularly significant within coastal waters (Wernberg et al., 2023).

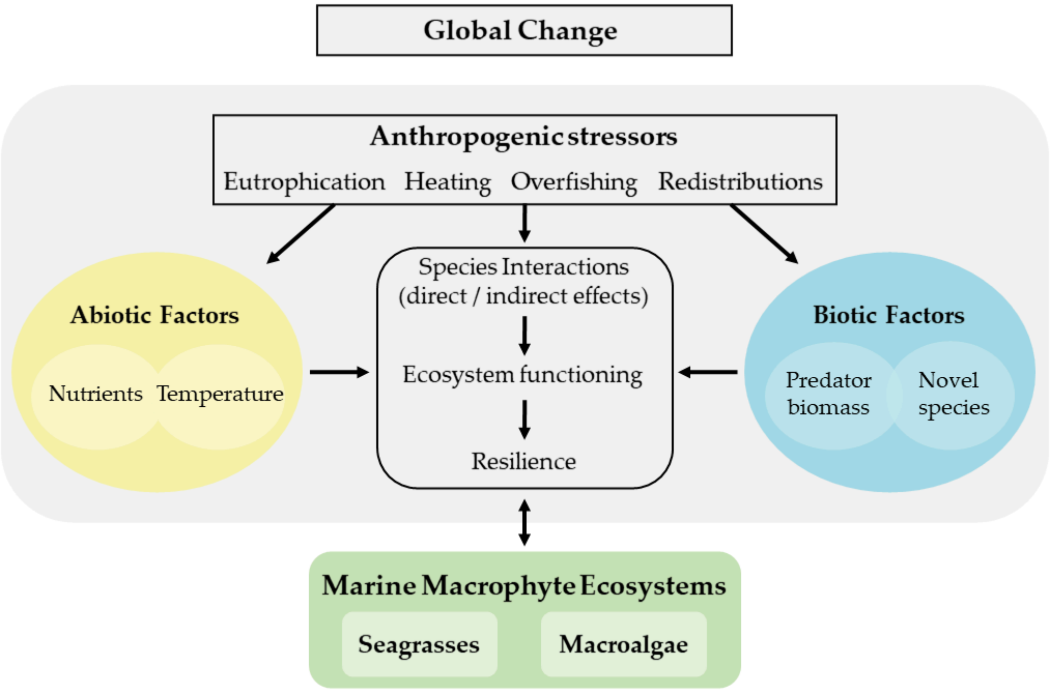


Figure 1.2. Influence of global change on marine vegetated habitats. Sources of anthropogenic stress directly or indirectly shape abiotic and biotic contexts, altering species interactions. These human-mediated impacts affect the functioning of macrophyte ecosystems, eroding their resilience and determining the persistence capacity of macrophyte species and their associated biodiversity.

1.4.1. Eutrophication and light limitation impacts on marine vegetation

As primary producers, the growth, abundance, and distribution of seagrass and macroalgae species are essentially limited by underwater irradiance and light availability at the canopy (Duarte, 1991; Dennison et al., 1993). Human activities have led to alarming reductions in the quality and clarity of coastal waters, largely due to inadequate waste treatment and changes in land use (Erftemeijer & Lewis, 2006; Airoldi & Beck, 2007; Burkholder et al., 2007; Mangialajo et al., 2008). This decline in water quality is widely acknowledged as one of the principal threats to the health of seagrass meadows and macroalgal forests in recent decades (Orth et al., 2006;

Krause-Jensen et al., 2007; Waycott et al., 2009). Eutrophication has, therefore, led to light limitation, affecting the vast majority of marine macrophytes in two main ways (Krause-Jensen et al., 2007; Short et al., 2011). First, by reducing water transparency, it reduces the maximum depth at which marine macrophytes can thrive. Specifically, phytoplankton blooms limit light availability and diminish the chances for macrophytes to persist at depth (Duarte, 1991; Sant & Ballesteros, 2021). Second, in shallow areas, nutrients contribute to the overgrowth of epiphytes and fast-growing algae that compete for light with seagrasses and forest-forming species (Burkholder et al., 2007; Pinedo et al., 2007). Thus, light limitation can trigger abrupt ecosystem collapses with flow-on consequences for their associated biodiversity (Walker & McComb, 1992; van der Heide et al., 2007).

Marine macrophytes exhibit specific capacities to cope with light limitation (Lee et al., 2007; Sant & Ballesteros, 2021). The species-specific capacity to acclimatize to reduced light has been studied using the minimum light requirements (MLR) at the canopy level as a proxy of species survival in seagrass and macroalgal beds (Lee et al., 2007; Sant & Ballesteros, 2021). Global minimum and maximum depth observations of seagrasses have also provided insights into their depth colonization ranges, providing a baseline for each species under optimum light conditions (Short et al., 2011). In addition, macroalgae are commonly characterised by high spatial competition, leading to tight depth-zonation patterns that can reveal optimum species performances at different light conditions (Sant & Ballesteros, 2021). Light limitation impacts are of particular concern in deeper waters as macrophyte distributions are commonly constrained at their deep edge (Short et al., 2011; Sant & Ballesteros, 2021). Hence, regardless of whether they are caused by anthropogenic pressures or natural depth gradients, some species of seagrass and macroalgae are more vulnerable than others to reduced light conditions. While anthropogenic reductions in light availability may be of greater concern at regions with lower natural levels of light penetration, it is clear that species with more restrictive MLR or found over narrower depth ranges may be more prone to local or regional contractions (Short et al., 2011). Understanding how seagrass and macroalgae species harvest light and if there are specific strategies at distinct organizational scales that can cope better with light attenuation is, therefore, a critical factor to be solved. Enlarging our ecological knowledge in this direction could help refocus research and management efforts on species, meadows, or forests more vulnerable to light reduction impacts.

1.4.2. Overfishing, trophic cascades and alteration of herbivory patterns

The overexploitation of fish stocks has long attracted the attention of ecologists for their potential indirect impacts on the degradation and total collapse of extensive ecosystems dominated by marine vegetation (Steneck et al., 2002; Eklöf et al., 2008; Filbee-Dexter & Scheibling, 2014; Heithaus et al., 2014). Free from their usual predators, herbivore outbreaks can trigger catastrophic depletions of marine macrophytes (Estes et al., 2011; Ling et al., 2015; Christianen et al., 2023). Trophic cascades (i.e., indirect effects of predator presence/absence on marine vegetation via herbivore control) show substantially greater effects on marine ecosystems compared to other aquatic and terrestrial ecosystems (Shurin et al., 2002), which also vary at local or regional scales, making them even more difficult to predict and manage. Indeed, ongoing pressures and context-dependent conditions interact in ways that are not always intuitive, leading to shifts that occur earlier or later than anticipated (Ling et al., 2009a; Conversi et al., 2015; Boada et al., 2017). Hence, in an ocean without predators (Myers & Worm, 2003), it is fundamental to understand the influence of abiotic (see Section 1.4.3.) and biotic factors that shape the strength of plant-herbivore interactions, that is, those between macroalgae or seagrasses, and herbivores (Bakker et al., 2016; Wood et al., 2017). These factors, often determined by the surrounding environment, play a decisive role in predicting the strength of these interactions and their impact on ecosystem vulnerability (Borer et al., 2005; Poore et al., 2012; Boada et al., 2017).

1.4.3. Anthropogenic influences on abiotic environments and species interactions

Macroalgal forests and seagrass meadows are vulnerable to other human influences on abiotic conditions besides light limitation in coastal waters derived from nutrient enrichments (see Section 1.4.1). For example, seawater warming has caused macroalgal forests and seagrass meadows to experience extensive thermal stress, massive mortalities, and range contractions over recent decades (Marbà & Duarte, 2010; Smale, 2020; Wernberg et al., 2023). While a substantial body of research has investigated the direct effects of global change on biodiversity (e.g., Sala et al., 2000), it may induce less obvious biotic impacts via alteration in species interactions (Tylianakis et al., 2008). This variation in species interactions can have greater impacts on ecological communities than the human-induced change in environmental conditions itself (Ockendon et al., 2014). For instance, regarding plant-herbivore interactions, nutrient enrichments in marine benthic ecosystems can stimulate macrophyte growth and effectively buffer the control exerted by herbivores (Burkepile & Hay, 2006; Boada et al., 2017). In addition, as temperatures rise at the pace of global warming, it influences both herbivore and macrophyte metabolic rates. This is expected to affect animal behaviour, intensifying feeding rates and herbivore consumption demands in response to such metabolic needs or due to alterations in dietary resource preferences (Kordas et al., 2011; Pagès et al., 2018; Buñuel et al., 2021; Santana-Garcon et al., 2023). In the case of marine macrophytes, although expected to increase their productivity in regions close to the poles (Hyndes et al., 2017; Krause-Jensen et al., 2020), they are also already suffering range contractions or seeing their resilience eroded in temperate seas (Smale et al., 2013; Wernberg et al., 2016). Moreover, ocean warming is simultaneously inducing the tropicalization of temperate seas, leading to novel species interactions that can drive the fate of macrophyte ecosystems (see Section 1.4.4.).

1.4.4. Range shifts under global change: The rise of tropicalization

While human activities such as the removal of geographical barriers or increased maritime transport facilitate the introduction and spread of numerous species (Hulme, 2009; Castellanos-Galindo et al., 2022), anthropogenic heating also favours the pole-ward expansion of marine organisms (Smale, 2020; Krause-Jensen et al., 2020). Many of these species rely on increased seawater temperatures to keep on the move toward higher latitudes and find new environments that fit their biological demands (Bennet et al., 2021). In the so-called tropicalization (i.e., the increased prevalence of tropical species in historically temperate areas that have since warmed due to global change), novel interactions form as native temperate species encounter range-extending species (Vergés et al., 2014a; Hyndes et al., 2017; Zarzyczny et al., 2023). These tropical species usually exert a higher pressure on temperate ecosystem resources than their native counterparts, which might result in widespread macrophyte loss (Sala et al., 2011; Vergés et al., 2014b; Vergés et al., 2016; Wernberg et al., 2016; Smale, 2020). By affecting habitat-forming species, tropicalization will also sooner or later affect key native herbivore species (Yeruham et al., 2020). Interactions between these herbivores might be crucial for such evolutionary-novel communities as they are responsible for structuring temperate macrophyte communities (Gilman et al., 2010; Wood et al., 2017). While the ultimate mechanisms whereby range-extending species (or vagrants) succeed in unfamiliar areas remain poorly understood (Stuart-Smith et al., 2021; Miller et al., 2023), it is critical to identify which species traits help some species to enter and later colonize temperate latitudes; helping us understand range-extension patterns and species interactions in tropicalized ecosystems (Vergés et al., 2019; Nagelkerken et al., 2023).

Behavioural traits or the display of adaptive behaviours on the invasion front line can help the establishment of range-extending (or invasive) species in new locations (Holway & Suarez, 1999; Smith et al., 2018). While the role of behavioural interactions remains unresolved in most of these ongoing intrusions (Coni et al., 2022), social species capable of forming mixed-species shoals could obtain similar benefits as those of single-species shoals (see Paijmans et al., 2019). However, these interactions are not without costs and may be a function of the novel environment rather than a behavioural carry-over from their tropical heritage. *Abudefduf sexfasciatus*, for instance, only formed mixed-species shoals in temperate areas of south-eastern Australia, but not in its natural tropical domains (Matis, 2018). Native species, in contrast, might need time to learn to interact and develop resistance mechanisms against invaders (Santamaría et al., 2022). Hence, species traits and behavioural interactions might be crucial to favour or put resistance to the intrusion and subsequent establishment of range-extending species (Azzurro et al., 2014; Smith et al., 2018; Donelson et al., 2019). Thus, the outcomes of these interactions are (likely) highly dependent on the specific interactors forming the assemblage (Paijmans et al., 2020; Coni et al., 2021). This highlights the importance of investigating each emerging interaction in detail to help understand the fate of ongoing invasions and also to assess potential impacts on macrophyte communities in tropicalized temperate ecosystems (Vergés et al., 2014a; Zarzyczny et al., 2023).

1.5. Resilience in marine vegetated ecosystems: Mechanisms and concepts

Global change is eroding the resilience of seagrass meadows and marine forests. In this thesis, resilience is defined as the capacity of ecosystems to preserve function in the face of disturbances, including its two key components, resistance and recovery (Levin & Lubchenco, 2008; Kilminster et al., 2015; O'Brien et al., 2018). The gradual loss of resilience resulting from constant anthropogenic pressures has made ecosystems dominated by marine vegetation, as well as other foundation species, particularly prone to sudden collapses to less productive and diverse states (Scheffer et al., 2001; Mumby et al., 2007). As global change drivers like nutrient enrichments, anthropogenic heating, or the arrival of invasive species (among others) intensify their effects, these collapses have emerged throughout the world's seas (e.g., Ling et al., 2009; Vergés et al., 2014b; Wernberg et al., 2016; Boada et al., 2017). In seagrass meadows or macroalgal forests these catastrophic transitions often relates to reductions in underwater light availability (van der Heide et al., 2007; Carr et al., 2010) or increases in herbivore abundance (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015; Christianen et al., 2023). The nonlinearities inherent in these systems have long fascinated field and theoretical ecologists (see Holling, 1973; May, 1977); however, the present era of global change has made these transitions very real as many ecosystems teeter on the brink of irreversible collapse (Wernberg et al., 2023; Ling & Keane, 2024).

Under such pressures, macrophyte ecosystems can shift to alternative and highly stable states (van der Heide et al., 2007; Carr et al., 2010; Filbee-Dexter & Scheibling, 2014). These *bistable* systems can display two stable states in a given location and for a given level of stress (Adams et al., 2018). For an ecosystem that expresses *bistability*, one stable state typically represents a healthy, undisturbed version of the ecosystem, whereas the other represents its degraded version. In the case of seagrass meadows and macroalgal forests, a set of attributes and feedback mechanisms have been described as determinants of their ability to cope with environmental stress (Ling et al., 2015; Maxwell et al., 2017). Thus, while habitat-forming species modify the physical environment within their beds, creating more conducive environmental conditions for other species, which define them as ecosystem engineers (Thomson et al., 2015; Bulleri et al., 2018); they also facilitate their own presence through multiple potential feedback loops (Nyström et al., 2012; Maxwell et al., 2017; Mayol et al., 2022). For instance, seagrass leaves and shoots help reduce water flow, lowering physical stress and enhancing sediment trapping from the water column, improving light penetration within meadows and ultimately reinforcing seagrass growth (Ralph et al., 2007; Adams et al., 2016; Adams et al., 2018). However, this will only occur as long as these feedback loops are strong enough (Maxwell et al., 2017). Although feedback loops help sustain the presence of macrophytes (i.e., self-reinforcing), they have the potential to perpetuate the reverse state as well (i.e., self-dampening) (Nyström et al., 2012; Ling et al., 2015). Following the same example, as meadows degrade and seagrass declines, its absence permits increased current and wave velocities that promote sediment resuspension, higher turbidity, and physical stress, which together prevent the establishment of seedlings and the perpetuation of an unvegetated and stable bare sand state (van der Heide et al., 2007; Carr et al., 2010). Given how feedback loops can shape the nonlinear dynamics that influence the resistance and recovery (i.e., resilience) of macrophyte ecosystems, these systems serve as excellent models for ecological research (Filbee-Dexter & Scheibling, 2014; O'Brien et al., 2018). Moreover, all these reasons affecting ecosystem dynamics of marine vegetated habitats (among others) make restoration efforts very complex (van Katwijk et al., 2016), being therefore crucial to prevent these potential losses rather than attempting a challenging restoration once the system is lost (Scheffer et al., 2001; van der Heide et al., 2007).

1.6. The Mediterranean Sea: A natural laboratory for global change

The Mediterranean Sea, situated between the North Atlantic Ocean and the tropical Red Sea, is the largest semi-enclosed sea on Earth. It is characterised by low nutrient values, high salinity, and a (warm-)temperate regime (Coll et al., 2010). However, it is also defined by inherent natural environmental variability, primarily along its longitudinal gradient. This variability involves crucial gradients of temperature, nutrients, and salinity (Agusti et al., 2017; Santana-Garcon et al., 2023; Nikolaou et al., 2023). Despite occupying less than 1% of the world's surface ocean, it hosts 6.4% of its marine biodiversity, including a large number of endemic species (Boudouresque et al., 2017). Although it makes the Mediterranean Sea a hotspot of biodiversity (Lejeusne et al., 2010; Boudouresque et al., 2017), it is also severely affected by anthropogenic pressures, including high urbanization levels, overfishing, maximum temperatures fluctuations, species invasions, among a wide range of other drivers of global change (Airoldi & Beck, 2007; Sala et al., 2012; Cramer et al., 2018).

Although anthropogenic heating is warming the world's seas, the Mediterranean has experienced a warming trend 3.7 times higher than the global ocean over the last 40 years (Pisano et al., 2020). It amounts to a rise of 0.38 °C per decade and an increase in the likelihood of marine heatwaves and mass mortality events (IPCC, 2019; Garrabou et al., 2022). This increase in temperature is leading to the collapse of Mediterranean native biodiversity at the warmer edges (Yeruham et al., 2015; Albano et al., 2021), as well as an increase of range-extending tropical species as the environment changes (Lejeusne et al., 2010; Vergés et al., 2014b). The Mediterranean coast is also among the most densely populated on Earth (Airoldi & Beck, 2007). Human activities to meet the needs of such a disproportionately high population have caused intense impacts on their coastal habitats directly linked to land transformation, overfishing, and the introduction of invasive species (Lejeusne et al., 2010). Large-scale agriculture transformation, livestock farming, and increased coastal urbanization intensify nutrient discharge into coastal waters (e.g., Ouaissa et al., 2023). This alteration of coastal biogeochemical cycles has promoted degradations in water quality, inducing phytoplankton or algal blooms that could radically alter the traditional composition of their oligotrophic coastal benthic communities (Coll et al., 2010; Agusti et al., 2017). Macroalgal beds and seagrass meadows are particularly at risk from these alterations (Ralph et al., 2007). In addition, the Mediterranean has been fished since ancient times, and with the increasing demand for marine resources, the mean trophic level of catches has declined significantly (Pauly et al., 1998) to the point that in 2014, 91% of its fish stocks were already overfished (Cramer et al., 2018). Overfishing has caused a loss of functional predation, leading to indirect cascading effects and resulting, for instance, in sea urchin outbreaks and overgrazing episodes in macroalgal forests (Sala et al., 1998). Finally, while the geography of the Mediterranean defines its characteristic temperate biota derived from the Atlantic Ocean (Lejeusne et al., 2010), maritime transport and the opening of the Suez Canal have allowed approximately 1000 tropical species to successfully infiltrate Mediterranean ecosystems (Castellanos-Galindo et al., 2022; Zenetos et al., 2022). Among the Lessepsian species that have settled in the eastern Mediterranean, rabbitfishes have caused dramatic transformations of shallow rocky reefs dominated by marine forests that are now depleted in productivity and diversity (Sala et al., 2011; Vergés et al., 2014b).

2. Objectives

The objectives and research questions of this thesis aim to understand how habitat-forming species respond and acclimatize to the rapidly changing conditions posed by anthropogenic global change. This thesis focuses on marine macrophytes *sensu lato* (both seagrasses and macroalgae) as foundation species of soft and rocky substrates, exploring their interactions with herbivores (i.e., sea urchin and fish species) and their environment, and with a particular emphasis on Mediterranean systems. I use multiple methodological approaches to address these questions, including the sampling of environmental gradients across the Mediterranean Sea, meta-analytic approaches, and mechanistic and statistical models in order to understand how species respond to change. In particular, I focus on species-specific traits at different organizational levels to understand how species strategies vary in response to anthropogenic stressors. This thesis seeks to provide essential ecological insights for more effective ecosystem management and conservation, helping mitigate the ongoing impacts of global change. The thesis is split into four objectives:

The first objective is to evaluate the effect of physiological photo-acclimatization and self-facilitation mechanisms in shaping seagrass resistance and resilience to light deprivation. In **Chapter 3**, I use model-based approaches to explore potential coping mechanisms seagrass species employ to deal with light limitation, using seagrass minimum light requirements (MLR) as a proxy of plant resistance. I then build and parameterize deterministic models of plant carbon balance based on field evidence for *Cymodocea nodosa*.

The second objective seeks to assess the influence of species-specific seagrass attributes and traits in determining their global maximum vertical distributions (i.e., depth range). For this, I examine the effects of seagrass size (using rhizome diameter as a proxy), functional resilience strategies (i.e., colonizing, opportunistic, and persistent species), and acclimatization potential (i.e., in physiological, morphological, structural, and growth traits) on their species-specific depth distribution ranges. In **Chapter 4**, I conduct a systematic review of existing literature and perform a series of meta-analyses to test how these factors influence seagrass vertical distribution.

The third objective explores how the relationship between (macroalgae) habitat production and herbivore consumption (i.e., *Paracentrotus lividus* and *Arbacia lixula* sea urchin species) changes in response to distinct endogenous and exogenous factors across the Mediterranean Sea. I estimate the relationship between herbivory and production by measuring the size of individually-produced sea urchin grazing halos across different ecological contexts (i.e., distinct nutrients and temperature conditions, protection regimes, macroalgal habitat types, and depths). In **Chapter 5**, I use grazing halos as the response variable that integrates multiple interacting factors influencing the relative vulnerability of macroalgal communities to herbivory.

The fourth objective examines how native fish species (i.e., *Sarpa salpa* and *Sparisoma cretense*) and Lessepsian range-extending tropical herbivores (*Siganus luridus* and *Siganus rivulatus*) interact by creating novel shoaling configurations in a tropicalizing transitional area and altering their respective foraging activity. In **Chapter 6**, I include observational field data in generalized linear models to evaluate: (i) novel shoaling configurations and size of shoals based on their composition where native and range-extending species co-exist, (ii) the strength of mixed-species associations, and (iii) how fish foraging activity is mediated by species identity, bout rates, individual length, shoal type and shoal size. Knowledge of these novel interactions will help provide powerful insights into the impact of range-extending herbivores on Mediterranean macrophyte ecosystems.

Advisors’ report

We, Dr. Teresa Alcoverro Pedrola and Dr. Jordi Boada Garcia, research scientists at the Blanes Center for Advanced Studies (CEAB), and Dr. Matthew Philip Adams, senior lecturer at Queensland University of Technology (QUT) as advisors of the Doctoral Thesis entitled “Species interactions, ecosystem functioning and the resilience of marine vegetated ecosystems in a global change era”,

INFORM that the research developed by Mario Minguito Frutos for his Doctoral Thesis has been organized into four chapters, corresponding to the two published scientific papers and the two completed manuscripts currently under review listed above with their corresponding impact factors, quartiles, deciles, and areas of knowledge. The thesis contains a General Introduction, a General Discussion, and a General Conclusions section that comprises the main findings reached in this thesis,

and we CERTIFY that Mario Minguito Frutos has led the research in this thesis, actively participating in all the tasks of the different studies conducted within this thesis: setting the hypothesis and objectives, organizing the fieldwork and data collection, conceiving and performing the data analyses that support the results, and leading the writing and revision process of all the manuscripts already published and those that are currently under review.

Finally, we CERTIFY that the co-authors of the publications that endorse this Doctoral Thesis will not use them as part of any other national or international Doctoral Thesis.

Blanes, 15th May 2024

Dr. Teresa Alcoverro Pedrola　　Dr. Jordi Boada Garcia　　Dr. Matthew Philip Adams

Matthew Ad

Chapter 3

Quantifying the role of photo-acclimatization and self-facilitation for seagrass resilience to light deprivation

Minguito-Frutos, M., Adams, M. P., Alcoverro, T., Vilas, M. P., Alonso, D., Mayol, E., Bernardeu-Esteller, J., Marín-Guirao, L., Ruiz, J. M., & Boada, J. (2023). Quantifying the role of photoacclimation and self-facilitation for seagrass resilience to light deprivation. *Frontiers in Plant Science*, *14*, 1186538. https://doi.org/10.3389/fpls.2023.1186538.

Abstract

Light gradients are ubiquitous in marine systems as light reduces exponentially with depth. Seagrasses have a set of mechanisms that help them to cope with light stress gradients. Physiological photo-acclimatization and clonal integration help to maximize light capture and minimize carbon losses. These mechanisms can shape plants' minimum light requirements (MLR), which establish critical thresholds for seagrass survival and help us predict ecosystem responses to the alarming reduction in light availability posed by global change. Using the seagrass *Cymodocea nodosa* as a case study, we compare the MLR under different carbon model scenarios, which include photo-acclimatization and/or self-facilitation (based on clonal integration) and that were parameterized with values from field experiments. Physiological photo-acclimatization conferred plants with increased tolerance to reducing light, approximately halving their MLR from 5-6% surface irradiance (SI) to ≈ 3% SI. In oligotrophic waters, this change in MLR could translate to an increase of several meters in their depth colonization limit. In addition, we show that reduced mortality rates derived from self-facilitation mechanisms (promoted by high biomass) induce bistability of seagrass meadows along the light stress gradient, leading to abrupt shifts and hysteretic behaviors at their deep limit. The results from our models point to (i) the critical role of physiological photo-acclimatization in conferring greater resistance and ability to recover (i.e., resilience), to seagrasses facing light deprivation and (ii) the importance of self-facilitating reinforcing mechanisms in driving the resilience and recovery of seagrass systems exposed to severe light reduction events.

Keywords: *minimum light requirements, physiological photo-acclimatization, bistability, resilience, Cymodocea nodosa.*

3.1. Introduction

Seagrasses provide multiple goods and services to humans, such as nursery habitat for fish species, coastal protection against erosion, water quality improvement, carbon sequestration, and buffering capacity against ocean acidification (Duarte et al., 2013; Unsworth et al., 2019a; Ricart et al., 2021). One of the main reasons for the global decline of seagrasses is coastal eutrophication and the subsequent reduction of light availability, which contracts the space where seagrasses can thrive (Cloern, 2001; Orth et al., 2006; Burkholder et al., 2007; Waycott et al., 2009). Light limitation reduces photosynthetic rates of seagrasses, altering their overall carbon balance (Ralph et al., 2007; McMahon et al., 2013), and subsequently leading to net carbon losses which is likely a primary control of seagrass decline (Moreno-Marín et al., 2018; Adams et al., 2020). Indeed, seagrass ecosystems shift to a bare sand state when light availability drops below critical tolerance thresholds, with entire seagrass meadows collapsing after major light limitation events (Walker & McComb, 1992; Preen et al., 1995; van der Heide et al., 2007). For long-term changes in light availability, these thresholds are commonly known as minimum light requirements (MLR). MLR therefore determine the critical light availability for survival of seagrasses over ecologically-relevant time frames and are calculated with light values at maximum colonization depth (Collier et al., 2016). Because of their relevance to sustain meadow persistence, MLR have been identified for numerous seagrass species distributed worldwide (e.g., Erftemeijer & Lewis, 2006; Lee et al., 2007).

Understanding the processes conferring seagrasses with increased resistance to disturbances becomes essential to forecast and prevent the loss of these habitat-forming species. Since light plays the most pivotal role in modulating plant growth and depth limits (Dennison, 1987; Duarte, 1991), changes in seagrass responses to light reduction are a likely pathway by which resistance is conferred to them. Seagrasses respond to light deprivation with a well-defined sequence of changes, the first of which is physiological photo-acclimatization (Waycott et al., 2005). Physiological photo-acclimatization refers to the ability of plant leaves to increase their efficiency of converting light into photosynthate and/or decrease respiration demand. The presence or absence of physiological photo-acclimatization can be identified by measuring changes in both the maximum photosynthetic rates and photochemical efficiency of seagrass leaves in response to changes in their local light environment (Cayabyab & Enríquez, 2007). Under light limitation, plants physiologically acclimatize through two strategies: enhancing light harvesting efficiency (e.g., adjusting metabolic demand of leaf tissues, increasing total chlorophyll, reducing the chlorophyll *a:b* ratio, etc.), and/or minimizing carbon losses (i.e., carbon allocation strategies) (Olivé et al., 2013; Silva et al., 2013). For instance, the higher content of total chlorophyll (as well as other altered pigments) in the seagrass *Cymodocea nodosa*, together with its carbon allocation strategy, have been argued as the underlying reasons for its superior ability to cope with light deprivation compared to *Zostera marina* (Silva et al., 2013). In addition, seagrasses can also acclimatize to low light by increasing shoot size and reducing shoot density (i.e., self-thinning) in order to optimize light capture by the canopy (Enríquez et al., 2019). These strategies are critical for maintaining a positive carbon balance and reducing MLR (Campbell et al., 2007; Silva et al., 2013). However, seagrass species are not all equal, and a greater ability to acclimatize certain traits can confer plants an improved carbon balance and reduced MLR, allowing seagrasses to survive in environments with lower light availability (Ruiz & Romero, 2001; Minguito-Frutos et al., 2023). Hence, the MLR for different seagrass species may depend substantially on the magnitude of its photo-acclimatization capacity, which itself can be mediated by the contextual conditions where that population resides (Erftemeijer & Lewis, 2006; Cayabyab & Enríquez, 2007). Local contexts, referring to light but also to thermal natural histories, have influenced the strategies of marine macrophytes in responding to abiotic impacts such as light reduction (Ruiz & Romero, 2003; Robledo & Freile-Pelegrín, 2005; Yaakub et al., 2014) or marine heatwaves (Nguyen et al., 2020; Schubert et al., 2021). In particular, seagrasses growing in suboptimal light environments have their MLR altered and show different photosynthetic performance compared to those growing in optimal conditions (Ruiz & Romero, 2003; Yaakub et al., 2014).

In addition to these well-defined acclimatization responses (Waycott et al., 2005), seagrass ecosystems may also be characterised by the occurrence of feedbacks leading to the emergence of nonlinear dynamics (van der Heide et al., 2007; McGlathery et al., 2013). When sufficiently strong, feedbacks can push seagrass meadows to express bistable behaviors with two possible stable states (seagrass and bare sand) for the same level of external stress (Maxwell et al., 2017; Adams et al., 2018). Bistable behaviors may arise as a consequence of increased light stress provoking abrupt transitions at the deep edge of seagrass meadows (Mayol et al., 2022). For example, if reinforcing mechanisms driven by plant presence exists, and if such mechanisms act to reduce the mortality rates of a stressed seagrass bed (i.e., self-facilitation mechanisms), they can lead to bistability as explored in Mayol et al. (2022) (see Fig. 3.1). In that recent work, it was found that bistable behaviors could potentially arise due to clonal integration, which refers to the ability of seagrass species to translocate resources between connected ramets (Terrados et al., 1997; Nielsen & Pedersen, 2000). However, under light stress gradients, mortality increases resulting in shoot density decrease and this lower biomass could significantly modify the local environment by reducing sediment trapping, increasing damage from erosion, reducing physical integration, reducing anchoring and amplifying toxicity from eutrophication (Duarte & Sand-Jensen, 1990; Olesen & Sand-Jensen, 1994; Vidondo et al., 1997; van der Heide et al., 2007; van der Heide et al., 2008; Collier et al., 2009). Overall, seagrasses will display a set of responses to cope with light stress gradients linked to changes in biomass that eventually affect mortality rates, but it is so far unclear whether photo-acclimatization itself is a nonlinear process able to cause bistability.

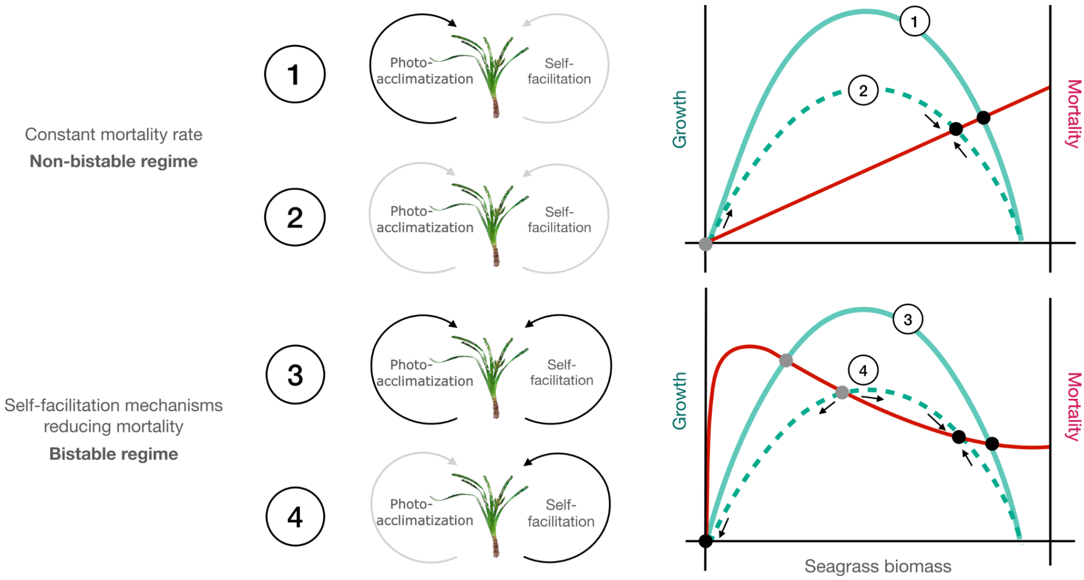


Figure 3.1. Conceptual diagram describing the different models explored. Green curves represent seagrass growth rates as a function of biomass up to a certain maximum carrying capacity. Red lines represent seagrass mortality rates. Equilibrium points are represented by grey (unstable) and black (stable) dots at the intersection between growth and mortality curves. In the absence of self-facilitation (1 and 2 upper panel), mortality increases with biomass and intersects growth curves forming stable equilibria. In contrast, self-facilitation mechanisms (3 and 4 lower panel) reduce seagrass mortality as biomass increases, promoting the emergence of unstable equilibria leading to bistability (two stable equilibria separated by an unstable equilibrium point). Moreover, plants able to photo-acclimatize (solid lines) both in non-bistable (1) and in bistable regimes (3) are expected to use light more efficiently and increase their growth, compared to those that cannot (dashed lines 2 and 4).

Mechanistic models provide a useful tool to explore and untangle the effects of causal processes on ecosystem behaviour (Burd & Dunton, 2001). Such models may help to elucidate the effects of physiological photo-acclimatization and self-facilitation mechanisms (e.g., mechanisms related to a reduction in mortality associated with large biomasses) on identifying MLR and bistability behaviors in seagrass beds. In addition, models incorporating data-calibrated seagrass responses to light reduction can predict seagrass carbon balance (Adams et al., 2020) and quantify their resilience to light limitation (Adams et al., 2018). Hence, predictions of suitably-designed mechanistic models can indicate how plants respond to light reduction (Burd & Dunton, 2001). If seagrasses represented by such models exhibit nonlinear responses and/or alternative stable states, these predictions are critical to inform management actions that could alleviate the light pressure in time before an abrupt change in seagrass ecosystem state, which may be potentially irreversible.

The aim of this study is thus to assess seagrass biomass responses and resilience to four different conditions: the presence (or absence) of physiological photo-acclimatization as light reduces, and the presence (or absence) of self-facilitation mechanisms (represented here by clonal integration) as biomass reduces. To achieve the study's aim, we built and parameterized deterministic models of carbon balance using data for the Mediterranean seagrass *C. nodosa* gathered in field experiments (Marín-Guirao et al., 2022) and field light gradients (Mayol et al., 2022) where both mechanisms have been described. These models do not aim to incorporate all mechanisms influencing seagrass dynamics; rather, the presented models focus on a few relevant mechanisms with the aim of uncovering gaps in scientific knowledge (Burd & Dunton, 2001 and references therein). Our predictions demonstrate how the MLR and potential bistability of seagrass ecosystems is dependent on each of the four proposed models, and thus yield guidance for what new information should be sought if one or more of these ecosystem properties (MLR and bistability) is of interest for decision-making in environmental management.

3.2. Materials and methods

3.2.1. Study system

Cymodocea nodosa (Ucria) Ascherson 1869 is a subtidal seagrass species native and widely distributed throughout the Mediterranean, extending in the East Atlantic coasts including the Canary Islands (Garrido et al., 2013). It is considered a fast-growing, medium-size opportunistic species with remarkable phenotypic plasticity that inhabits a broad range of environments, including those with more fluctuating environmental conditions (Olesen et al., 2002; Olivé et al., 2013; Silva et al., 2013; Peralta et al., 2021). *C. nodosa* forms dense monospecific meadows between the water surface and 40 m depth (Terrados & Ros, 1992; Short et al., 2011), exhibiting often abrupt declines in shoot density at their depth limits compatible with alternative stable states caused by self-facilitation mechanisms (Mayol et al., 2022). This plastic seagrass species is characterised by a strong photo-acclimatization potential, altering its photosynthetic-irradiance (*P-I*) parameters as light is reduced, to optimize its light use efficiency (Olivé et al., 2013; Silva et al., 2013; Marín-Guirao et al., 2022).

3.2.2. Model description

To quantitatively assess the influence of physiological photo-acclimatization on seagrass ecosystem properties, we examined four models of plant responses to light reduction (Fig. 3.1; Table 3.1). In two of the four models, it was assumed that plants photo-acclimatize (Fig. 3.1; scenarios 1 and 3) to changes in light availability by adjusting their photosynthetic-irradiance (*P-I*) parameters (for physiological mechanisms which potentially cause these parameter adjustments see e.g., Marín-Guirao et al., 2022). In the other two models (Fig 3.1; scenarios 2 and 4) and for comparison, it was assumed that plants cannot photo-acclimatize.

Table 3.1. Equations used in the physiological photo-acclimatization models.

Eqn.	Model equations	Which scenarios used in?
(1)	$\frac{dB}{dt} = K\,\frac{1}{1+\,[BAR]}\left(\frac{1}{2}P-\,(R+\,[RRR][BAR])\right)B\,\left(1-\frac{B}{N}\right)-\delta(B)$	①,②,③,④
(2)	$P = \frac{P_{max}\,I}{I+\,I_k}$	①,②,③,④
(3)	$P_{max}(I) = P_{gmax} + \frac{P_{gmin}-P_{gmax}}{1+\,e^{\lambda_P(I-y_{cP})}}$	①,③
(4)	$I_k(I) = I_{kmax} + \frac{I_{kmin}-I_{kmax}}{1+\,e^{\lambda_K(I-y_{cK})}}$	①,③
(5)	$R(I) =\, R_{max} + \frac{R_{min}-R_{max}}{1+\,e^{\lambda_R(I-y_{cR})}}$	①,③
(6)	$\delta(B) =\, d_0\,B$	①,②
(7)	$\delta(B) = \left(\frac{1+\,e^{-\lambda_B B_0}}{1+\,e^{\lambda_B(B-B_0)}}\right)d_0 B$	③,④

In the models without photo-acclimatization, carbon balance is based on the following three *P-I* parameters: maximum gross photosynthetic rate P_{max} (in units of mg O_2 g^{-1} above-ground [ABG] dry weight [DW] h^{-1}), saturation irradiance I_k (μmol quanta m^{-2} s^{-1}) and above-ground respiration R (mg O_2 g^{-1} ABG DW h^{-1}). In the models that include photo-acclimatization, each of these three parameters P_{max}, I_k and R possess a nonlinear dependence on the benthic irradiance I (μmol quanta m^{-2} s^{-1}) as detailed later in this section. We parameterized our models in terms of the saturation irradiance parameter I_k instead of the (also commonly used) photosynthetic efficiency α due to our recent finding that the species-specific ability of seagrasses to acclimatize the parameter I_k better explains these species' ability to cope with light reduction and colonize depth ranges (Minguito-Frutos et al., 2023). Below-ground respiration by roots and rhizomes (Fourqurean & Zieman, 1991; Burd & Dunton, 2001) was also included in the carbon balance of all four models. Specifically, it was assumed that the rate of below-ground respiration per unit below-ground biomass was 1/10 of the maximum rate of above-ground respiration per unit above-ground biomass (Staehr & Borum, 2011), analogous to ten-fold differences in turnover rate observed between above-ground and below-ground biomass compartments (Vonk et al., 2015). This assumption was mathematically characterized by the constant parameter [*RRR*] = R_{max}/10 (where [*RRR*] denotes root/rhizome respiration in units of mg O_2 g^{-1} below-ground [BG] DW h^{-1}). The ratio of below-ground biomass to above-ground biomass, required here, was denoted by [*BAR*]. [*BAR*] can be highly variable in the field but typically its order of magnitude is one (see e.g., Pérez et al., 1994; Collier et al., 2017), so for simplicity its default value was set to one in all four models. However, we also explored the effect of increasing [*BAR*] above one in later simulations.

The difference between each of the two models that included photo-acclimatization and those that excluded photo-acclimatization was the absence or presence (Fig. 3.1; upper and lower panel, respectively) of self-facilitation (clonal integration) reducing mortality rates as biomass increases (see Mayol et al., 2022). We included self-facilitation in our analysis since it may be crucial in favoring natural or induced recovery of seagrasses (van Katwijket al., 2016; Moksnes et al., 2018). In the models where this self-facilitation was absent, the seagrass mortality rate (δ) was set to a constant equal to d_0 (in units of h^{-1}) so that the biomass lost due to mortality is always proportional to the current biomass of seagrass. In contrast, when self-facilitation was present, this mortality rate (δ) depended nonlinearly on the current total biomass of the seagrass state (mortality is reduced at high biomass), as detailed later, in the next section.

All four models used an ordinary differential equation to track the total seagrass biomass B (in units of g total DW m^{-2}). Models employed the common logistic growth assumption that biomass can accumulate up to some maximum carrying capacity (g total DW m^{-2}). The carrying capacity N represents, therefore, the maximum population that a system can sustain, depending on various limited resources such as food or space. In our models, we assumed that growth is maximized at ½ N and that restricted space diminishes production at higher biomass levels as a result of self-shading (Burd & Dunton, 2001). We assumed equal amounts of carbon fixation to the amounts of O_2 evolved/fixed during photosynthesis-respiration (Fourqurean & Zieman, 1991; Adams et al., 2017), to convert between carbon exchange rates (in units of mg O_2 g^{-1} ABG DW h^{-1}) and growth rates (in units of h^{-1}). We firstly introduced a factor (1/1+[*BAR*]; in units of g ABG DW g^{-1} total DW) to account for the products of photosynthesis and respiration allocated to net growth of below-ground tissues. Secondly, we introduced a conversion factor *K* (g total DW mg^{-1} O_2) to account for the total biomass produced per net mass of oxygen evolved (for further information see Appendix A: Supplementary Text A1). Combining all of the above considerations, the four investigated models all possess the form

$$\frac{dB}{dt} = K\frac{1}{1+[BAR]}\left(\frac{1}{2}P - (R + [RRR][BAR])\right)B\left(1 - \frac{B}{N}\right) - \delta(B), \quad (1)$$

where the factor of 1/2 in front of the gross photosynthesis rate term *P* accounts for the average difference in time over which photosynthesis and respiration (*R*) processes are occurring (12 hours per day vs 24 hours per day, respectively). The gross photosynthesis rate *P* (mg O_2 g^{-1} ABG DW h^{-1}) is implemented using the standard Michaelis-Menten formulation (Pérez & Romero, 1992; Marín-Guirao et al., 2022; Mayol et al., 2022),

$$P = \frac{P_{max}\, I}{I + I_k}, \quad (2)$$

where *I* is the instantaneous light (photosynthetically active radiation, in units μmol quanta m^{-2} s^{-1}).

3.2.3. Modelling physiological photo-acclimatization to light limitation

In the two models where photo-acclimatization is absent, the parameters for photosynthesis and respiration (P_{max}, I_k and *R*) are set to constant values (corresponding to observed values of these parameters in seagrasses acclimatized to high light conditions). Conversely, in the two models where photo-acclimatization is present, these three parameters are assumed to possess a nonlinear dependence on the benthic irradiance I. Here we provide justification for the mathematical formulations $P_{max}(I)$, $I_k(I)$ and $R(I)$ that are assumed in the two photo-acclimatization models.

Based on the data shown in Fig. 3.2 (adapted from Marín-Guirao et al., 2022; see also Appendix A: Table A1), all three parameter functions $P_{max}(I)$, $I_k(I)$ and $R(I)$ can be feasibly represented by sigmoidal functions (curves in Fig. 3.2; Appendix A: Table A2). Thus, for the photo-acclimatization models we assumed that:

$$P_{max}(I) = P_{gmax} + \frac{P_{gmin} - P_{gmax}}{1 + e^{\lambda P(I - y_{cP})}}, \tag{3}$$

$$I_k(I) = I_{kmax} + \frac{I_{kmin} - I_{kmax}}{1 + e^{\lambda K(I - y_{cK})}}, \tag{4}$$

$$R(I) = R_{max} + \frac{R_{min} - R_{max}}{1 + e^{\lambda R(I - y_{cR})}}, \tag{5}$$

In equations (3) and (4) that are related to photosynthesis, P_{gmax} and I_{kmax} represent the maximum gross photosynthetic rate for seagrass acclimatized to high light conditions (mg O_2 g^{-1} ABG DW h^{-1}) and the saturation irradiance for seagrass acclimatized to high light conditions (μmol quanta m^{-2} s^{-1}), respectively. As irradiance I declines, the values of these two parameters decline towards minimum values: P_{gmin} which represents the maximum gross photosynthetic rate for seagrass acclimatized to low light conditions, and I_{kmin} which represents the saturation irradiance for seagrass acclimatized to low light conditions. The slopes (λ_P, λ_K) and the inflection points (y_{cP}, y_{cK}) of the curves in equations (3) and (4) determine the strength of the declines for P_{max} and I_k, respectively (Table 3.2). Similarly, in the above-ground respiration equation (5), R_{max} and R_{min} represent the leaf respiration rates (mg O_2 g^{-1} ABG DW h^{-1}) for seagrass acclimatized to high and low light conditions respectively, and the slope λ_R and the inflection point y_{cR} have analogous definitions to λ_P, λ_K and y_{cP}, y_{cK} (Table 3.2).

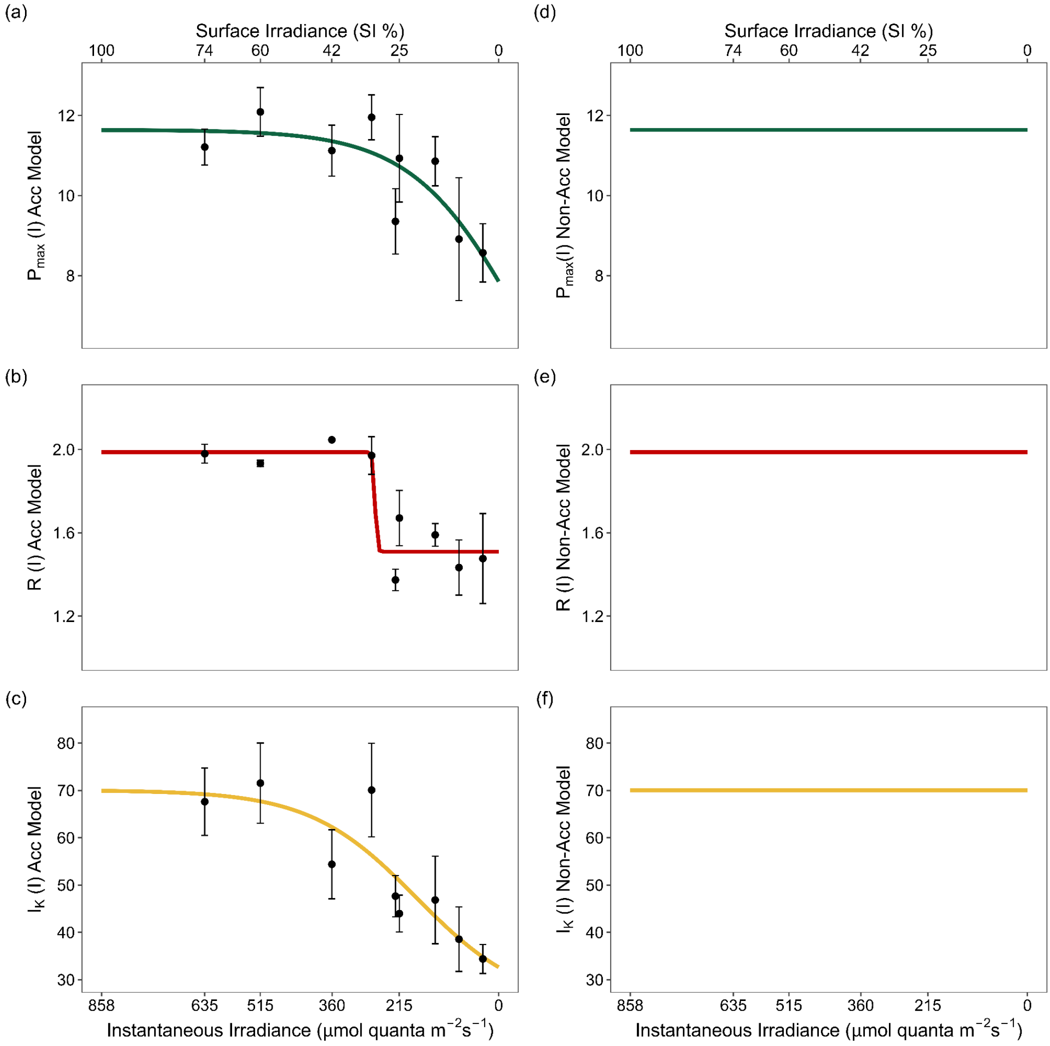


Figure 3.2. Physiological photo-acclimatization models compared (left vs right panels) under the light stress gradient. Y-axes represent values for each physiological mechanism along the gradient: maximum gross photosynthesis P_{max}, (a) vs (d); above-ground respiration R, (b) vs (e); and saturation irradiance I_k, (c) vs (f). P_{max} and R are shown in units of mg O_2 g^{-1} ABG DW h^{-1} and I_k in µmol quanta m^{-2} s^{-1}. X-axes represent light values of total instantaneous irradiance (µmol quanta m^{-2} s^{-1}) (bottom) and percentage of surface irradiance (SI) (top). X-axes values ranged from 858.04 µmol quanta m^{-2} s^{-1} of instantaneous irradiance that equaled 100% SI after conversions derived from field shading experiments. While lines in left panels represent the best fit curve to the nine levels of light stress (black dots corresponding to 74, 60, 42, 32, 26, 25, 16, 10, and 4% SI) for each physiological mechanism in field shading experiments; lines in right panels are set to constant values corresponding to their maximum values observed at high light conditions.

Table 3.2. Values of models parameters. Full justification of these parameter values is provided in Supplementary Text A1.

Parameter	Value	Description	Units	Reference
Non-acclimatization Model				
P_{gmax}	11.64	Maximum Photosynthesis	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
I_{kmax}	70.04809	Saturation Irradiance	$\mu mol\ quanta\ m^{-2}s^{-1}$	Marín-Guirao et al., 2022
R_{max}	1.987	Above-ground Respiration	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
Acclimatization Model				
P_{gmax}	11.64	P_{max} (high light)	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
P_{gmin}	2.096	P_{max} (low light)	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
λ_P	0.008524	P_{max} Slope	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
y_{cP}	-49.1	P_{max} Threshold	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
I_{kmax}	70.0.4809	I_k (high light)	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	Marín-Guirao et al., 2022
I_{kmin}	24.54396	I_k (low light)	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	Marín-Guirao et al., 2022
λ_K	0.00863	I_k Slope	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
y_{cK}	177.45783	I_k Threshold	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
R_{max}	1.987	Above-ground Respiration (high light)	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
R_{min}	1.509	ABG Respiration (low light)	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
λ_R	0.4567	ABG Respiration Slope	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
y_{cR}	267.1	ABG Respiration Threshold	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
Below-ground Parameters				
$[BAR]$	1	Below-Above Ratio	-	Pérez et al., 1994; Collier et al., 2017
$[RRR]$	0.1987	Roots/Rhizomes Respiration	$mg\ O_2/(g\ BG\ DW \cdot h)$	Staehr & Borum, 2011
Biomass and Growth/Mortality Parameters				
K	0.001075	Conversion Efficiency	$g\ \ total\ DW/mg\ O_2$	Zharova et al., 2008; Nielsen & Pedersen, 2000
N	100	Carrying Capacity	$g\ total\ DW\ m^{-2}$	
d_0	0.000116	Mortality Rate	h^{-1}	Mascaró et al., 2014
λ_B	0.05	Facilitation Slope	$(g\ ABG\ DW\ m^{-2})^{-1}$	Mayol et al., 2022
B_0	10	Threshold Facilitation	$g\ ABG\ DW\ m^{-2}$	Mayol et al., 2022

These curves were fitted to the data obtained in field experiments (Marín-Guirao et al., 2022) by employing a robust and efficient implementation of the Levenberg-Marquardt algorithm for solving nonlinear least squares problems (via the *minpack.lm* R package; Elzhov et al., 2022). The nonlinear least squares estimates of the parameters obtained from this model-data fitting, along with other parameters sourced from the literature for use in our models, are listed in Table 3.2 and justified in Appendix A: Supplementary Text A1.

3.2.4. Modelling seagrass mortality

To test the influence of seagrass mortality in the carbon balance models we considered two different mortality functions. In the first function, we assume the absence of self-facilitation (Fig. 3.1; scenario 1 and 2), so seagrass mortality (δ) responds constantly (d_0) to the current seagrass biomass (B) and presents the form:

$$\delta(B) \; = \; d_0 \, B. \tag{6}$$

In the second function, self-facilitation (Fig. 3.1; scenario 3 and 4) is assumed to yield a nonlinear relationship between the mortality rate (δ) and seagrass biomass (B) according to (Mayol et al., 2022),

$$\delta(B) \; = \; \left(\frac{1 + e^{-\lambda_B B_0}}{1 + e^{\lambda_B (B - B_0)}} \right) d_0 \, B, \tag{7}$$

where parameters λ_B (units of inverse biomass) and B_0 (units of biomass) control the shape of the nonlinear relationship between mortality rate and seagrass biomass.

3.2.5. Solving the models: Determining minimum light requirements

To quantify how the four presented models of seagrass carbon balance are affected by the reduction of benthic irradiance I, we performed numerous mathematical evaluations of the model expression for dB/dt shown in Eqn. 1. To do so, we assumed that daily averaged light I_{daily} (i.e., light dose over one day) was approximately equal to half of a constant instantaneous light value I received during daylight hours, i.e., I_{daily} (mol quanta m^{-2} d^{-1}) in Marín-Guirao et al. (2022) ≈ ½ I (instantaneous irradiance in μmol quanta m^{-2} s^{-1}). We then calculated the equivalent percentage of surface irradiance (SI = 100%-0%), and solved all models up to their carrying capacity (N = 100 g total DW m^{-2}). After solving the four models of seagrass response to limiting light conditions, we determined the MLR of each model as the minimum quantity of benthic irradiance (both as instantaneous light received during daylight hours in μmol quanta m^{-2} s^{-1} and as daily averaged light in % SI) that allows a positive rate of change for seagrass biomass, dB/dt (g total DW m^{-2} h^{-1}).

To evaluate the influence of physiological photo-acclimatization and self-facilitation (clonal integration) on the stability of seagrass ecosystems, we calculated the equilibrium points resulting from each of the models. These equilibrium points can be stable (Fig. 3.1 *black points*) or unstable (Fig. 3.1 *gray points*), depending on whether the system tends towards an equilibrium point or moves away from them, respectively. When self-facilitation is present, the system can potentially express two stable equilibria separated by an unstable equilibrium point (a situation known as bistability). However, when self-facilitation does not occur, unstable equilibrium points are not expected to emerge and bistability would not take place. Thus, we used the R *rootSolve* package (Soetaert, 2009), which identifies all the equilibrium points within the pre-specified range, as well as whether they represent stable or unstable equilibria.

3.2.6. Quantifying the ecological resilience to light limitation

Ecological resilience was quantified following the definition in Adams et al. (2018) for those models that expressed bistability:

$$Resilience = \frac{B_{stable} - B_{unstable}}{B_{stable}} \, x \, 100 \qquad (8)$$

In this equation, B_{stable} and $B_{unstable}$ are the strictly positive values of seagrass biomass (g DW m^{-2}) representing stable and unstable equilibrium points, respectively. In bistable ecosystems, the ecological resilience calculated from Eqn. (8) will always fall between 0% and 100%, with the system being more resistant to disturbance as the calculated resilience approaches 100%.

3.3. Results

Our models predicted that photo-acclimatization decreases the MLR of *C. nodosa* from 5.8% SI to 3.4% SI (Fig. 3.3a), when other nonlinear mechanisms (i.e., reduction in mortality rate from clonal integration) are absent. Photo-acclimatization does not result in bistable behaviors of seagrass ecosystems (one stable equilibrium for each model in Fig. 3.3a), despite it being a nonlinear process itself.

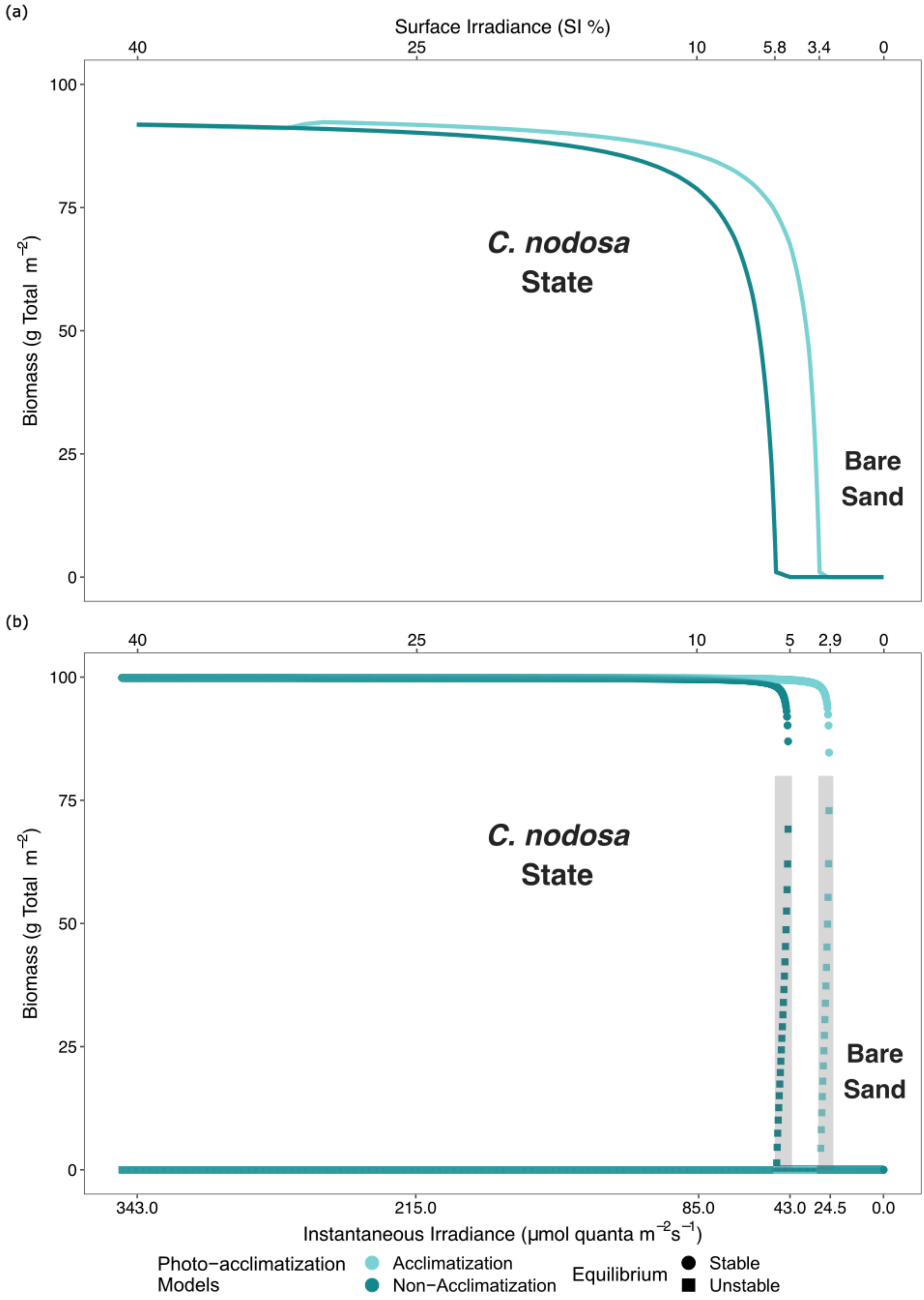

(a)
Surface Irradiance (SI %)
40
25
10
5.8
3.4
0
100
75
50
25
0
Biomass (g Total m^{-2})
C. nodosa
State
Bare
Sand
(b)
40
25
10
5
2.9
0
100
75
50
25
0
Biomass (g Total m^{-2})
C. nodosa
State
Bare
Sand
343.0
215.0
85.0
43.0
24.5
0.0
Instantaneous Irradiance (µmol quanta $m^{-2}s^{-1}$)
Photo−acclimatization Models
Acclimatization
Non−Acclimatization
Equilibrium
Stable
Unstable

Figure 3.3. Minimum light requirements (MLR) are depicted for the four presented models: (a) physiological photo-acclimatization and non-acclimatization models in absence of self-facilitation (clonal integration) and, (b) photo-acclimatization models in presence of self-facilitation. Physiological photo-acclimatization models are shown in light blue (acclimatization) and dark blue (non-acclimatization). In the presence of self-facilitation, bistability arises and circles (stable) and squares (unstable) represent equilibrium types. The shaded area in (b) represents the bistable region predicted by the models.

The inclusion in our models of the clonal integration mechanism (i.e., self-facilitation), also reduced the MLR, but not as substantially as the photo-acclimatization mechanism. Models predicted MLR of *C. nodosa* to be 5.1% SI and 2.9% SI in the absence and presence of photo-acclimatization, respectively (Fig. 3.3b), when self-facilitation was introduced.

The self-facilitation (i.e., mortality reduction as plant biomass increases) also yielded bistability within specific ranges of benthic irradiance values, regardless of whether photo-acclimatization was present or not (shaded areas in Fig. 3.3b). Hence, in the absence of photo-acclimatization, the seagrass ecosystem formed by *C. nodosa* was bistable when the average daily irradiance was between 5.1% SI and 5.8% SI; and in the presence of photo-acclimatization, this ecosystem was bistable when the average daily irradiance was between 2.9% SI and 3.4% SI. The photo-acclimatization mechanism also permitted a greater range of irradiance values over which the seagrass has maximal resistance to disturbance (Fig. 3.4).

We also explored the effect of changing the below-ground to above-ground biomass ratio on the MLR predicted by our four models. Crucially, we found that as the ratio of below-ground biomass to above-ground biomass ([*BAR*]) increases, there is a substantial increase in the MLR for plants both with and without photo-acclimatization capacities (Fig. 3.5). However, plants that photo-acclimatize cope better with a relative increase of the biomass ratio between below- and above-ground tissues, except when self-facilitation is absent and a threshold is exceeded (MLR at [*BAR*] equal to 9, ~26.2% SI compared to ~41.5% SI) (Fig. 3.5 left panel). After this threshold ([*BAR*] = 9) the MLR of *C. nodosa* that do not possess self-facilitation mechanism increases abruptly. On the contrary, in a system where self-facilitation is acting, and [*BAR*] is equal to 10, the MLR of *C. nodosa* increases gradually – together with photo-acclimatization the MLR only reaches ~15.6% SI (Fig. 3.5 right panel).

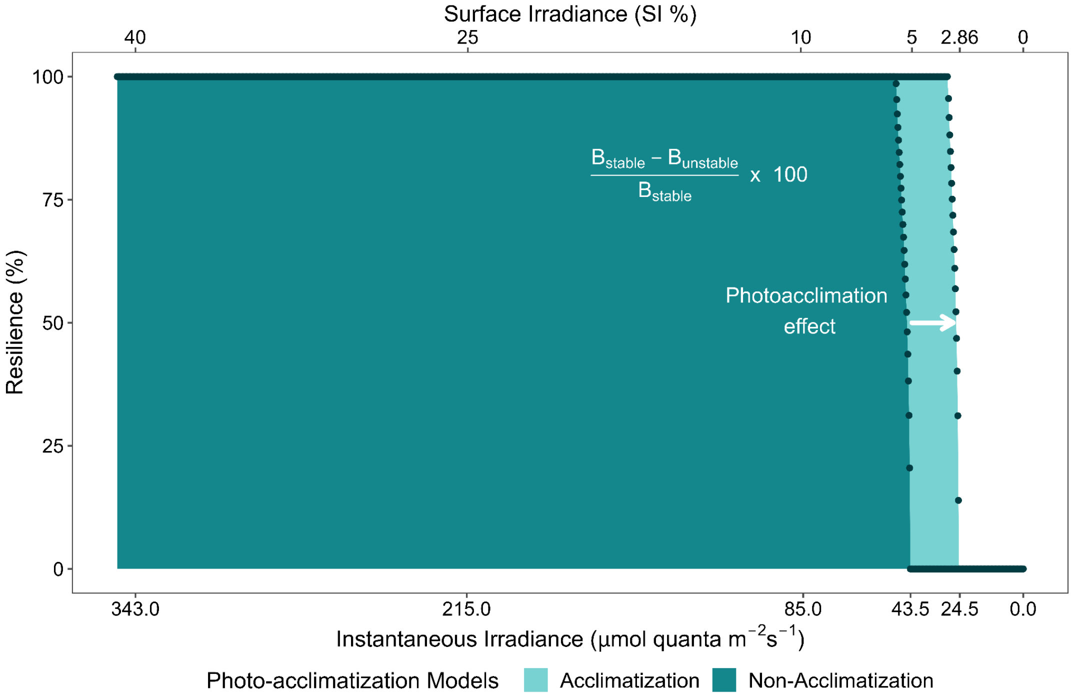


Figure 3.4. Ecological resilience for physiological photo-acclimatization (light blue) and non-acclimatization (dark blue) models to light limitation, as a function of benthic irradiance (in instantaneous irradiance and % SI). Resilience is calculated following the mathematical definition provided in Adams et al. (2018) which has its basis in the conceptual definition provided in Gunderson (2000). Dots represent the calculated values of resilience (%) as a function of the values of instantaneous irradiance (μmol quanta m^{-2} s^{-1}) or surface irradiance (%SI), for each model.

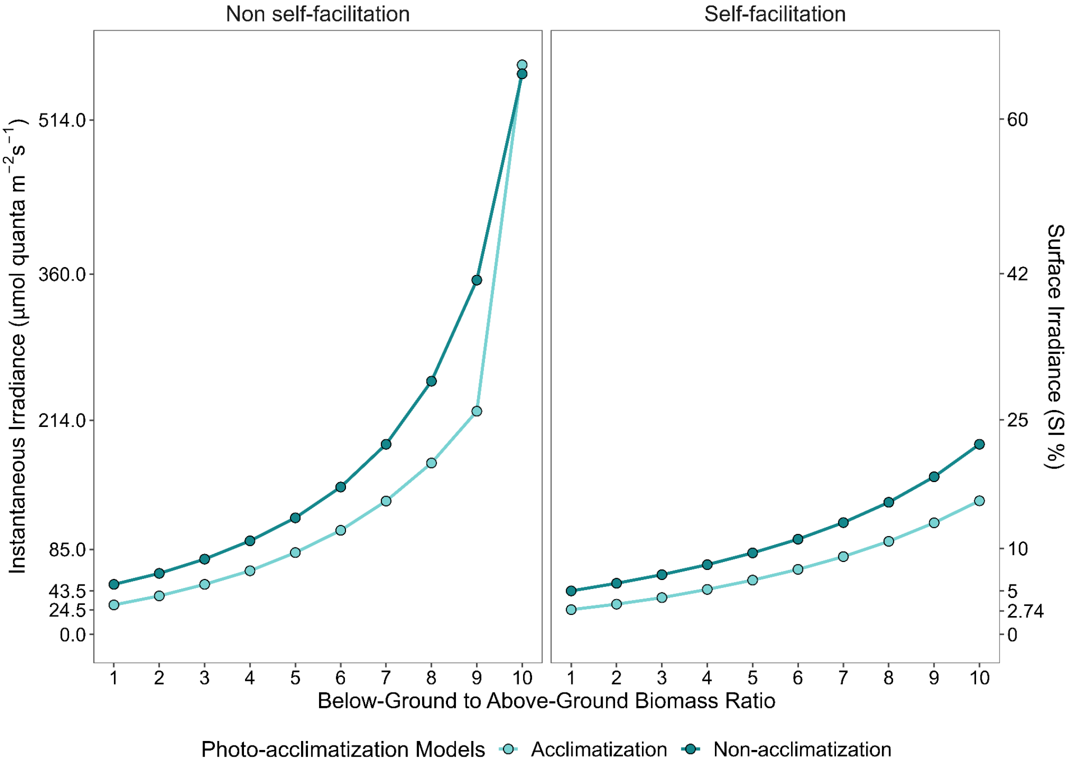


Figure 3.5. Predicted minimum light requirements as a function of below-ground to above-ground biomass ratio (model parameter [*BAR*]), for plants that express physiological photo-acclimatization (light blue) or not (dark blue). Left and right panels represent the absence and presence of self-facilitation, respectively.

3.4. Discussion

In this modelling study, we used data from intensive field experimentation to test the effect of physiological photo-acclimatization on the minimum light requirements (MLR) and, then resilience, of seagrasses performing contrasting physiological strategies to cope with light stress gradients. Specifically, our models predict that the ability of *C. nodosa* to photo-acclimatize to low light approximately halves its threshold of collapse (MLR). In addition, the presence of self-facilitation mechanisms such as clonal integration, alleviating mortality rates with increasing biomass, can result in bistability and decrease MLR even further. On the other hand, photo-acclimatization increases the resilience of bistable meadows to light reduction by increasing plant resistance and their ability to recover (O'Brien et al., 2018), but it cannot yield bistability in seagrass beds. Therefore, the results from our models point to the critical role of physiological photo-acclimatization in conferring resilience to seagrasses against light deprivation, and also illustrate that other nonlinear mechanisms (if present) can cumulatively contribute to this resilience and shape the recovery of seagrass ecosystems exposed to light reduction.

Using our modelling approach, we provide a coarse quantification of the MLR of *C. nodosa*, which can reorganize its photosynthetic apparatus to resist light limitation, and compare this to the equivalent MLR predicted if such plants are unable to photo-acclimatize. Our study uses data from field shading experiments that identified patterns of physiological acclimatization mechanisms of *C. nodosa* to light-limiting conditions (see Marín-Guirao et al., 2022). MLR predicted through our mathematical modelling approach (2.9% – 3.4% SI for plants with and without self-facilitation respectively) are comparable to those found by previous experimental studies (e.g., 4.4% SI (Olesen et al., 2002) and 7.3% – 10.2% SI (Dennison et al., 1993)). Of particular note, a halving of MLR can yield a contraction of $\approx$ 1 m to $\approx$ 10 m at the deep limit, depending on the values of the light attenuation coefficient (k = 0.07 to k = 0.57 respectively, see Dennison et al., 1993; as calculated using the standard light extinction equation provided in Dennison, 1987).

The photo-acclimatization-mediated reduction in MLR is mainly related to *C. nodosa*'s capacity to decrease both its leaf respiration demand and saturation irradiance I_k as benthic irradiance decreases. Reducing leaf respiratory losses is critical for seagrasses to survive periods of light stress, as leaf respiration typically accounts for the majority of respiratory requirements in seagrasses (Fourqurean & Zieman, 1991; Masini et al., 1995). The decline in above-ground respiration observed at low light environments is a common photo-acclimatization mechanism in *C. nodosa* (Olivé et al., 2013; Marín-Guirao et al., 2022), but also among other seagrass species, making the outcomes found in this study potentially applicable to other seagrasses

(Ruiz & Romero, 2001; Ruiz & Romero, 2003; Collier et al., 2009; Collier et al., 2012). In fact, several species of different genera have been found to reduce their above-ground tissues to balance the energetic demand under impoverished light environments (Mackey et al., 2007; Collier et al., 2012). Similarly, some seagrass species have been shown to reduce their total leaf area (i.e., self-thinning) as a strategy to cope with light reduction at depth, increasing their overall production (Enríquez et al., 2019). Our finding that reduced I_k at low light levels boosts the carbon balance of *C. nodosa* agrees with previous findings for this species (Olivé et al., 2013) and other seagrasses (Ruiz & Romero, 2001; Campbell et al., 2007). Interestingly, we also found that even though P_{max} decreases as benthic irradiance declines, this did not cause a detrimental effect on carbon production compared to plants unable to photo-acclimatize (constant P_{max}). This occurred because the reductions in both respiration demand and I_k of plants able to acclimatize, counteract the simultaneous reduction of P_{max}, as light decreases. Therefore, in the present work we have been able to demonstrate how the cumulative changes in multiple physiological parameters at low light, allow seagrasses to more efficiently harvest light, compared to those plants with less variability in their physiological response. These results are in agreement with field experiments that found the plastic *C. nodosa* to be more resilient under adverse light conditions compared to other less plastic seagrasses like *Zostera marina* (Silva et al., 2013) or *Posidonia oceanica* (Olesen et al., 2002).

The results of our work show that presence of self-facilitation mechanisms, such as clonal integration leading to reduced mortality rates with increasing biomass, further reduces the MLR of *C. nodosa*, but also makes the ecosystem prone to bistability. Clonal integration might be the main reinforcing feedback in clonal seagrass plants (Nielsen & Pedersen, 2000), although a wide range of reinforcing feedbacks (e.g., enhancing sediment trapping, providing physical protection, etc.) could act similarly in reducing seagrass mortality with increasing biomass (Burkholder et al., 2007; Maxwell et al., 2017). Unlike self-facilitation mechanisms, photo-acclimatization alone did not cause bistability in the ecosystem formed by *C. nodosa*. Thus, we show that nonlinear trajectories in acclimatization mechanisms (i.e., photo-acclimatization) do not always lead to the emergence of bistability and may not always be the cause of alternative stable states (McGlathery et al., 2013), but are still drivers of threshold behaviors that challenge the management of these ecosystems (van Katwijk et al., 2016). The presence of multiple alternative states (i.e., seagrass and bare sand states) for a given level of irradiance (i.e., bistability) is an indicator of hysteresis, which carries significant additional impediments for the recovery of the ecosystem as multiple feedbacks acting in the alternative state can reinforce its persistence (Moksnes et al., 2018). Given the prevalence of self-facilitation mechanisms alleviating mortality, the presence of bistability is a plausible scenario (van der Heide et al., 2007; Carr et al., 2010) in the ecosystems sustained by seagrasses independently of their photo-acclimatization capacities.

As is the case for many coastal ecosystems, seagrasses are exposed to multiple coexisting stressors (hurricanes or storms, overgrazing, etc.) eroding their resilience (Ruiz et al., 2009; Carlson et al., 2010; Infantes et al., 2011). These disturbances often cause uneven distributions of below- and above-ground plant tissues (i.e., leaves and rhizomes), eventually altering the below-ground to above-ground biomass ratio ($[BAR]$). We found that this ratio is essential for understanding resilience of seagrasses to light-limiting conditions. As $[BAR]$ increases, MLR increase too, making *C. nodosa* more vulnerable to light limitation. High below-ground to above-ground biomass ratios (e.g., $[BAR] \geq 10$) can be particularly challenging for maintaining positive carbon balance after heavier losses of photosynthetic tissues due to herbivory (Ruiz et al., 2009). In these situations, the effect of the physiological photo-acclimatization on increasing seagrass resilience to light deprivation may not be sufficient to counteract the effects of external stressors unless other compensatory mechanisms are also present (e.g., reduced respiration in the below-ground tissues, not investigated in this study). Reallocation of plant material between below-ground and aboveground tissues could also potentially be a strategy to boost carbon availability in periods when photosynthesis is suboptimal (Zimmerman et al., 1995; Alcoverro et al., 1999). However, large below-ground structures can also paradoxically be considered a heavy burden in periods of reduced light due to their respiratory requirements (Fourqurean

& Zieman, 1991; Hemminga, 1998; Alcoverro et al., 2001). For this reason, further investigation is required to understand the actual role of below-ground tissues, which may increase the predictive power of seagrass production models and, therefore, their utility for making effective management decisions (Burd & Dunton, 2001). In the current era of global change, understanding the limits of acclimatization capacity under the cumulative effects of human impacts on seagrasses influencing their resilience becomes imperative (Adams et al., 2020).

3.5. Conclusion

Overall, the goal of these models was to assess the effect of *C. nodosa*'s photo-acclimatization capacity on reducing their MLR (increased resistance) and enhancing its resilience to light deprivation. To accomplish this, our models included few essential mechanisms, making easier to understand the gaps in our knowledge and did not include all relevant processes influencing seagrass carbon balance (Burd & Dunton, 2001). Given this, we found that in all the scenarios explored, transitions followed nonlinear dynamics. However, unlike self-facilitation, photo-acclimatization did not lead to bistability of *C. nodosa*'s seagrass beds. Nonlinearities carry critical implications for the predictability of abrupt shifts in the ecosystems formed by seagrasses, particularly for those exhibiting bistable behaviors (due to potential hysteresis). Our results foresee that under increasing light disturbances related to global change (Unsworth et al., 2019b), seagrass species that have evolved greater photosynthetic plasticity might be less vulnerable to anthropogenic reductions in light availability. Equally important, our models demonstrate that seagrass ecosystems that possess self-reinforcing mechanisms to reduce their mortality rates when biomass is high can be bistable.

Since not all species are equally able to acclimatize to light reduction (Minguito-Frutos et al., 2023) nor do the meadows they form possess the same ecosystem components, there is an imminent need to identify differences in species acclimatization capacity and prevalence of feedback mechanisms (Maxwell et al., 2017). This will help create management plans that account for species-specific vulnerability to stressors as light deprivation. Considering that light limitation is the main factor affecting seagrasses at different organizational scales: physiological, morphological and population (Ralph et al., 2007), our study therefore contributes to an improved understanding of seagrass ecosystem functioning which is valuable for conservation efforts. Specifically, we show how plastic seagrasses such as *C. nodosa* with potentially multiple reinforcing feedbacks give a wider operational space for managerial action to conserve the ecosystems formed by these species. Continued strategies to manage and conserve seagrass ecosystems can help to avoid sudden collapses in seagrass beds, which in some cases could be potentially irreversible (Lee et al., 2007; van der Heide et al., 2007).

Chapter 4

Species-specific acclimatization capacity of key traits explains global vertical distribution of seagrass species

Minguito-Frutos, M., Boada, J., Pagès, J. F., Marco-Méndez, C., Arthur, R., Adams, M. P., & Alcoverro, T. (2023). Species-specific acclimatization capacity of key traits explains global vertical distribution of seagrass species. *Global Ecology and Biogeography*, *32*(6), 976-986. https://doi.org/10.1111/geb.13673.

Abstract

The global vertical depth distribution of seagrass species remains poorly understood. Locally, the abundance and distribution of seagrasses is determined by light penetration, but at global levels each seagrass species has very distinct maximum distributional depth ranges, indicating that plant-associated traits must also influence their specific depth ranges. Seagrass-specific attributes, such as plant size or architecture, growth or reproductive strategy and their physiological and/or morphological acclimatization potential, have been suggested to be responsible for this variety of vertical distributions. We investigate here whether these species-specific traits drive differences in the global maximum vertical distribution of seagrasses. We tested whether the species-specific maximum vertical distribution of seagrasses can be predicted by (i) their rhizome diameter (a proxy for plant size), (ii) their functional resilience (growth/reproductive strategy), or (iii) their acclimatization capacity. For the last aspect, we used a systematic review followed by meta-analytical approaches to select key seagrass traits that could potentially acclimatize to extreme light ranges across different seagrasses. We found that vertical distribution is best explained by the species-specific acclimatization capacity of various seagrass traits, including saturation irradiance (physiological trait), leaves per shoot (morphological trait) and above-ground biomass (structural trait). In contrast, our results indicate no predictive power of seagrass size or growth/reproductive strategy on the vertical distribution of seagrasses. Across the globe, the ability of seagrass species to thrive at a wide range of depths is strongly linked to the species-specific acclimatization capacity of key traits at different organizational levels.

Keywords: *acclimatization, depth, light, seagrasses, species traits, vertical distribution.*

4.1. Introduction

Like every other photosynthetic marine species, the abundance and distribution of seagrasses along the vertical gradient are strongly determined by light (Duarte, 1991a; Duarte et al., 2007). Light attenuates sharply with depth in the ocean, placing increasing demands on the photosynthetic machinery of the plant, and beyond a point, few species can cope (Dennison et al., 1993). Underwater irradiance is determined by the light attenuation coefficient (k), which, in turn, is mediated by a range of abiotic and biotic factors (e.g., eutrophication leading to phytoplankton blooms, natural or anthropogenic turbidity and sedimentation, latitude, topography; Lee et al., 2007). The parameter k has, on its own, been proposed as a powerful predictor of seagrass depth limits (Duarte, 1991a; Duarte et al., 2007). However, in similar environmental conditions, distinct seagrass species have very different abilities to colonize depth ranges (Lee et al., 2007). For example, in the Mediterranean Sea, *Posidonia oceanica* can colonize waters between 0 and 45 m in very clear conditions, whereas *Zostera noltii*, in the same conditions, has a highly restricted distributional range (between 0 and 10 m) (Short et al., 2011). Variations in seagrass strategies might drive differences in species-specific vertical distributions (i.e., the maximum depth ranges that each seagrass can colonize) (Short et al., 2011), raising the question of what traits and at which organizational level (from physiological to meadow scale) allow some species to occupy vast depth ranges, whereas others remain always limited to shallow waters across their global distribution.

Seagrasses are not a species-rich group but differ considerably in their vertical colonization abilities. Although most seagrass species are able to colonize the very shallowest waters (with some exceptions; Short et al., 2011), the vertical distribution in most seagrasses seems to be determined largely by their depth limit. At a global level, species such as *Posidonia sinuosa* can be found from shallow waters to a maximum of 15 m. In stark contrast, species such as *Halophila stipulacea* can have very large vertical colonization ranges and have been recorded from 0 to 70 m (Short et al., 2011). Thus, different seagrass species have characteristic maximum vertical distributional ranges independent of their environmental conditions. Several species-specific traits of seagrasses, such as plant size/architecture and growth/reproductive strategy (Duarte, 1991a), or physiological and morphological adaptations (Dennison et al., 1993) have been proposed to account for this variance in species-specific seagrass depth limits. It is possible that large species colonize a wider range of depths given their capacity to store carbohydrates in rhizomes and their larger photosynthetic tissue, which are crucial to compensate for plant carbon gains at light-poor depths for extended periods (Alcoverro et al., 1999). In contrast, larger sizes can also be a burden for respiration in the same light-limiting conditions (Alcoverro et al., 2001). Differences in photophysiology might also allow some species to photosynthesize more efficiently in reduced light conditions (Bité et al., 2007; Silva et al., 2013). Vertical distribution can also vary between seagrass functional resilience linked to their life history, including growth or reproductive strategies in response to disturbances (Kilminster et al., 2015). Species with a high capacity for spatial recolonization and competition (fast-growing or pioneer species) (Fourqurean et al., 1995) might be advantaged by quickly colonizing deeper locations. However, seagrasses of very different sizes, rhizome diameters and growth strategies have been recorded with similar depth ranges. For instance, *P. oceanica* (large and "persistent" sensu Kilminster et al., 2015) and *H. stipulacea* (small and "colonizing" sensu Kilminster et al., 2015) both have extremely wide vertical ranges, from 0 to 45 and 70 m, respectively. The ability to colonize wide vertical ranges and adjust to changing light conditions is therefore dependent not merely on species-specific traits, but on the acclimatization potential of those traits (Schubert et al., 2018).

Studies describing specific acclimatization abilities of different seagrasses to light limitation are common, focusing on different levels of organization (i.e., physiological, morphological, structural or growth). These studies typically use field shading experiments or naturally occurring depth gradients (Ruiz & Romero, 2001; Collier et al., 2009; Enríquez et al., 2019; Marín-Guirao et al., 2022). The few studies that include more than one species observe that some species are characterised by more plastic phenotypes and traits that allow them to cope better with low-light environments than others (Olesen et al., 2002; Bité et al., 2007; Silva et al., 2013). In a similar vein, recent studies with several Mediterranean macroalgae show that their depth distributional range is closely related to species-specific photo-acclimatization capacities and light-harvesting strategies (Sant & Ballesteros, 2021). However, most studies of light acclimatization in seagrasses focus on a single species and often do not study plant responses across organizational levels (Schubert et al., 2018). A more holistic approach is required to understand how the ability of species to acclimatize by modulating particular seagrass traits can mediate differences in their vertical distribution.

In this study, we assessed whether the global maximum vertical distribution of seagrass species (obtained from Short et al., 2011) could be predicted by a series of species-specific plant attributes/traits (including size or growth/reproductive strategies) or the inherent acclimatization potential of traits (physiological, morphological, structural or growth traits). The average species-specific traits associated with size (Duarte, 1991b; Marbà & Duarte, 1998; Roca et al., 2016) and growth/reproductive strategies (Kilminster et al., 2015) were obtained from the literature, and the acclimatization capacity of the physiological, morphological, structural or growth traits was obtained with a systematic review and a meta-analytical approach.

4.2. Materials and methods

4.2.1. Relationship between the maximum vertical distribution of seagrass species and their size and growth/reproductive strategy

We tested the relationship between the maximum recorded vertical distribution (i.e., maximum depth range of colonization ever recorded) of seagrasses around the world (data from Short et al., 2011) and two potential predictors (i) rhizome diameter (data from Duarte, 1991b; Marbà & Duarte, 1998; and Roca et al., 2016), and (ii) growth/reproductive strategy (data from Kilminster et al., 2015), with two separate linear models. For the first model, we used data from 37 species and 11 different seagrass genera, and for the second we used data of 62 species grouped into five different categorical predictors (colonizing, colonizing–opportunistic, opportunistic, opportunistic–persistent and persistent; sensu Kilminster et al., 2015). Model assumptions were checked visually and statistically using the functions of the *DHARMa* R package (Hartig, 2022). Assumptions were met adequately after logarithmic and square root transformation of the response variable “vertical distribution” for the first and second models, respectively (Zuur et al., 2009).

4.2.2. Relationship between maximum vertical distribution and seagrass trait acclimatization potential

We tested the relationship between the globally maximum recorded vertical distribution of different seagrass species (data from Short et al., 2011) and selected key seagrass traits that could potentially acclimatize to extreme low-light conditions. To identify traits with potential acclimatization capacity, we first conducted a systematic review followed by a meta-analytical approach. Our review examined studies that included seagrass traits data in field shading experiments (with extreme low values vs. control) and depth-based studies comparing shallow versus depth limit (or close to) values. To be included in our study, the publication had to provide information on seagrass trait responses to light reduction at different organizational levels: (i) physiological [saturation irradiance (grouping data from I_k and E_k), maximum photosynthetic rate (grouping data from P_{max} and ETR_{max}) or photosynthetic efficiency (α)]; (ii) morphological (leaf length, leaf width or leaves per shoot); (iii) structural (shoot density or above-ground biomass); or (iv) growth (shoot growth). We selected works published between 1982 and 2020. The search was conducted in Web of Science (WOS), with the following string for title, abstract and keywords: (seagras* OR eelgras* OR turtlegras*) AND (“shad*” OR “depth” OR “bathymetric distribution*” OR “light*”) AND (“photosynthe*” OR “photo-physio*” OR “photo-acclima*” OR “acclima*” OR “morpho*”); and in Scopus with the following search string: TITLE-ABS-KEY((seagras* OR eelgras* OR turtlegras*) AND (“shad*” OR “depth” OR “bathymetric distribution*” OR “light*”) AND (“photosynthe*” OR "photo-physio*" OR "photo-acclima*" OR "acclima*" OR "morpho*")) AND (LIMIT-TO (SUBJAREA, "AGRI") OR LIMIT-TO (SUBJAREA, "ENVI") OR LIMIT-TO (SUBJAREA, "EART")). These two searches yielded 617 and 695 scientific papers, in WOS and Scopus, respectively. Our final list did not include 11 relevant publications that we included manually in the list of selected studies, in addition to one publication conducted with collaborators, for which we had data prior to publication. For more details on the systematic review and meta-analyses (literature review, inclusion criteria, data extraction, calculation of the effect size and data analyses), see the Appendix B: Supplementary Text B2. After scrutinizing all these publications, we ended up with a total of 78 scientific studies (see Fig. 4.1; Table B1 in Appendix B). The final list summarizing the number of publications, studies and species, grouped by trait, that we finally selected, is shown in Table 4.1. The Fig. B1 in Appendix B shows the species for which data meeting the criteria were available and the traits that were evaluated for each of them. We therefore obtained data on species-specific acclimatization potential to light reduction that were pooled by trait (effect sizes of each physiological, morphological, structural or growth trait) to be used as predictors of seagrass vertical distribution in the linear models. Once effect sizes were obtained for each chosen trait, we fitted linear mixed-effects models (LMMs) with a logarithmic transformation of the response variable, maximum recorded vertical distribution ('Vertical distribution'). In the model, we also included 'Article' as a random factor and incorporated the weights obtained from the separate meta-analytical models to provide robustness to linear models. We tested the effect of the random factor based on the Akaike information criterion (AIC) and likelihood ratio tests (Zuur et al., 2009). Thus, we used LMMs or linear models (LMs) when the random effect did not provide useful information to the model. Whenever possible (sample size permitting), linear models also included the effect of the type of study (experimental shading or depth-based study) and their interaction ('Effect size' and 'Type of study'). Model assumptions were checked visually and statistically using functions from the R package *DHARMa* (Hartig, 2022). When residuals did not meet the assumption of homogeneity of variances (i.e., leaves per shoot), we estimated the model coefficients and *quasi-t* Wald test, using the

“HC4m” proposed by Cribari-Neto and da Silva (2011), as the corrected estimates of the covariance matrix for inconstant variances (heteroscedasticity).

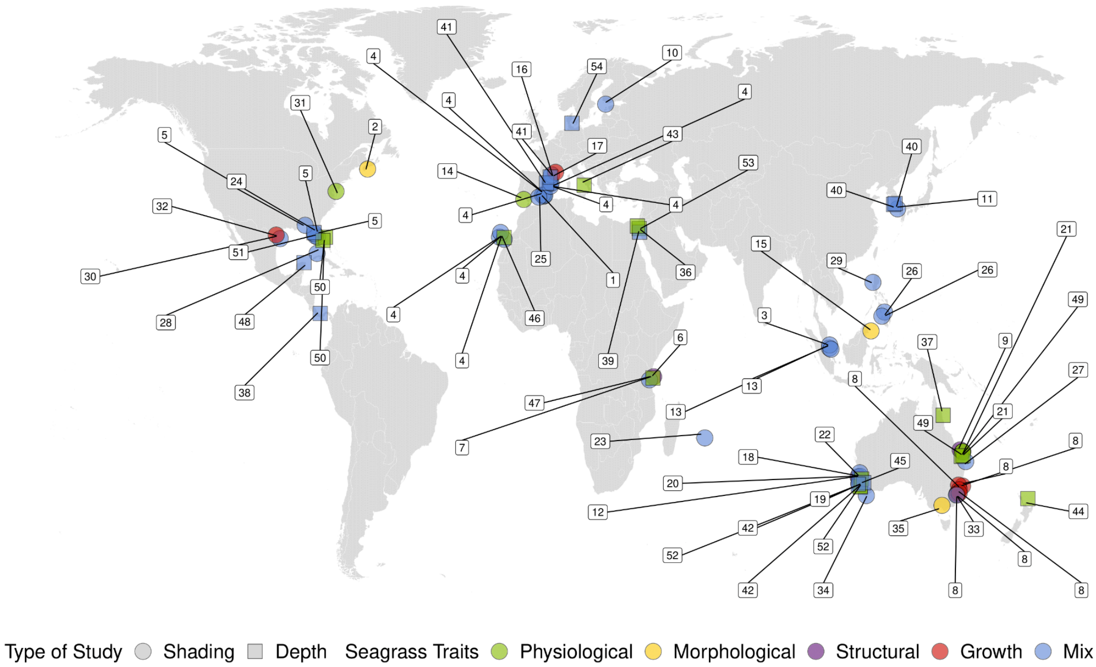


Figure 4.1. Results of the literature review. Shape shows the type of study (manipulative shading and depth-based studies) and colour the type of trait (physiological, morphological, structural and growth) studied in each publication (54 publications and 78 studies). The numbers related to each point represent the ID number corresponding to each publication in the Supporting Information (Appendix B: Table B1).

Table 4.1. Search results ordered by type of trait. Number of articles, studies and species for shading and depth-based investigations meeting our criteria.

Type of Trait	Trait	Publications	Studies	Species
Physiological	Saturation Irradiance (I_k and E_k)	17	35	13
	Maximum Photosynthesis (P_{max} and ETR_{max})	25	45	14
	Photosynthetic Efficiency (α)	22	40	14
Morphological	Leaf Length	19	26	13
	Leaf Width	16	24	9
	Leaves per Shoot	11	16	7
Structural	Shoot Density	25	49	15
	Aboveground Biomass	19	27	12
Growth	Shoot Growth	20	42	13

4.3. Results

4.3.1. Relationship between the maximum vertical distribution of seagrass species and their size and growth/reproductive strategy

We found no evidence of a relationship between the vertical distribution of seagrass species and rhizome diameter (our proxy for seagrass size, P = 0.823; Fig. 4.2a; Table B2 in Appendix B). In addition, there was no evidence of systematic differences in the vertical distribution of seagrasses according to their growth/reproductive strategies (using the classification of Kilminster et al. (2015); P = 0.178; Fig. 4.2b; Table B3 in Appendix B).

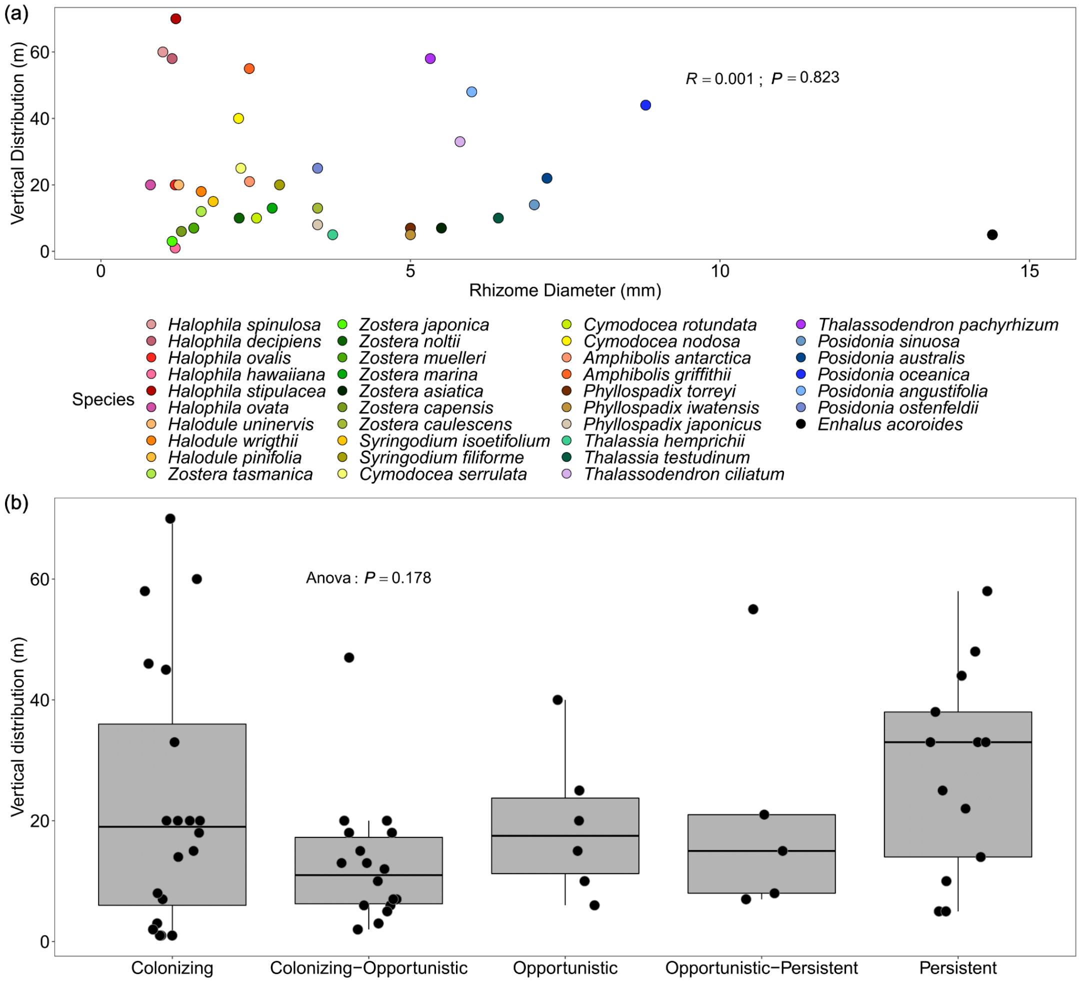


Figure 4.2. (a) Relationship between rhizome diameter and the maximum vertical distribution (i.e., maximum depth range of colonization) of 37 seagrass species. (b) Relationship between the maximum vertical distribution of 62 seagrass species and their classification according to seagrass growth/reproductive strategies. Points in panel (b) have been jittered horizontally to avoid overlapping.

4.3.2. Relationship between maximum vertical distribution and seagrass trait acclimatization potential

Selecting seagrass traits with acclimatization potential: Separate meta-analyses

According to the results of our meta-analyses, there was evidence of an overall effect for seven of the nine traits studied in response to reduced incoming light: saturation irradiance (I_k), maximum photosynthesis (P_{max}), photosynthetic efficiency (α), leaves per shoot (LXS), shoot density ($Sh.Dens$), above-ground biomass ($Ab.b$) and shoot growth ($Sh.G$) (Fig. 4.3; see Table B4 in Appendix B). In contrast, leaf length ($L.Length$) and leaf width ($L.Width$) did not show an overall effect in response to contrasting light environments. We found very strong evidence for saturation irradiance (P < 0.0001) and strong evidence for maximum photosynthesis (P = 0.0012) decreasing as a result of light reduction, and data revealed strong evidence for an influence of light reduction in increasing photosynthetic efficiency (P = 0.0015). In the case of morphological traits, there was moderate evidence for a decrease in the number of leaves per shoot (P = 0.0165) with light reduction, but there was no evidence for an influence of light reduction on leaf length (P = 0.2490) or width (P = 0.8739). There was also very strong evidence for structural traits, such as shoot density (P < 0.0001) and above-ground biomass (P < 0.0001), decreasing in lower light treatments. Finally, we found very strong evidence for shoot growth declining with light reduction (P = 0.0002).

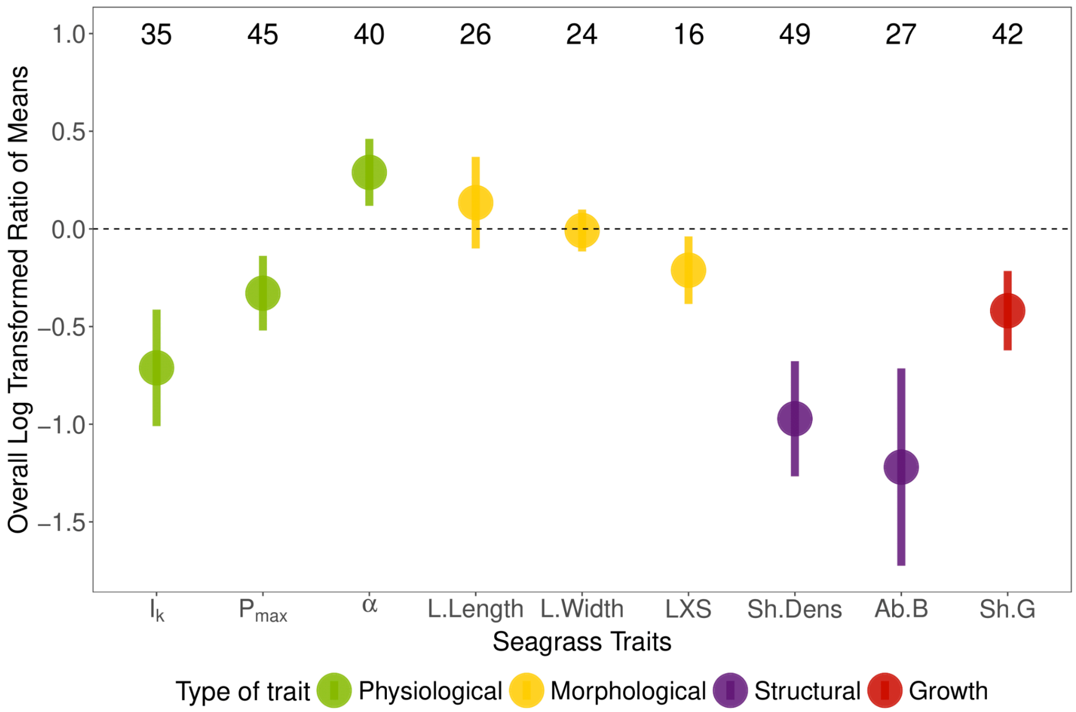


Figure 4.3. Overall effect sizes against light reduction calculated for each seagrass trait. Colours define the type of trait: physiological (green), morphological (yellow), structural (purple) and growth (red). Numbers above each trait represent the number of scientific studies for each seagrass trait analysed (for further explanation of these numbers, see Table 4.1). Seagrass traits shown from left to right, I_k, saturation irradiance; P_{max}, maximum photosynthesis; α, photosynthetic efficiency; L.Length, leaf length; L.Width, leaf width; LXS, leaves per shoot; Sh.Dens, shoot density; Ab.B, above-ground biomass; Sh.G, shoot growth.

Influence of the selected traits on seagrass maximum vertical distribution

The acclimatization potential of the seagrass traits saturation irradiance, number of leaves per shoot and above-ground biomass (Fig. 4.4; Fig. 4.5) clearly explained the maximum vertical distribution of the analysed seagrass species. We found strong evidence for acclimatization potential (i.e., weighted effect sizes) of saturation irradiance (physiological trait) explaining the vertical distribution of seagrasses (P = 0.004; Table B5 in Appendix B), in addition to very strong evidence for the acclimatization potential of leaves per shoot (morphological trait; $P < 0.001$; Table B6 in Appendix B) and moderate evidence for above-ground biomass (structural trait; $P = 0.0288$; Table B6). In contrast, there was no evidence for the acclimatization potential of any other traits providing an adequate explanation of the vertical distribution of seagrasses (Table B5).

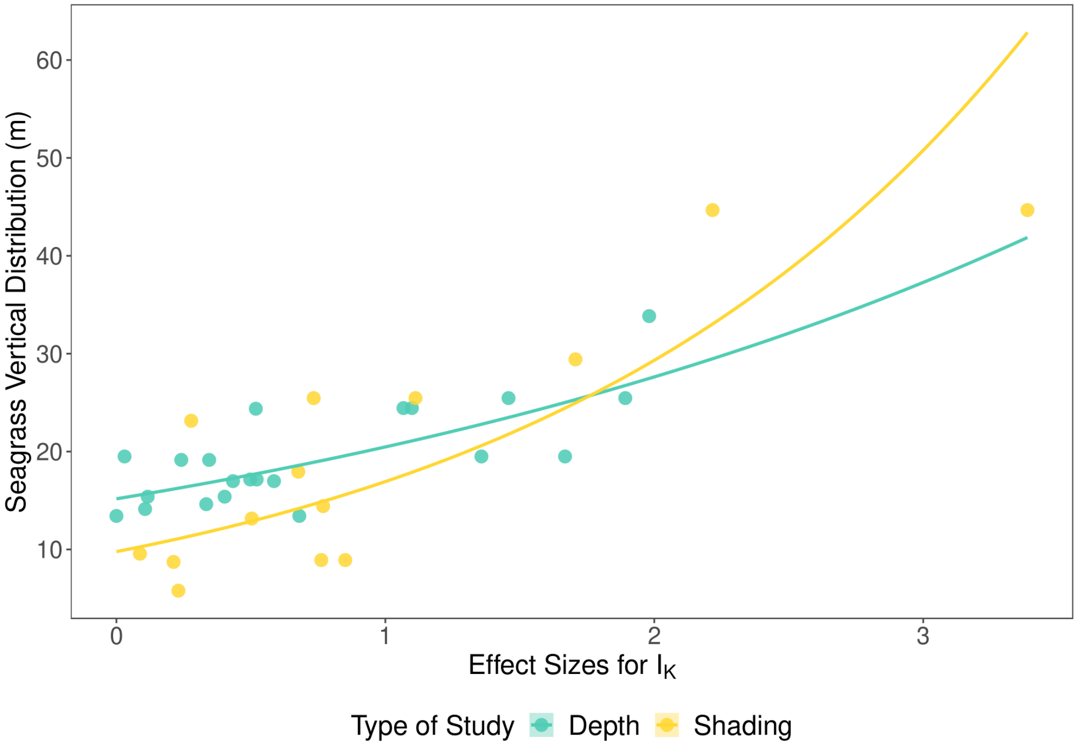


Figure 4.4. Relationships between seagrass maximum vertical distribution (in metres) and predictor variables, effect sizes (acclimatization potential for saturation irradiance, I_k) and type of study (depth-based and field shading). Data points represent distribution of standardized partial residuals of the fitted linear mixed model, where continuous lines represent the model fit through the data.

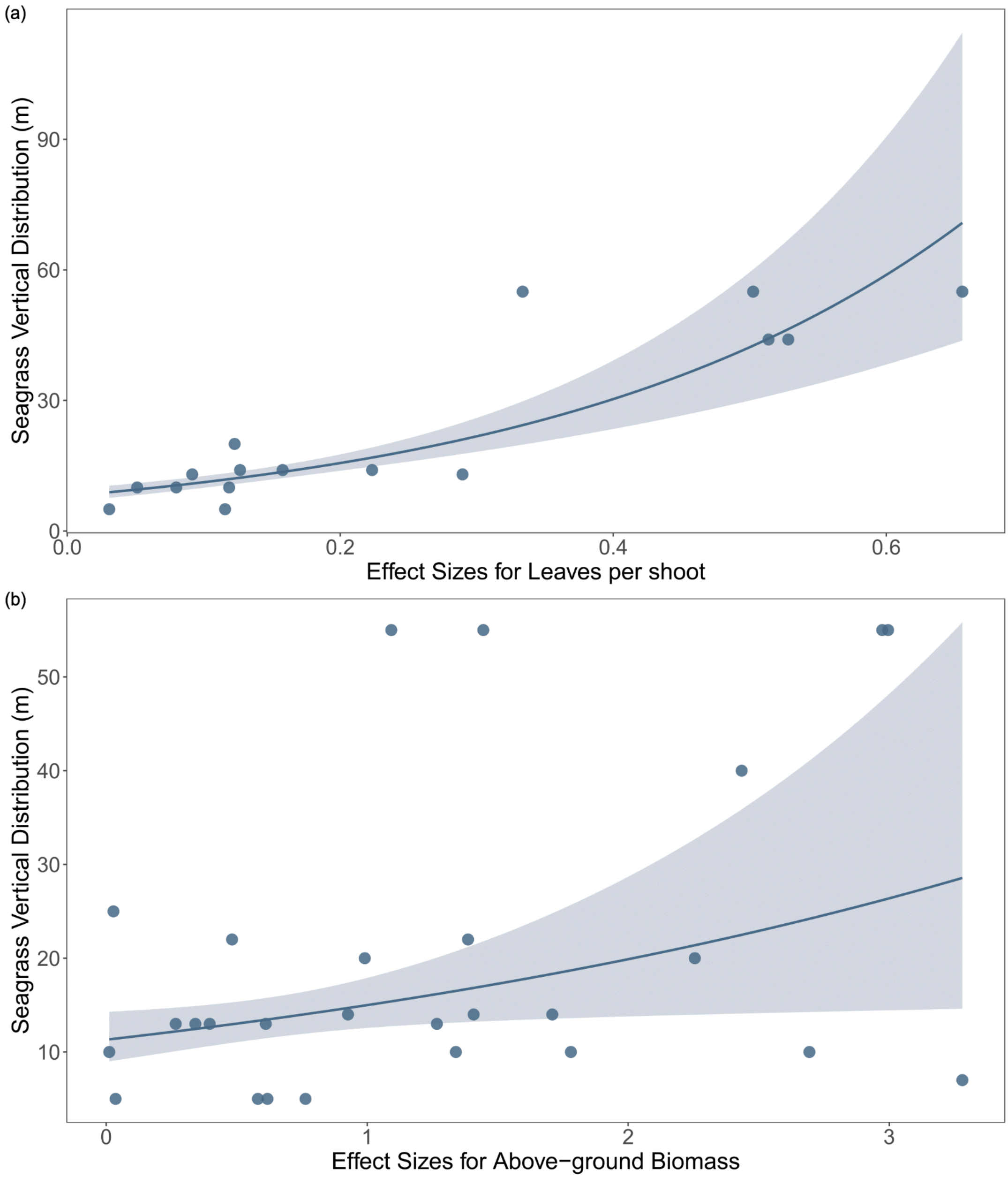


Figure 4.5. Relationships between seagrass maximum vertical distribution (in metres) and predictor variables, effect sizes: acclimatization potential for (a) leaves per shoot and (b) above-ground biomass. Data points represent distribution of standardized partial residuals of the fitted linear model, where continuous lines represent model fit through the data and the shades show 95% confidence intervals.

4.4. Discussion

The reducing transparency of coastal seas is one of the surest imprints of human pressures on nearshore waters. Photosynthetic dependence places firm limits on how much reduction in water quality marine plants can take (Duarte, 1991a; Dennison et al., 1993), and the upward march of once-extensive seagrass meadows over the last few decades is a clear sign of accelerating environmental stress (Waycott et al., 2009). What is additionally worrying about the light requirements of seagrass meadows is that these systems are often strongly nonlinear in their behaviour (Marín-Guirao et al., 2022), implying that restoration of water clarity might not guarantee meadow recovery (Katwijk et al., 2016). Understanding what allows some species to occupy wide depth distributions whereas others remain limited to much shallower ranges is therefore crucial to determine the differential susceptibility of seagrass assemblages to reduced water quality. Our survey of a large proportion of seagrass species world-wide indicates that their vertical distribution scales with acclimatization potential in key physiological, morphological and structural traits associated with low light. This ability transcends species size or functional groups, with trait acclimatization capacity found across species with large differences in rhizome width (our proxy for species size) or plant strategies. In addition, we found that these traits were not limited to a single organizational level but were a mix of physiological, morphological and structural traits. Of the traits we explored, the vertical distribution of seagrass species was best explained by the degree of species-specific capacity to reduce saturation irradiance (physiological trait), along with the capacity to reduce leaves per shoot and above-ground biomass (morphological and structural traits, respectively) as light conditions worsened.

4.4.1. Seagrass maximum vertical distribution and species size

Despite the strong negative relationship between the light attenuation coefficient (*k*) and the depth limit of seagrass meadows (Duarte et al., 2007), light availability alone cannot accurately predict species-specific vertical distributions of seagrasses

(Koch, 2001). Earlier studies have already highlighted the striking interspecific differences in seagrass depth ranges, which were attributed to seagrass growth strategies or architecture (Duarte, 1991a). For instance, it has been proposed that larger rhizomes are linked to better carbon allocation abilities, which could help to boost the carbon balance of plants against declines in benthic light and promote seagrass growth through increased carbohydrate reserves (Alcoverro et al., 1999). Our results, however, conclusively rule out plant size or architecture, which is strongly related to rhizome diameter (Duarte, 1991b), as the primary predictor of seagrasses colonizing deeper depths. In fact, large rhizomes might place a heavy respiratory burden on plant physiology at depth or during periods of severe light reduction (Duarte, 1991a; Fourqurean & Zieman, 1991; Hemminga, 1998; Alcoverro et al., 2001). This respiratory demand might well offset the reserve advantages of larger rhizomes. Having large rhizomes to allocate resources has clear advantages and might provide seagrasses with considerable resilience to seasonal light trends or in the face of disturbances such as herbivory, sedimentation or occasional light reduction (Ruiz & Romero, 2003; Vergés et al., 2008; Roca et al., 2014). However, the maintenance costs of this architecture make it untenable in low-light conditions (Hemminga, 1998), and some species might have to trade off resistance to short-term light deprivation against a larger vertical distribution.

4.4.2. Seagrass maximum vertical distribution and growth/reproductive strategy

Our results show no evidence that growth/reproductive strategies reflect differences in the vertical distribution of seagrass species. Colonizing, opportunistic, persistent and their intermediate life-history strategies are a useful way to classify seagrasses of the world in relationship to their functional resilience. As conceived by Kilminster et al. (2015), they combine a range of species-specific attributes, including shoot turnover, sexual maturity and investment in dormant seeds, to characterise how species are likely to respond to disturbances. Colonizing plants are characterised by faster growth rates, shorter time to sexual maturity and a higher investment in dormant seeds. Persistent species, in contrast, adopt a contrasting strategy, taking longer to reach maturity, growing more slowly and investing more in vegetative growth. Opportunistic species adopt a mixed strategy (Kilminster et al., 2015). It has been suggested that some of these traits, such as a reduced leaf/shoot turnover in persistent species, might be a long-term tolerance mechanism against reduced light conditions. For a relatively minor loss of acquired resources, plants could maintain large amounts of biomass, to cope with light reduction better (Olesen et al., 2002). However, what emerges from our analysis is that resilience strategies do not clearly map to vertical distribution.

4.4.3. Seagrass maximum vertical distribution and trait acclimatization potential

The ability to deal with reducing light conditions represents a slightly different set of physiological challenges from other environmental or biotic stressors and requires a unique set of plant strategies. Thus, what separates species with the largest vertical distributions, such as *P. oceanica*, *Cymodocea nodosa*, *H. stipulacea* or *Amphibolis griffithii*, is not so much their morphologies (they have diverse above- and below-ground structures) or their resilience strategies (which differ considerably among them), but the remarkable acclimatization potential in their physiological and morphological responses with changing light (Ruiz & Romero, 2001; Mackey et al., 2007; Silva et al., 2013; Tuya et al., 2019). In contrast, species with lower acclimatization capacity in their photosynthetic traits have never been observed at great depths. These photosynthetically limited species include *P. sinuosa* (Collier et al., 2008), *Syringodium filiforme* (Major & Dunton, 2000) and *Thalassia testudinum* (Enríquez et al., 2019). Interestingly, the photo-acclimatization responses identified in this analysis range from physiological acclimatization through to the ability to modify morphologies and above-ground structure. Studies of individual species identify this acclimatization potential as being essential in dealing with light reduction (Ruiz & Romero, 2001; Bité et al., 2007; Campbell et al., 2007; Collier et al., 2009; Silva et al., 2013); our approach allows us to generalize this across species, linking it clearly to depth distributions.

Perhaps unsurprisingly, higher physiological acclimatization capacity in the photosynthetic machinery of the plant is crucial to their ability to occupy a wide range of light regimes. As light conditions reduce with depth, only species with the ability to acclimatize by counterbalancing their carbon gains can persist (Ruiz & Romero, 2001; Ruiz & Romero, 2003). This response is typically the primary mechanism by which plants deal with light reduction (Ralph et al., 2007; Collier et al., 2012; McMahon et al., 2013). Of the three physiological parameters we examined, the reduction in the saturation irradiance (I_k) allows plants, albeit at the cost of also reducing their maximum photosynthesis, to obtain higher photosynthetic efficiencies in low-light conditions (Marín-Guirao et al., 2022). Past studies have highlighted that a photo-acclimatization response in this trait might explain more efficient use of light, in addition to differences in vertical distribution for a limited set of species (Bité et al., 2007; Campbell et al., 2007). For instance, a recent paper by Park et al. (2021) indicates that interspecific variation in physiological traits, among other traits, helps to explain differences in the vertical distribution of three *Zostera* spp. (*Zostera japonica*, *Zostera marina* and *Zostera caespitosa*). Likewise, Silva et al. (2013) showed that *C. nodosa*, with larger vertical distributions, is better photosynthetically adapted to low-light conditions than the less plastic *Z. marina*. Our study shows that the acclimatization potential of physiological traits, specifically the ability to modulate I_k, works across species and powerfully predicts the vertical distributions that might hold across the seagrass assemblage.

Acclimatization potential as a determinant of vertical distribution was also found at higher levels of plant organization. Across the assemblage, seagrasses showed considerable intraspecies variability in morphological, structural and growth traits, with a few notable exceptions. Crucially, the ability of the plant to reduce leaves per shoot and above-ground biomass explained species-specific vertical distributions. Many large seagrass species that form dense meadows (*P. oceanica*, *C. nodosa* and *A. griffithii* among them) adopt a leaf-reduction mechanism (defoliation) to minimize self-shading, an ideal strategy when colonizing deeper, darker locations (Ruiz & Romero, 2001; Mackey et al., 2007). For these species, defoliation might serve to mobilize carbohydrates (Silva et al., 2013). In addition, carbohydrate losses could be minimal if the leaf loss is restricted to older leaves, which make a minor contribution to carbon production (Alcoverro et al., 1999). This is also an ideal method for reducing the costs of above-ground respiration in impoverished light environments (Fourqurean & Zieman, 1991; Mackey et al., 2007; Collier et al., 2009). However, species showing limited ability to modify their leaves per shoot or above-ground biomass, compared with other species (for instance, *T. testudinum*, *Thalassia hemprichii* or *P. sinuosa*), are confined to shallower waters (Collier et al., 2009). Of the traits we measured, leaf dimensions (length and width) demonstrated a poor ability to change with light limitation across all species. This reduces the ability of seagrass species to expand their photosynthetic areas or (by growing taller) access shallower, more light-rich waters. For instance, leaf length and width have been found to decrease with light reduction in species such as *P. sinuosa* (Collier et al., 2009). In general, leaf morphology might be an unreliable predictor of seagrass responses to low-light environments (Tuya et al., 2019). Instead, at the deeper ends of their vertical distributions, seagrass species adopt strategies to minimize energy expenditure with structural modifications.

Across the assemblage, shoot density and shoot growth reduced, in general, with light reduction for most species in our dataset. Although the pattern of decline with reducing light was similar within species and within studies (see Fig. B2 in Appendix B), the acclimatization potential of these traits did not adequately explain the specific vertical distributions of seagrasses. Declines in shoot density are strongly linked to the ability to store carbohydrate reserves, particularly in larger species possessing larger rhizomes (Alcoverro et al., 2001). Nevertheless, for structural traits, the relatively short timing and duration of shading studies might have influenced our results (Collier et al., 2009). In fact, for experimental studies, long-term responses are expected to see the effect of light not only in the survival, but also in the full development of true meadows at their edges.

A potential limitation of our study is that we did not control for other abiotic factors that vary with depth that could also play a role in determining vertical depth distributions (Beer & Waisel, 1982; Carr et al., 2010). We limited our investigation to depth-based studies and shading manipulative experiments, where the only modified condition was light reduction. Our purpose was to obtain metrics related to plant identity that could explain depth distribution, but we cannot disentangle whether other factors, such as turbulence or sediment grain size, or overall differences between temperate and tropical waters additionally influenced these patterns. Our results are based on only a subset of species, because we do not yet have a comprehensive understanding of the responses of many seagrass species to reduced light. Shading experiments or comparative depth-based studies do not exist for all seagrass species, but represent c. 30% of the entire seagrass pool. As previous studies have already highlighted, our ability to generalize is necessarily circumscribed by gaps in research effort (McMahon et al., 2013). Moreover, this lack of species representation combines with an unequal distribution of our data across the entire range of depths suitable for seagrasses, which could have shaped the results found in this study.

4.5. Conclusion

What seems clear is that seagrass species use different strategies, at different levels of organization, to colonize deeper locations. Physiological acclimatization is geared towards maximizing their light-harvesting strategy in the deep, whereas higher-level strategies are directed at minimizing costs and reducing plant architecture. These strategies work in tandem. The seagrass species with the greatest vertical distribution were able to acclimatize physiological, morphological, and structural traits (I_k, leaves per shoot, and above-ground biomass) simultaneously. A combined acclimatization ability at physiological and higher levels is what makes these species particularly successful across the entire depth gradient.

Although the decline in the areal extent of seagrass meadows is easy to see as coasts succumb to a host of local and global stressors, the vertical contraction of meadows is often less visible. Yet it is one of the surest signs of an ecosystem in decline and serves as a warning of worsening ecological conditions. Identification of the mechanisms by which different seagrass species thrive within their natural depth ranges is crucial to establish species-specific baselines against which to measure this retreat and calibrate recovery programmes. Seagrass species have different vulnerabilities to declining light conditions, with some being particularly sensitive to even small changes in light regimes. What our work shows is that the ability to deal with reduced light is not linked to a few specialized traits, but with the acclimatization potential to modify trait parameters at physiological, morphological and structural levels. There are, however, limits to trait acclimatization, and many meadows are increasingly depth-restricted as stressors increase. Reversing this retreat will require concerted and coordinated efforts to improve water quality but are essential to conserve the diversity and function of seagrass meadows across their depth range.

Chapter 5

Grazing halos reveal differential ecosystem vulnerabilities in vegetated habitats

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Abstract

As global change modifies the biotic and abiotic conditions of vegetated ecosystems, they are increasingly susceptible to overgrazing events. Although herbivory represents a natural force controlling the abundance of primary producers, marine macrophyte communities are particularly vulnerable to experiencing abrupt and catastrophic collapses triggered by marine herbivores, most notably by sea urchins. While herbivore abundance is often a strong predictor of impending ecosystem collapse, the large natural variability across macrophyte ecosystems makes it difficult to generalize these predictions. How close an ecosystem is to overconsumption depends, eventually, on the critical relationship between habitat primary production and herbivore consumption, which considerably varies across ecological contexts. Here, we used grazing halos produced by individual sea urchins to characterise how producer-consumer interactions vary upon mediated by endogenous (i.e., species-specific traits) and exogenous factors (i.e., environmental factors influencing biotic and abiotic contexts) across the Mediterranean Sea in order to assess the relative vulnerability of their macroalgal communities to overgrazing. There were strong variations in the production-consumption relationship across the Mediterranean basin. Sea urchin species identity significantly influenced this vulnerability, with *Arbacia lixula* producing grazing halos more than twice as large as *Paracentrotus lividus*. Sea urchin halos increased consistently with herbivore size and across depth. However, sea urchin size also interacted with nutrient conditions, increasing ecosystem vulnerability as nutrient availability decreased. In addition, species identity interacted with other context-specific factors such as habitat type, predator-induced fear, and seawater temperature, which only influenced *P. lividus* halos. Our results emphasize how variable overgrazing vulnerability can be, depending on a broad range of interacting species- and site-specific factors characteristic of each local context. While tracking herbivore abundance and ecosystem states is important to assessing overgrazing vulnerability, we need to shift focus to a better understanding of local forces mediating producer-consumer interactions. Although the drivers pushing ecosystems to collapse may be global, protecting vegetated ecosystems from overgrazing will require bespoke integrative approaches that address contextual complexity, which is often inherently local.

Keywords: *plant-herbivore interactions*, *ecosystem vulnerability*, *overgrazing*, *sea urchins*, *macroalgal forests.*

5.1. Introduction

Plant-herbivore interactions shape the structure and functioning of the world's ecosystems (Wood et al., 2017; Trepel et al., 2024). Although herbivory is a critical function across ecosystems, its relative importance as a structuring agent is highly variable (Worm et al., 2002; Burkepile & Hay 2006; Jia et al., 2018). The role of herbivory in regulating the abundance of primary producers is typically much more pronounced in aquatic ecosystems, where herbivores can remove up to ten times more plant biomass than their terrestrial counterparts (Bakker et al., 2016). Herbivory rates are particularly high in marine benthic ecosystems, where herbivore activity can result in an average reduction of 68% of producer abundance (Poore et al., 2012). As global change gathers pace, its cumulative impacts erode the resilience of marine vegetated habitats, making them notably prone to high rates of herbivory (Strain et al., 2014; Filbee-Dexter & Wernberg, 2018). In addition, local anthropogenic impacts like overfishing have decimated marine predator communities worldwide, disrupting food webs and causing population explosions of herbivores, resulting in trophic cascades characteristic of marine ecosystems (Sala et al., 1998; Shurin et al., 2002; Myers & Worm, 2003).

As their populations grow, marine herbivores can severely deplete highly productive macrophyte ecosystems (Steneck et al., 2002; Barrientos et al., 2022; Christianen et al., 2023). Once critical herbivory thresholds are breached, ecosystems may shift rapidly towards impoverished and highly stable alternative states devoid of vegetation (Eklöf et al., 2008; Filbee-Dexter & Scheibling, 2014). The inherent hysteresis of these depauperate states makes recovery pathways highly protracted; a simple reduction in herbivore numbers (i.e., stressor) does not guarantee a return to the original vegetated state (Scheffer et al, 2001; Ling et al., 2015). While herbivore numbers are clearly important in determining these trajectories, a host of other factors influence the nonlinear dynamics shaping the resistance and recovery (i.e., resilience) of macrophyte ecosystems (Conversi et al., 2015; Wood et al., 2017). There is now mounting evidence showing that marine regime shifts can be mediated by: (i) endogenous factors associated with specific herbivore and macrophyte traits (Vergés et al., 2014b; Barrientos et al., 2022), (ii) exogenous abiotic factors related to climatic-driven seawater temperature or site-specific nutrient conditions (Wernberg et al, 2016; Boada et al., 2017), (iii) exogenous biotic factors influencing predator control over herbivores (Steneck et al., 2002; Sala et al., 1998), or (iv) interaction between some of these (Ling et al., 2009a; Sala et al., 2012; Conversi et al., 2015). Given this complexity of response, preventing marine vegetated habitats from tipping over in the first place is likely the most robust strategy for their management (Scheffer et al., 2001). The difficulty often is, however, identifying clear integrative measures that reliably signal changes in ecosystem structure and function, and that can serve as an index of changing plant-herbivore interactions (Worm et al., 2002; Burkepile & Hay, 2006; Wood et al., 2017).

Herbivorous sea urchins are some of the most notorious barren-forming organisms worldwide (Shurin et al., 2002; Ling et al., 2015). Sea urchin numbers have been often seen as robust predictors of imminent macrophyte collapse, with numerous studies focusing on determining the abundances at which sea urchins could trigger catastrophic regime shifts (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015). However, while quantitative approaches have been successful at identifying thresholds of herbivory stress for each local context, the ability to generalize such estimates across macrophyte ecosystems is frustrated by the considerable natural variation in biotic and abiotic factors and their effect on site-specific productivities and herbivory (Mann, 1973; Pessarrodona et al., 2022a). Most of this variance is related to specific endogenous traits of both macrophytes and herbivores and with exogenous factors that together determine the productivity of each habitat and set the context for such plant-herbivore interactions (Burkepile & Hay 2006; Poore et al., 2012). Macroalgal-dominated ecosystems range from thin turfs to highly structured macroalgal forests with a diverse set of morphofunctional types, varying considerably in their structural and functional resistance to herbivory (Hereu et al., 2008; Filbee-Dexter & Wernberg, 2018). In addition, primary production can vary considerably between habitats (Mann, 1973; Dayton, 1985), with the productivity of a healthy kelp forest being up to ten times higher than intertidal macroalgae, and both being considerably more productive than turf-dominated ecosystems in temperate regions (Smale et al., 2013; Filbee-Dexter & Wernberg, 2018). Similarly, herbivorous sea urchin species differ in their biological or ecological traits such as individual morphometry, diet preferences, and/or behaviour; which can mediate their foraging and feeding preferences and, therefore, herbivory pressures on macroalgal forests (Wangensteen et al., 2011; Agnetta et al., 2013).

Besides endogenous traits, exogenous abiotic factors such as nutrients, temperature, and light can shape both macrophyte primary production (Dayton, 1985; Sant & Ballesteros, 2021) and herbivore consumption rates between regions or across depths (Boada et al., 2017; Nikolaou et al., 2023). Under oligotrophic or light-limiting conditions, decreased primary production and compensatory grazing by sea urchins (among other behavioural changes) both alter the production-consumption relationship, making macroalgal systems much more prone to catastrophic collapses than regions with higher nutrient availability (Dayton, 1985; Boada et al., 2017; Nikolaou et al., 2023). Non-lethal temperature increases can enhance primary production, but may also modify herbivore metabolic requirements, which affects the balance of these interactions (O'Connor, 2009; Pagès et al., 2018). Among the exogenous biotic factors that influence this relationship, the presence of predators can shape herbivore behaviour by inducing fear that indirectly influences herbivory rates and reduces their impacts on macroalgal forests (Hereu, 2005; Pessarrodona et al., 2019; Pagès et al., 2021).

Central to overgrazing vulnerability is the fundamental relationship between habitat productivity and herbivore consumption (Suskiewicz & Johnson, 2017). While many factors may shape the vulnerability of vegetated ecosystems to collapse (Hereu et al., 2008; Conversi et al., 2015), this production-consumption ratio most clearly describes how close a system is to overconsumption. While several studies have explored how the production-consumption relationship is modified by endogenous or exogenous factors, most have tested these factors individually or in laboratory conditions (Suskiewicz & Johnson 2017; Kriegisch et al., 2019). Scaling these studies up to whole ecosystems is critical to determine context-specific vulnerabilities of macroalgal communities (Conversi et al., 2015; Wood et al., 2017). Here, we explore how the vulnerability of temperate macroalgae communities is mediated by endogenous factors, including species/habitat identity and sea urchin size; and exogenous factors such as predator-induced fear, nutrient, temperature, and light conditions; which influence the strength of the production-consumption interaction (Fig. 5.1a). For this, we assessed the balance between productivity and herbivory by measuring sea urchin grazing halos of two key species of sea urchins (Fig. 5.1b,c). Grazing halos are commonly found associated with physical refuges and are characterised by a sharp transition of macroalgal-habitat to bare rock substrate. We assumed that, when maintained by a single urchin, a halo represents the per capita relationship between the production of the habitat and the rate of herbivore consumption. The size of these halos therefore integrates the influence of context-specific, endogenous and exogenous factors, and allows us to explore the resilience of the macroalgal community across space. We evaluated the factors that mediated the productivity-herbivory relationship by measuring the size of grazing halos over a wide range of sites in the Mediterranean Sea spanning gradients of nutrient conditions, temperatures, depths, and protection regimes (Fig. 5.1a).

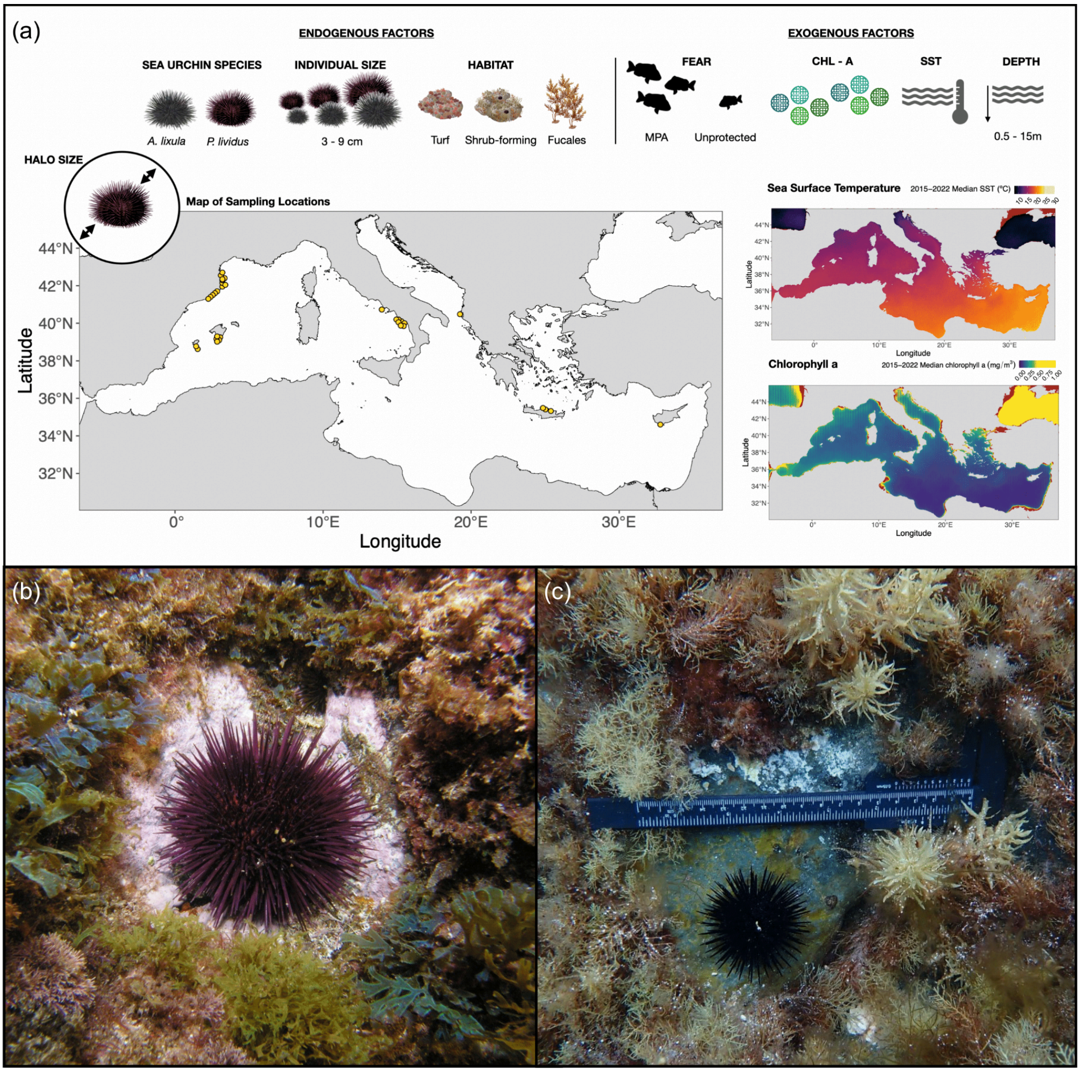


Figure 5.1. (a) Schematic representation of the endogenous and exogenous factors influencing the relationship between primary production and herbivore consumption (i.e., grazing halos) and shaping the vulnerability of macroalgal forests to herbivory. (a) Halos were measured in 32 locations (yellow points) across the Mediterranean Sea. Maps on the right panel show the median sea surface temperature (top) and median chlorophyll *a* (bottom) for the study period between 2015 and 2022, as an example of the spatial gradient of nutrients and seawater temperature in the Mediterranean Sea (data extracted from NOAA's ERDDAP service). Chlorophyll *a* values higher than 1 mg m^{-3} are depicted in red. (b), (c) Grazing halos produced by *P. lividus* and *A. lixula*, respectively.

5.2. Materials and methods

5.2.1. Study area and species

The Mediterranean is a confined and highly human-modified sea. It is an excellent model to test the impacts of global change as many of its drivers are more strongly felt than in the rest of the oceans (Cramer et al., 2018). For instance, the rate of warming is more than threefold faster in the Mediterranean than in the global ocean (Pisano et al., 2020). In addition, coastal waters have become increasingly oligotrophic over the past decade in response to warming (Agusti et al., 2017). At the same time, this sea has experienced a high level of local anthropogenic pressure, and overfishing has been (and still is) a major stressor, exhibiting some of the lowest values of fish biomass for shallow reefs (Sala et al., 2012; Cramer et al., 2018). The Mediterranean Sea is characterised by pronounced spatial gradients for crucial environmental variables such as nutrients, temperature, and salinity (Nikolaou et al., 2023; Santana-Garcon et al., 2023), making it ideal to test the main drivers modifying our oceans today.

Our study focuses on shallow rocky reefs dominated by macroalgal communities where drastic sea urchin overgrazing events can occur (Sala et al., 1998; Boada et al., 2017). When undisturbed, these vegetated habitats are dominated by macroalgae of the order Fucales (mainly *Cystoseira sensu lato*) and other shrub-forming macroalgal communities (Ballesteros, 1989). These macroalgal communities are critical ecosystem engineers in benthic sublittoral Mediterranean assemblages, which are of paramount ecological importance, accounting for most of the biomass and production of these shallow ecosystems (Ballesteros, 1989). These macroalgal-dominated communities are also in decline due to a host of local and global forces, being often replaced by simplified habitats dominated by algal turfs or urchin barrens (see e.g., Sala et al., 1998; Giakoumi et al., 2012; Pessarrodona et al., 2021). *Paracentrotus lividus* and *Arbacia lixula* are ubiquitous sea urchin species in Mediterranean rocky reefs, able to form barrens where healthy macroalgal forests used to thrive (Kempf, 1962; Bulleri et al., 1999). Despite the similarity between these two sea urchin species, they differ in fundamental features. Crucially, species-specific differences in morphometric traits make them differentially vulnerable to predation, affecting their behaviour, movement and, hence, their potential herbivory pressure on macroalgal beds (Guidetti & Mori, 2005; Agnetta et al., 2013; Agnetta et al., 2015). As foragers, they also have distinct dietary preferences: *P. lividus* is a strict herbivore, grazing on species of macroalgae and turf, whereas *A. lixula* is a more functional omnivore (with a clear carnivorous tendency) that acts as a "bulldozer" when moving across macroalgal forests, rooting out all macroalgae as it forages for benthic organisms (Wangensteen et al., 2011; Agnetta et al., 2013; Agnetta et al., 2015).

5.2.2. Study design and measures of sea urchin halos

We explored the relationship between habitat productivity and sea urchin consumption by measuring grazing halos along gradients of nutrients, temperature, light and contrasting management protection regimes at multiple locations across the Mediterranean Sea. The size of these halos (i.e., using halo diameter as a proxy) represents a useful indicator of the net balance between macroalgae production and sea urchin consumption and can help evaluate how different sets of endogenous and exogenous factors of biotic and abiotic nature alter the strength of these producer-consumer interactions (see Fig. 5.1a). Halos are patches of bare rock on the macroalgal-dominated bottoms maintained by sustained sea urchin grazing (see Fig. 5.1b,c), typically associated with small refugia (Ling & Johnson, 2012; Pessarrodona et al., 2019). While the halo size probably does not represent absolute herbivory pressure, the urchin does not wander far from its refuge (Hereu, 2005), focusing the bulk of its grazing on the area around it (Bulleri, 2013), which allows us to use halo size as a comparative measure between locations.

We measured the diameter of 1218 individually-produced sea urchin halos formed by *P. lividus* (n = 917) and *A. lixula* (n = 301) in 32 locations across the Mediterranean Sea (Fig. 5.1a). The data was collected from 2015 to 2022. The sampling period spanned from mid-March (except April) to mid-October. At each sampled region we surveyed the site actively searching for grazing halos by snorkelling or scuba diving. Sea urchin barrens were excluded since they preclude the identification of halos. At each chosen area, we actively looked for (i) solitary sea urchins so we could attribute its herbivory to a single individual and (ii) individuals larger than three cm, since smaller sea urchins rarely generate distinctive halos (Pessarrodona et al., 2019). We measured the halo diameter either *in situ* with a ruler, or *ex situ* by taking a picture with a scale and analysing the images with the software ImageJ.

5.2.3. Endogenous and exogenous factors shaping halo size

For each halo observation we noted the sea urchin species (*P. lividus* or *A. lixula*), its test diameter without spines (measured between the spines with a vernier calliper), the morphologic type of foundation species (separating communities dominated by ephemeral algae forming a horizontal mat; turfs, arborescent shrub-forming macroalgae with complex three-dimensional structure, and canopy-forming macroalgae of the order Fucales; as defined by Monserrat et al. (2022)), and depth. In addition, we used information on the level of protection (two categories, areas with any protection level or completely unprotected coastal areas) (Hereu, 2005); and data on chlorophyll *a* and sea surface temperature (SST), were collected for each study site, using the NOAA's ERDDAP service through the *rerddap* R package (Chamberlain, 2022). From each dataset, we selected the annual maximum chlorophyll *a* and maximum SST at each study location in the year in which the data were collected. During data extraction, we excluded any chlorophyll *a* outliers from the datasets used for modelling. Outliers were identified as inconsistent peaks within the time series.

5.2.4. Data analysis

We evaluated the relationship between 'Halo size' (i.e., halo diameter measured in cm) and different endogenous and exogenous factors using linear mixed-effects models (LMMs). To assess the distribution of the response variable we used the *fitdistrplus* R package (Delignette-Muller & Dutang, 2015). We applied a maximum likelihood estimate method to fit the data to three likely distributions (gamma, log-normal and Weibull), whose model fittings were evaluated visually and statistically (Appendix C: Table C1).

To test the effect of predictors on 'Halo size', we fitted a set of candidates LMMs with log-normal distribution of errors (Appendix C: Table C1), using the *lmerTest* R package (Kuznetsova et al., 2017). These models integrated, therefore, the effect of both endogenous factors - 'Species' (two levels: *A. lixula* and *P. lividus*), 'Size', 'Habitat type' (three levels: turf, shrub-forming and Fucales); and exogenous factors - 'Protection level' (two levels: protected and unprotected locations, as a proxy for predator-related fear); 'Annual maximum chlorophyll *a*', 'Annual maximum SST', and 'Depth'. 'Location' (32 levels) and 'Sampling period' (seven levels, one per month) were set as random factors, including random slopes for each 'Species' within each 'Location'. We disregarded the use of random slopes for each 'Species' within each sampling period due to matrix singularity issues (insufficient levels to include 'Sampling period' in *A. lixula* models). The most informative model was chosen based on Second-Order Information Criterion (AICc) and likelihood ratio tests, and using the variance inflation factor to assess collinearity among explanatory variables (Burnham & Anderson, 2004; Zuur et al., 2009). This general model (i.e., including both species together) was confirmed by applying multi-model inference and an iterative stepwise procedure using the *dredge()* function in the *MuMIn* R package (Bartoń, 2022) (Appendix C: Table C2). Our preliminary results showed differences among species, so we applied the same criteria to fit LMMs for each species separately thus testing the relationship between species-specific halos and all predictor variables. 'Location' and 'Sampling period' were included as random factors only in the *P. lividus* model (insufficient levels to include 'Sampling period' in *A. lixula* model).

In all cases, model assumptions were visually and statistically explored using the functions in the *performance* R package (Lüdecke et al., 2021). In the general model, despite logarithmic transformation, model residuals did not meet the assumption of normality. However, fixed effects in LMMs have been found to be sufficiently robust to violations of residuals normality (Schielzeth et al., 2020). To examine the level effect of the different categorical predictors analysed, we ran Tukey post-hoc analyses for pair-wise comparisons using the *multcomp* R package (Hothorn et al., 2008).

5.3. Results

The results of the two types of models included in this study (i.e., a general model including both species together (Appendix C: Table C3) and species-specific models (Appendix C: Table C4)), to explore the relationship between habitat productivity and sea urchin consumption, showed that both exogenous and endogenous factors influenced the size of grazing halos. However, the importance of different predictors varied among sea urchin species as explained by our species-specific models (Table C4). In our general model, species identity strongly affected halo diameter ($P < 0.001$; Table C3); in fact, *A. lixula* grazing halos were more than twice as large as *P. lividus* grazing halos (overall mean ± se = 27.9 ± 0.96 vs 12.5 ± 0.26 cm, respectively; Fig. 5.2). In this model, the predictor "Species" also showed interaction effects with the annual maximum chlorophyll *a* ($P = 0.010$; Table C3) and habitat type ($P = 0.004$; Table C3). Halos were larger in areas with lower nutrients, but only for sea urchins larger than 4 cm test diameter ($P < 0.001$; Table C3). The significance of this size-dependent nutrient effect was also confirmed for each species separately (*A. lixula*, $P = 0.036$; *P. lividus*, $P < 0.001$; Table C4; Fig 5.3). *P. lividus* halos statistically varied with the type of macroalgal community, but not those of *A. lixula* (*A. lixula*, $P = 0.158$; *P. lividus*, $P < 0.001$; Table C4; Fig. 5.3). The average halo size was larger in communities dominated by Fucales (*A. lixula*, mean ± se = 35.4 ± 5.25; *P. lividus*, mean ± se = 14.5 ± 0.62) than in habitats dominated by shrub-forming macroalgae (*A. lixula*, mean ± se = 28.2 ± 1.17; *P. lividus*, mean ± se = 12.2 ± 0.31) or turfs (*A. lixula*, mean ± se = 25.7 ± 1.65; *P. lividus*, mean ± se = 9.4 ± 0.31). However, our species-specific model outputs (Fig. 5.3), which integrate the natural variability associated with other predictors of halo size, only detected significantly larger halos in turf grounds than in habitats dominated by shrub-forming algae for *P. lividus* (Appendix C: Table C5).

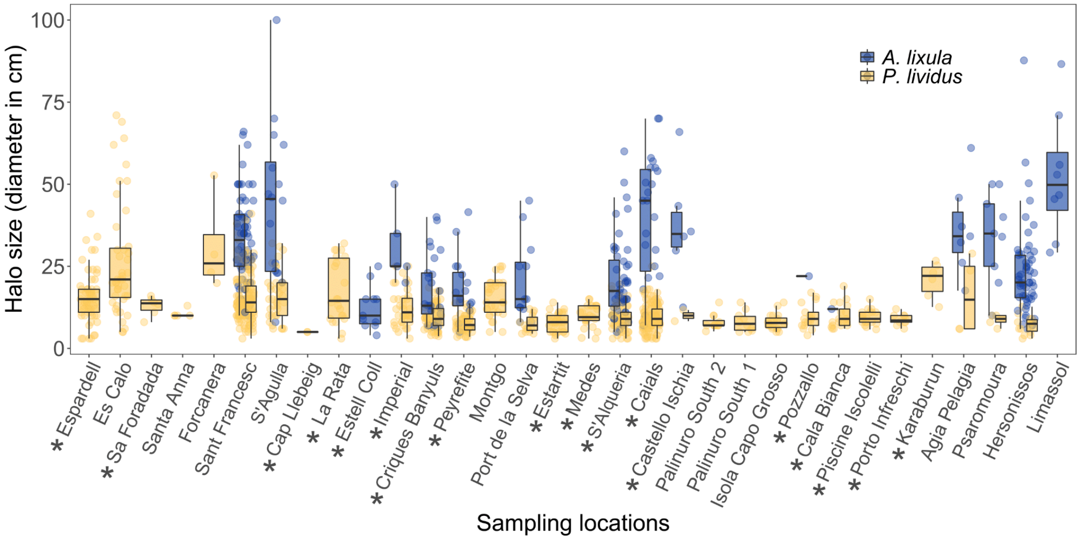


Figure 5.2. Halos measured across sampling locations in the Mediterranean Sea grouped by sea urchin species: *A. lixula* and *P. lividus*. Locations are ordered by longitude and *a*sterisks indicate that they are within an area with some level of protection.

Our general model results indicate that the management protection level (proxy of predator-induced fear) had a strong negative effect on halo sizes (*P* = 0.002; Table C3). Halos were larger outside marine protected areas (MPA) than inside them for both *A. lixula* (MPA: mean ± se = 23.6 ±1.34; outside: mean ± se = 31.3 ± 1.29) and *P. lividus* (MPA: mean ± se = 10.6 ± 0.23; outside: mean ± se = 15.4 ± 0.53). In the species-specific model, only *P. lividus* showed this effect (*P* = 0.003; Table C4; Fig. 5.3), whereas *A. lixula* did not (*P* = 0.285; Table C4; Fig. 5.3). Our data only revealed weak evidence (*P* = 0.055; Table C3) of a potential effect of annual maximum SST on halo size for both species; however, when analysed separately, they showed a positive effect of SST on halos produced by *P. lividus* (*P* = 0.026; Table C4; Fig. 5.3) and no effect on *A. lixula* halos (*P* = 0.807; Table C4; Fig. 5.3). Conversely, we found very strong evidence for a positive effect of depth on halo size (*P* < 0.001; Table C3), which was consistent across species (*A. lixula*, *P* = 0.037; *P. lividus*, *P* < 0.001; Table C4; Fig. 5.3).

Our selected general LMM model (Table C2) accounted for a high proportion of the variance in our data as shown by the proportion of the variance explained by both fixed and random effects (conditional R^2 = 0.78) and that explained only by fixed effects (marginal R^2 = 0.53). In contrast, the species-specific models showed marked differences, as the LMM of *A. lixula* obtained a conditional R^2 = 0.54 and a marginal R^2 = 0.21, whereas the LMM for *P. lividus* approximately doubled these values (R^2 = 0.80 and R^2 = 0.47, respectively).

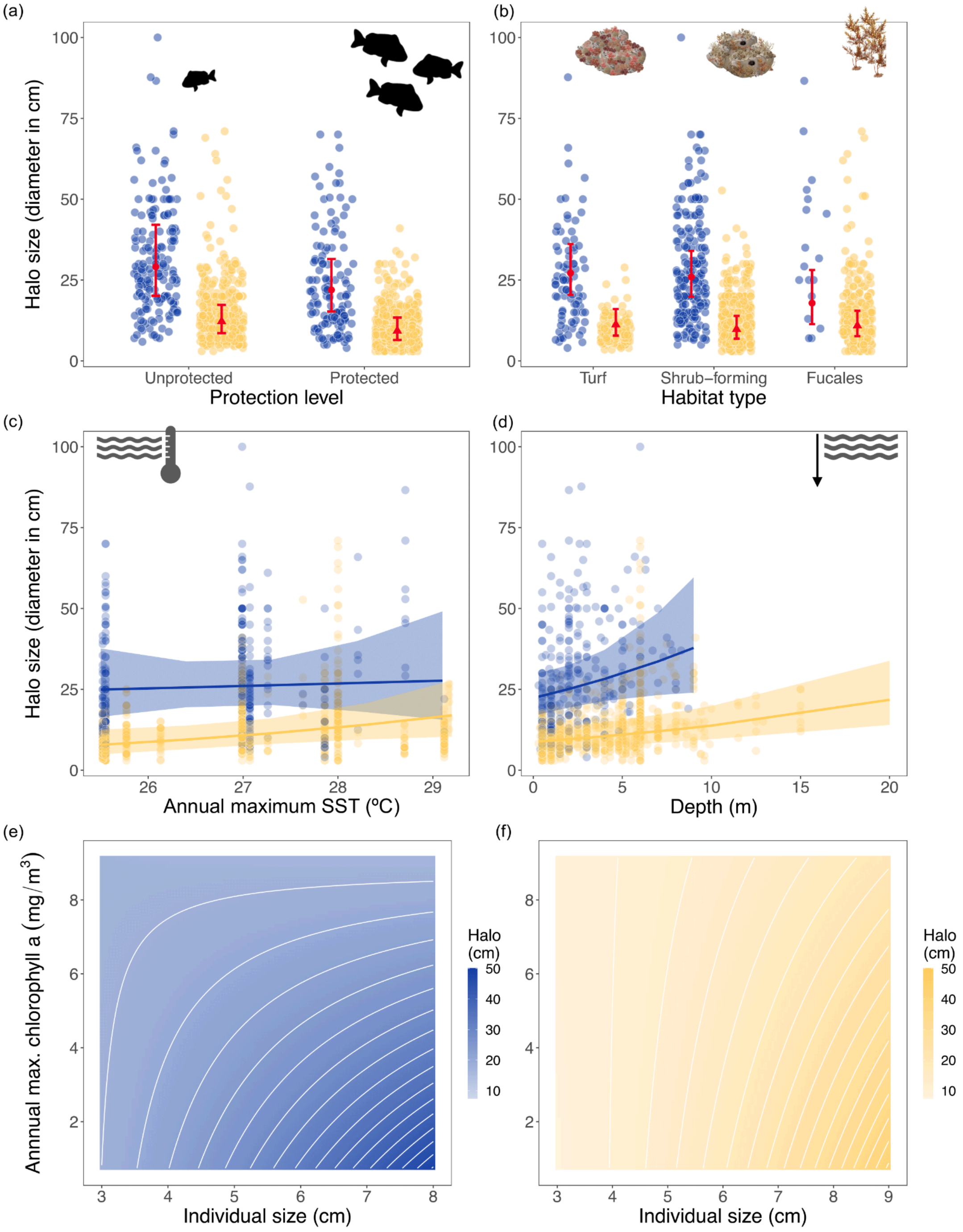

(a)
Halo size (diameter in cm)
100
75
50
25
0
Unprotected
Protected
Protection level
(b)
Turf
Shrub–forming
Fucales
Habitat type
(c)
Halo size (diameter in cm)
26
27
28
29
Annual maximum SST (ºC)
(d)
0
5
10
15
20
Depth (m)
(e)
Annnual max. chlorophyll a (mg/m³)
2
4
6
8
3
4
5
6
7
8
Individual size (cm)
Halo
(cm)
50
40
30
20
10
(f)
9
Individual size (cm)
Halo
(cm)

Figure 5.3. Data points represent *A. lixula* (blue) and *P. lividus* (yellow) halos measured in the field. Halos are explained by each predictor variable: (a) protection level, (b) habitat type, (c) annual maximum SST, (d) depth, and (e, f) the interaction between annual maximum chlorophyll *a* and sea urchin size. Data points are shown with fitted LMM (log-normal distribution) estimates (red points) or smooths, and 95% confidence intervals for each species-specific model. Heatmaps show the result of each species-specific model for the interaction between individual size and the annual maximum of chlorophyll *a*.

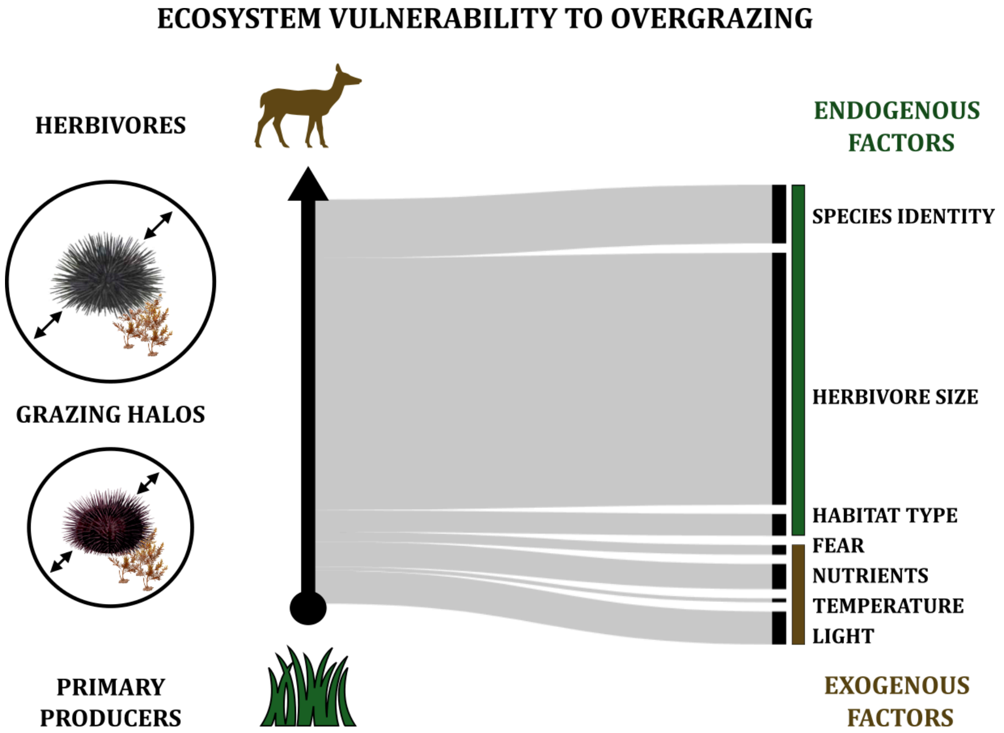


Figure 5.4. Schematic representation of the relationship between primary production and herbivore consumption (i.e., grazing halos) and the influence of endogenous and exogenous factors on plant-herbivore interactions (Sankey diagram adapted from model outcomes in this study).

5.4. Discussion

While, as a general rule of thumb, herbivore numbers are a powerful indicator of overgrazing episodes in vegetated ecosystems, this alone does not always represent an accurate predictor, since a host of context-dependent factors influence shifts to impoverished states devoid of vegetation (Eklöf et al., 2008; Hereu et al., 2008; Conversi et al., 2015; Ling et al., 2015). Our field study across the Mediterranean Sea shows that the relationship between macroalgal productivity and sea urchin consumption (i.e., halo size) is mediated by several endogenous and exogenous factors of biotic and abiotic nature that can shape ecosystem vulnerability to overgrazing collapses (Fig. 5.4). Sea urchin species differed in their foraging impact on macroalgal communities, reflecting differences in their life history traits. Although sea urchin sizes strongly determined these plant herbivore-interactions, this broad pattern was mediated by the type of habitat, exogenous abiotic factors such as depth, nutrients and temperature, and can be limited by exogenous biotic factors like fear.

Although several experimental studies have demonstrated that grazing rates can be modified by, among others, nutrients, temperature, fear, depth and plant anti-herbivory responses (Ling et al., 2009; Boada et al., 2017; Pagès et al., 2018; Kriegisch et al., 2019; Pessarrodona et al., 2019; Nikolaou et al., 2023; Santana-Garcon et al., 2023), the challenge has always been to integrate all these factors, since in natural conditions they often vary together in complex ways (Hereu et al., 2008; Wood et al., 2017; Kriegisch et al., 2019). The value of using individually-produced grazing halos is that they provide an ideal index by which herbivore (here sea urchins) consumption can be compared with inherent production values in real-world systems. With the assumption that halos exist at a steady state, the size of halos is a simple yet powerful integration of all the factors influencing the interaction between primary production and herbivore consumption. Using this basic measure our study shows that the strength of the interaction between macrophyte communities and herbivores is much more complex than population numbers alone can capture (Wood et al., 2017). Halting the retreat of marine macrophytes to overgrazing requires addressing the entire suite of endogenous and exogenous factors that shape their interactions.

Across the Mediterranean basin, the factor that most affected consumption rates was the size of individual sea urchins, regardless of species. Although sea urchins smaller than three cm were unable to produce a halo, since their rates of consumption were always lower than macroalgal production (Pessarrodona et al., 2019), beyond this threshold, halo diameters increased in length considerably with individual urchin size, as generally expected for herbivores (Bakker et al., 2016). The implication here is that sea urchin numbers, important as they are, may not be as critical as their demographic structure (Ling et al., 2019; Pessarrodona et al., 2019). While ecological indicators such as sea urchin biomass or abundance can partly account for the effect of herbivory impact, it is only beyond a certain size that sea urchin consumption begins to count towards overgrazing, and not in a simple linear way (Pessarrodona et al., 2019). The identity and traits of sea urchin species also matters, helping explain a large component of the variation in halo sizes. *P. lividus* is a selective feeder, grazing only on preferred types of vegetation (Agnetta et al., 2013; Agnetta et al., 2015). In contrast, the feeding strategy of *A. lixula* results in a 'bulldozer' effect, clearing the forest around it while feeding on a diverse set of benthic organisms (Wangensteen et al., 2011; Bulleri, 2013). The upshot of these foraging differences is that *A. lixula* halos tended to be twice the size of *P. lividus* halos and were not significantly influenced by most factors examined here, probably due to their omnivorous nature. Thus, community composition may also strongly influence the grazing and extirpation rates of macroalgal forests in shallow coastal communities where sea urchins thrive (Agnetta et al., 2013; Agnetta et al., 2015).

While the species- and size-specific differences we found in production-consumption ratios are likely self-evident, this relationship also varied with other, subtler, context-specific factors across the Mediterranean Sea. Within MPAs with some level of fisheries management, halo sizes were generally smaller, indicating that exogenous biotic factors like fear can significantly reduce grazing impact. This adds to the now large body of evidence of the importance of securing higher trophic functions, since their contribution to ecosystem resilience goes beyond their purely trophic effects (Sala et al., 1998; Steneck et al., 2002; Babcock et al., 2010, Ling & Johnson, 2012). Given that not all the MPAs in this study have strong fishing restrictions in place, our results may even underestimate the effect of fear. However, we need to be careful about how universally we assume that fear of predators operates since its effects were only significant for *P. lividus*, indicating that different sea urchin species may perceive and respond to risk in different ways (Pagès et al., 2021). Species-specific traits related to morphology, may determine their differential resistance to predation and elicit different responses to predator presence (Guidetti & Mori, 2005; Hereu, 2005).

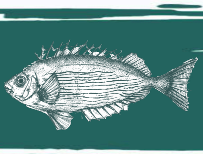
Nutrient rich areas of the Mediterranean also had smaller halos, given the higher algal production and lower sea urchin consumption rates in these waters, as has been demonstrated in other field and laboratory studies (Boada et al., 2017). Our analysis shows that other factors, such as the type of habitat, temperature and depth, can also influence grazing consumption ratios to differing degrees. While of less overall relevance, it is essential to consider them in any vulnerability assessment, since they may interact with other factors in ways that are not straightforward (Ling et al., 2009a; Conversi et al., 2015; Kriegisch et al., 2019). For instance, while deeper reefs are in general more prone to overgrazing as a result of reduced light penetration limiting algal production at depth, these deeper reefs may be protected from the more harmful *A. lixula* that is typically found in shallower reefs (Bulleri et al., 1999; Nikolaou et al., 2023). Similarly, although the largest halos were observed in habitats dominated by Fucales, turf grounds had a greater effect on the size of halos produced by *P. lividus* (see Appendix C: Table C5). This variation between raw field data and model estimates can be attributed to the virtual absence of larger-sized individuals at highly miniaturized turf grounds. Sea urchins in these habitats may be subject to higher levels of predator exposure or potential sedimentation impacts (Babcock et al., 2010; Kriegisch et al., 2019). Despite unbalanced data for some of our predictors (e.g., *A. lixula* halos on Fucales forests), these subtle but complex patterns highlight the value of using LMM models to integrate ecological responses mediated by a range of multiple interacting factors. Although they may be more difficult to interpret, they are much more representative of real-world systems, and avoid reductionistic assumptions of the relevance of single drivers (Bolker, 2008).

Nonetheless, the use of grazing halos has a few key assumptions and caveats. As mentioned before, we assume that the halos exist, on average, at a steady state, and are ‘fully formed’. Additionally, we assume that the sea urchin within each halo was solely responsible for its creation, and that it does the bulk of its feeding within these halos. Given what we know of sea urchin behaviour, these are simplifying but reasonable assumptions (Hereu, 2005; Ling & Johnson, 2012; Pessarrodona et al., 2019). The method cannot be used to quantitatively assess individual sea urchin effects in locations where they clump together to form combined halos or grazing fronts, since it is difficult in these circumstances to attribute grazing impacts to individual sea urchins. However, grazing halos are relatively common in most Mediterranean rocky reefs (Bulleri, 2013; Pessarrodona et al., 2019), providing a useful way to tease apart the relative importance of endogenous and exogenous factors that influence the relationship between production and grazing, and helping identify the relative vulnerability of macroalgal communities.

5.5. Conclusion

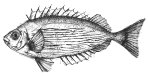
What do all these interactions mean for the vulnerability of vegetated ecosystems to overgrazing? The emphasis has long been on understanding herbivore population dynamics and their key drivers, intending to identify thresholds beyond which vegetated habitats exhibit catastrophic shifts to depauperate states devoid of vegetation (Steneck et al., 2002; Eklöf et al., 2008; Filbee-Dexter & Scheibling 2014; Ling et al., 2015). However, there are inherent difficulties in predicting and generalizing these ecosystem thresholds (e.g., see Conversi et al., 2015). Our study suggests that we need to shift our focus towards understanding the many context-specific interacting factors that influence plant-herbivore interactions, since these may provide better insights on the multiple underlying mechanisms of collapse. As our study shows, these interactions are often strongly influenced by the identity of the biotic agents involved and local environmental conditions like temperature, nutrients and/or predator presence, making predictions all the more complex (Boada et al., 2017; Pagès et al., 2018; Pessarrodona et al., 2019). To improve the robustness of our predictions at managerially meaningful scales, we need to move from measuring states to understanding interactions. The vulnerability of macrophyte ecosystems to collapse pivots on the strength of the production-consumption relationship. Understanding this interaction requires a deeper engagement with the many specific factors that influence it, and the local conditions that mediate it (Hereu et al., 2008; Boada et al., 2017; Pagès et al., 2018). When attempting to protect vegetated habitats from overgrazing, ecosystem managers need a bespoke, integrative approach suited to each region, community composition, and degree of protection. Ecosystems with similar biomasses of herbivores and macrophytes could exhibit markedly different vulnerabilities to catastrophic collapses, depending on local conditions (Ling et al., 2015). In general, nutrient enriched areas, with greater light availability, dominated by smaller herbivores of less impactful species and with a full complement of their predators, will be far more resilient to overgrazing events. Hence, in the current context of cumulative impacts resulting from global change, it becomes imperative to understand these context-specific differences to implement adequate management measures, whether they rely on securing trophic relationships, reducing anthropogenic pressures, controlling herbivore populations, or other forms of habitat management. Integrating universals with context specificity is critical, since real-world ecosystems dominated by vegetation are rarely, if ever, driven by a single controlling variable (Hereu et al., 2008; Conversi et al., 2015). Managing ecosystems requires us to engage meaningfully with this inherent complexity.

Chapter 6



Tropical range-extending herbivorous fishes shoal with native temperate species to gain foraging benefits

Minguito-Frutos, M., Buñuel, X., Marco-Méndez, C., Sanmartí, N., Skouradakis, G., Boada, J., Pagès, J. F., Alcoverro, T., & Arthur, R. Tropical range-extending herbivorous fishes shoal with native temperate species to gain foraging benefits. Under review in *Biological Invasions*.



Abstract

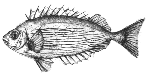
As temperate waters warm, species from tropical seas expand their ranges and colonize once inhospitable environments. This global process of tropicalization is creating novel species assemblages, where social species could gain significant benefits by allying with native temperate species in mixed-species groups. Social behaviours can influence herbivory dynamics in tropicalized communities, where the intrusion of tropical herbivores is exacerbating impacts on marine vegetation. The eastern Mediterranean Sea has witnessed widespread collapses of vegetated ecosystems since the arrival of tropical rabbitfishes *Siganus rivulatus* and *S. luridus*. As they have co-occurred for decades with the two native herbivores *Sarpa salpa* and *Sparisoma cretense*; here, we explored the association strength of these interactions and whether mixed-shoaling behaviours between native and range-extending fishes influenced foraging efficiency. We found 258 shoals, 76 (30%) composed exclusively of native species, 112 (43%) of rabbitfishes and 70 (27%) of species from both origins. Moreover, mixed-species shoals consisting solely of native species represent less than 3% of the total, while those of range-extending herbivores more than quadrupled these figures (14%). Pairwise association strengths indicated that *S. rivulatus* was the most gregarious species forming positive associations with *S. luridus* and *S. salpa*, whereas *S. cretense* was the least sociable species. Rabbitfishes, especially *S. rivulatus*, exhibited the largest bite rates, which increased with shoal size regardless of shoal type and suggesting greater foraging efficiency, since their bout rates remained unchanged. In contrast, *S. salpa* showed reduced foraging efficiencies only improving bite rates in large mono-specific shoals, and when bout rates were high. Bite rates of *S. cretense* were not affected by these variables. Range-extending rabbitfish have introduced mixed-species shoaling in the Mediterranean Sea. These novel social interactions resulted in asymmetric foraging benefits in favour of tropical herbivores, which, although highly specific, might shape herbivory pressures in tropicalized vegetated ecosystems.

Keywords: *range-extension, mixed-species foraging, species interactions, tropicalization, herbivory, rabbitfish.*

6.1. Introduction

Between a changing climate and free market-driven removal of (bio)geographical barriers, species are experiencing an unprecedented shift in their historical ranges (Pecl et al., 2017; Castellanos-Galindo et al., 2022). An upshot of this rapid global reshuffling is that species with no shared evolutionary history are being increasingly brought into contact with each other (Vergés et al., 2019). The resulting assemblages are entirely novel in their interactions, often causing larger impacts on natural communities than changing environmental conditions alone (Ockendon et al., 2014). These processes are of particular concern in the ocean, where, as seawater warms, marine species spread faster than terrestrial into once inhospitable environments (Poloczanska et al., 2013), giving rise to a tropicalization of temperate ecosystems around the world (Vergés et al., 2014a; Bennet et al., 2021; Zarzyczny et al., 2023). Much of the consequences of tropicalization depend on how native and range-extending species interact in these evolutionarily novel species encounters (Vergés et al., 2019; Stuart-Smith et al., 2021). It is likely that originating in more diverse and structurally complex habitats, tropical range-extending species have a wider behavioural repertoire that helps them occupy vacant ecological niches in temperate ecosystems with fewer biotic interactions (Steneck et al., 2017; Smith et al., 2018; Coni et al., 2022). However, range-extending species with similar functional niches to those found in temperate environments could also benefit from a preadaptation to their ecosystem functions (Miller et al., 2023).

Among range-extending species, gregarious species may be inherently better able to establish successfully in new locations (Holway & Suarez, 1999; Smith et al., 2018; Paijmans et al., 2020). By associating with native species, they could learn significantly through cultural transmission or imitation of the distribution and palatability of local resources (Brown & Laland, 2003). However, it is important to distinguish mere co-occurrence from mixed-species foraging (Blanchet et al., 2020). Foraging in mixed-species shoals is an interaction that can be mutually beneficial for all participating species either by reducing overall predation risk and vigilance

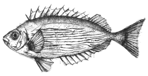


requirements, enhancing the probability of locating, capturing and collectively defending scarce resources, increasing swimming efficiency, etc. (Sridhar & Guttal, 2018; Paijmans et al., 2019). Nonetheless, it is important to distinguish whether these benefits accrue equally for all participants in mixed-species shoals (Paijmans et al., 2019). Certain species could potentially be more conspicuous to predators (Mathis & Chivers, 2003; Sridhar & Guttal, 2018), or when resources are scarce, species could be forced to compete for both food and space with more experienced or more efficient shoal participants (Krause & Ruxton, 2002; Coni et al., 2021). Hence, the ability to navigate these tradeoffs will vary with the species involved (see the findings of Paijmans et al., 2020 and Coni et al., 2021). What seems clear though, is that generalist strategies and plastic life history traits, in relation to both shoaling associations and foraging/feeding behaviours, may facilitate the expansion of range-extending species at its novel distribution edges (Smith et al., 2018; Monaco et al., 2020; Stuart-Smith et al., 2021; Coni et al., 2022).

How native and range-extending species interact in novel assemblages can have major impacts on the structuring and functioning of the temperate ecosystems they inhabit (Zarzyczny et al., 2023). The impacts of this wave of tropicalization can be particularly intense due to the spread of tropical herbivores (Vergés et al., 2014a), which often play strong top-down control on plant-dominated ecosystems (Poore et al., 2012; Bakker et al., 2016). Thus, herbivores are fundamental drivers of marine vegetation abundance, leading to substantial ecological changes, including regime shifts or functional extinctions in some extremes (Wernberg et al., 2016; Gangal et al., 2021). In fact, these tropical intruders have already driven catastrophic collapses of temperate macroalgal communities, producing massive reconfigurations in the structure and functioning of temperate reefs worldwide (Sala et al., 2011; Nakamura et al., 2013; Vergés et al., 2014b; Vergés et al., 2016). Hence, the arrival of range-extending species is expected to increase the richness, abundance, and functional diversity of herbivorous fish species (Zarco-Perello et al., 2020; Smith et al., 2021), exacerbating impacts on temperate primary producers (Vergés et al., 2014a;

Zarco-Perello et al., 2017) and, at some point, the competition for resources with temperate herbivores (Santana-Garcon et al., 2023).

With the opening of the Suez Canal in 1869, the Mediterranean Sea has witnessed a record number of incursions from the Red Sea and the Indian Ocean, with about 800-1000 Lessepsian species documented in its waters (Zenetos et al., 2022). This invasion, together with an unprecedented rise in the seawater temperature is accelerating the rate of successful establishment of range-extending species (Raitsos et al., 2010; Pisano et al., 2020; Zenetos et al., 2022). However, few range-extending species have been as successful as the two herbivorous rabbitfish, *Siganus rivulatus* (Forsskål, 1775) and *Siganus luridus* (Rüppell, 1828). First recorded in the eastern Mediterranean in Israel in 1924 (Steinitz, 1927), their arrival coincides with the loss of dense communities of canopy-forming macroalgae in favour of ecosystems dominated by thin turfs or bare rock (Sala et al., 2011; Vergés et al., 2014b; Nikolaou et al., 2023). Their success in Mediterranean rocky reefs has been attributed to several factors apart from warming seas (Giakoumi, 2014; Nikolaou et al., 2023). These factors include the significant ecophysiological and phenological plasticity of rabbitfish species (Hassan et al., 2003; Zarco-Perello et al., 2022), the virtual absence of large predators (Sala et al., 2012; Cramer et al., 2018), and the relative absence of herbivorous competitors. The Mediterranean has only two exclusively herbivorous fish species, the shoal-forming *Sarpa salpa* (Linnaeus, 1758) and the relatively solitary *Sparisoma cretense* (Linnaeus, 1758) (Verlaque, 1990; Bariche et al., 2004). Where these range-extending rabbitfish are present in the eastern Mediterranean, they are often observed co-occurring with native herbivores (see e.g., Santana-Garcon et al., 2023). Hence, here we tested if the potential association of rabbitfish with native temperate species can be an additional mechanism explaining their success and, eventually, the high herbivory pressure these Mediterranean rocky reefs experience (Nikolaou et al., 2023). Specifically, we hypothesize that tropical range-extending species, such as rabbitfish, may associate with native Mediterranean species to obtain larger foraging benefits in novel environments. By engaging in this associative foraging strategy, we expect an increase in shoal sizes and individual foraging



efficiency with potential consequences for native herbivorous fishes. We evaluated (i) the degree of association and mixed-shoaling behaviour between native and range-extending fishes where these four herbivores co-occur, and (ii) how different shoaling configurations based on species composition and size of the shoals influenced the foraging efficiency of native and range-extending species.

6.2. Materials and methods

6.2.1. Study area and design

Our study was conducted in the island of Crete (Greece), in the eastern Mediterranean basin, where two native species, the herbivorous bream, *S. salpa* and the parrotfish, *S. cretense* have co-occurred with the two range-extending rabbitfish, *S. rivulatus* and *S. luridus* for at least the last few decades (Stergiou, 1988; Magneville et al., 2022). Specifically, our study was designed to determine novel shoaling herbivore configurations in this tropicalizing transition zone, pairwise association strengths between native and range-extending species and to evaluate their effects on fish foraging activity. For this, we conducted in water fish surveys (see below for details on the different specific methodologies) around noon (between 11:00 am and 2:00 pm) to minimize the highly variant diurnal foraging activity of these species (Magneville et al., 2022). We selected seven locations (Agia Pelagia, Agios Ioannis, Vathi, Krassas, Elounda, Psaromoura, and Hersonissos) where herbivorous fish densities were high and all four species co-occur (see Fig. D1 in Appendix D for the map of the locations and data on species abundance). All surveys were carried out on snorkel in shallow rocky reefs (depth range 0 – 6 m). For further details on the study area and the abundance of herbivorous fish species, see Appendix D: Supplementary Text D3.

6.2.2. Determining shoaling configurations and species association strength

To quantify the occurrence of different shoaling configurations and the strength of species associations we collected data on the composition of independent shoals encountered in free swims (n = 258 shoals) distributed around the seven locations (see Fig. D1). Three observers conducted these surveys after inter-calibrating measurements to minimize variability. We sampled shoals opportunistically (the first observed regardless of size or composition) and each shoal was followed at a distance of a few meters until the fish were accustomed to the observer's presence. We recorded the species participating in every shoal and their abundance to determine the configuration of the encountered shoals and their strength of association.

6.2.3. Quantifying fish foraging activity as a function of shoal configuration

To determine if shoal size (i.e., number of fish individuals), shoal type (i.e., mono- or multi-specific), and/or fish individual length influenced fish foraging activity, we measured species-specific foraging activity (i.e., bite and bout rates) of focal herbivorous fish individuals in mono- or multi-specific groups (of all different combinations), along a gradient of shoal sizes. We recorded bite rates (bites min^{-1}) by visually counting the number of times the individual took distinct bites to the substrate within the observation period and bout rates (bouts min^{-1}) as the number of times the individual changed its spatial location between bites. To minimize ontogenetic effects (Buñuel et al., 2020), we followed individual fish larger than 10 cm in size within shoals of different types and sizes and observed their foraging activity for up to two minutes (Santana-Garcon et al., 2023). Observations included a 30-second acclimatization period for each sampled individual. Given the high rate of fissions and fusions in these mixed-species shoals, the average duration of our observations rarely exceeded one minute. We adjusted the time elapsed of our observations of mono-specific shoals to match that of multi-specific shoals. The observation was aborted if the fish showed evident responses to the observer or whether it changed its activity mode (e.g., from feeding to swimming) and was not recorded when its duration was less than or equal to 20 seconds. Thus, we measured the following parameters for every observation: (i) species identity of the focal individual; (ii) its length; (iii) the size of the shoal; (iv) the type of the shoal (mono- or multi-specific); and (v) the species present within the shoal. In total, we quantified the foraging activity of 294 focal individuals across all four species (*S. salpa*, n = 105; *S. luridus*, n = 56; *S. rivulatus*, n = 93; *S. cretense*, n = 40) in six of the seven shallow-water locations (we did not sample fish foraging activity in Agios Ioannis; Fig. D1).

6.2.4. Data Analysis

Shoaling configurations (species composition and size of the shoal)

We described shoaling configurations as the percent of fish groups according to their origins, including all the permutations of native and range-extending species (i.e., shoals of only native or range-extending, and shoals with species from both origins), concerning the total number of shoals found at the seven studied locations (n = 258 shoals, see above). These three shoaling configurations include data from mono- and multi-specific shoals. In addition, using a generalized linear mixed model (GLMM), we tested how the response variable 'Shoal size' varied among the different 'Shoal configurations' (fixed factor, three levels: native only, range-extending only, native and range-extending) and 'Shoal types' (fixed factor, two levels: mono- and multi-specific shoals). 'Location' was set as a random factor (seven levels). Thus, we fitted a GLMM with log-normal error structure after visually and statistically evaluating the fit of four likely distributions (gamma, log-normal, Weibull, and negative binomial) using the *fitdistrplus* R package (Delignette-Muller & Dutang, 2015) (see Table D2 in Appendix D: Section D2). To proceed with model selection, we followed an iterative stepwise procedure, starting with the response variable and the fixed and random predictor variables and selecting the model with the lowest AIC (Zuur et al., 2009). However, following Zuur et al. (2013), after considering log-likelihood ratio tests (LRTs) and AIC outputs, we dropped the 'Location' variable, as it accounted for a very small amount of the total variation of the model (estimate ± sd = 0.009 ± 0.097) and did not meet model assumptions. We then repeated the fitting process and selected the final (G)LM model (i.e., gaussian distribution) explaining 'Shoal size' as a function of 'Shoal configuration' (see Table D2).

Species association strength

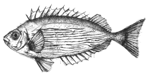
Pairwise species association strengths were evaluated based on species co-occurrence in shoals. All independent observations of shoals across all locations (n = 258 shoals, see above) were compiled in a presence-absence matrix with species in rows and shoals in columns. We used a randomization procedure using the *EcoSimR* R package (Gotelli et al., 2015) to generate 1000 null matrices from our observed matrix, maintaining row totals (species richness remains unchanged) and shuffling column totals (see Sridhar et al., 2012). This allowed us to test observed co-occurrences against expectations by chance alone. We then calculated an index of pairwise species association strengths (α) using the probabilistic formula:

$$\alpha = \frac{O - \mu}{\sigma},$$

where O is the number of species co-occurrences in our observed dataset, μ is the average of co-occurrences of that species pair in 1000 null matrices and σ is the standard deviation of the number of co-occurrences across the 1000 null matrices. α is a dimensionless index, where positive values indicate a stronger than expected co-occurrence (i.e., association), negative values indicate avoidance and zero indicates neutral or no interaction.

Fish foraging activity

We use generalized linear mixed models (GLMMs with gamma error structure) to assess individual fish foraging activities, that is, bite rates (bites per fish min^{-1}) and bout rates (bouts per fish min^{-1}), as a function of the fixed predictor variables ‘Species identity’ (*S. salpa*, *S. cretense*, *S. luridus*, and *S. rivulatus*), ‘Shoal type’ (mono- and multi-specific shoals), ‘Shoal size’, and ‘Individual length’ (n = 294; see Table S2). We also included bout rates as a fixed predictor in the models explaining bite rates. Although ‘Location’ was included as a random variable in these models, we dropped it following the above-mentioned criteria, as it accounted for a small amount of the total variance of the model of bite rates (estimate ± sd = 0.0058 ± 0.076). After fitting a general model to evaluate bite rates for all the species together and given the



significance of species identity in that model, we fitted a series of GLM models for each species separately.

All analyses were performed using the R language for statistical computing (R Core Team, 2023). We removed a few outliers (n = 6) of shoals greater than > 50 individuals from our dataset since it was difficult to get accurate measures of shoal size. We visually and statistically checked the assumptions of all GLMs (gaussian and gamma distributions) using the *performance* (Lüdecke et al., 2021) and *DHARMa* (Hartig, 2022) R packages, and plotted model outcomes using the estimates and 95% confidence intervals predicted by the R package *effects* (Fox & Weisberg, 2018).

6.3. Results

6.3.1. Novel shoaling configuration

We encountered a total of 258 shoals of fish herbivore species across the seven locations; 76 were composed only of native species (30% of observations), 112 consisted exclusively of range-extending species (43%) and 70 of species from both origins (27%) (Fig. 6.1). Native species formed multi-specific shoals with each other in less than 3% of all our observations, while range-extending rabbitfishes more than quadrupled this proportion (14%). Shoals consisting solely of native Mediterranean species (either in mono- or multi-specific groups) were smaller compared to shoals of range-extending species or shoals formed by native and tropical species ($P < 0.001$; Appendix D: Table D3; Fig. 6.1).

6.3.2. Species association strength

S. rivulatus was the most gregarious of all species (see Table 6.1), forming positive associations with the range-extending *S. luridus* ($\alpha = 1.52$) and the native *S. salpa* ($\alpha = 1.05$), and relatively neutral associations with the native *S. cretense* ($\alpha = -0.10$). In contrast, the rest of the herbivorous fish assemblage showed weak association values, with the native species *S. salpa* and *S. cretense* tending to avoid each other ($\alpha = -0.93$), as well as the range-extending *S. luridus* ($\alpha = -0.84$, $\alpha = -0.75$; respectively).

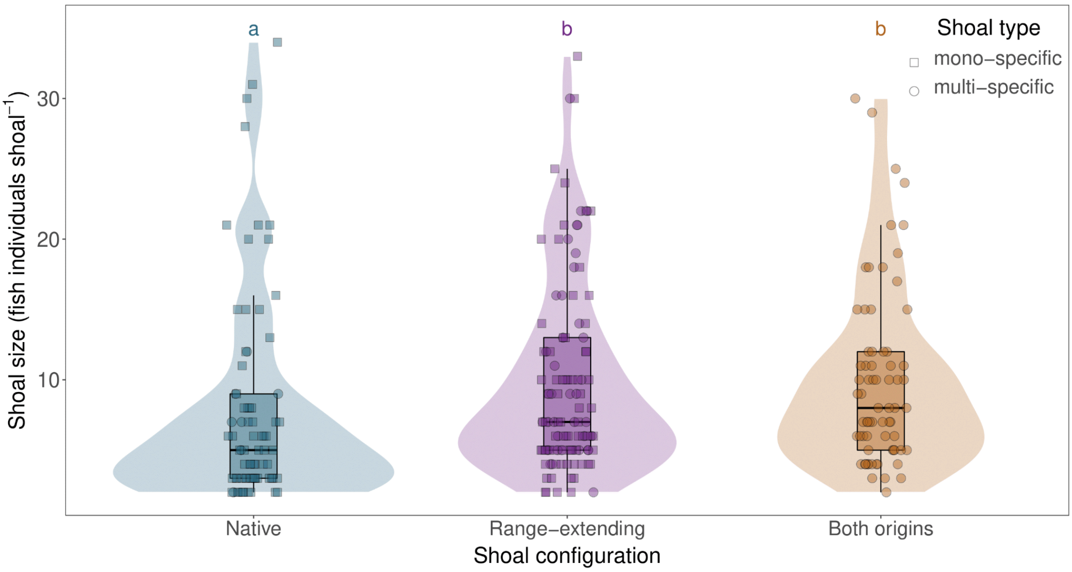


Figure 6.1. Relationship between the type of configuration and size of herbivorous fish shoals in Cretan rocky reefs. Shoal configurations refer to native Mediterranean species (*S. salpa* and *S. cretense*) in blue, range-extending rabbitfish (*S. luridus* and *S. rivulatus*) in purple, and species of both origins in brown. Squares and circles represent mono- and multi-specific shoals, respectively. Results of the Tukey test are shown with letters.

Table 6.1. Pairwise association strengths based on the co-occurrence matrix of shoals observed in the field. Positive values denote a higher degree of observed co-occurrences than expected by chance (i.e., positive association), while negative values point to avoidance.

	Sparisoma cretense	***Siganus luridus***	***Siganus rivulatus***
Siganus luridus	-0.75		
Siganus rivulatus	-0.10	1.52	
Sarpa salpa	-0.93	-0.84	1.05

6.3.3. Fish foraging activity

While bite rates varied strongly between herbivorous fishes ($P < 0.001$; Appendix D: Table D4; Fig. 6.2a), bout rates showed no relationship with species identity (Table D4; Fig. 6.2b). *S. rivulatus* had, in general, higher bite rates (mean + se = 36.01 ± 1.65 bites per min^{-1}) than all other species (mean + se = 27.29 ± 1.94, 21.47 ± 1.14 and 17.85 ± 1.06 bites per min^{-1} for *S. luridus*, *S. salpa*, and *S. cretense*, respectively) (Appendix D: Table D5; Fig. 6.2a). Bite rates of *S. luridus* were also significantly different from those of native species (Table D5; Fig. 6.2a).

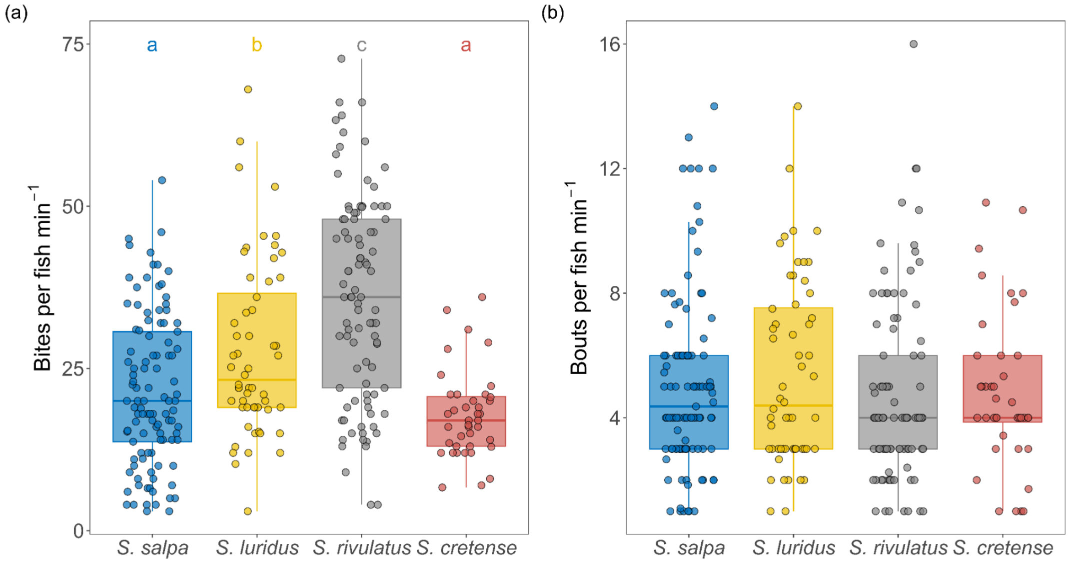


Figure 6.2. Relationship between fish foraging activity, that is, (a) bite rates (bites per fish min^{-1}) and (b) bout rates (bouts per fish min^{-1}); and species identity. Circles represent field observations of bite and bout rates per fish individual measured of each herbivorous species. (a) results of Tukey test are shown with letters; (b) no significant effect of species on bout rates was found.

Although, in general, bite and bout rates had a positive relationship with shoal size (*P* = 0.003; *P* = 0.012; respectively, see Table D4), it only positively influenced the bite rates of range-extending herbivores independently of shoal configurations (*S. rivulatus*, *P* < 0.001; and *S. luridus*, *P* = 0.049; Appendix D: Table D6; Fig. 6.3). However, there was an interactive effect between shoal size and shoal type on the bite rates of the native *S. salpa*. In multi-specific shoals (most of them with species of tropical origin), *S. salpa's* feeding activity did not increase with the size of the shoal compared to when shoaling in mono-specific groups (*P* = 0.041; Table D6; Fig. 6.3). The other species were indifferent to whether they shoaled mono-specifically or in multi-specific shoals (*S. rivulatus*, *P* = 0. 609; *S. cretense, P* = 0.614; no data presented for *S. luridus* as very few cases were observed in mono-specific shoals; Table D6). For *S. cretense* no effect of shoal size was observed on bite rates (*P* = 0.876; Table D6; Fig. 6.3). Although, overall, bite rates increased with bout rates (*P* < 0.001; Table D4), we only found strong evidence of this effect for *S. salpa* (*P* < 0.001; Table D6) and little or no effect for other species (Table D6; Fig. 6.4). Finally, despite bite rates decreased in general with fish individual length (*P* < 0.001; Table D4), only our species-specific model for *S. rivulatus* showed very strong evidence of this effect (*P* < 0.001) and no other effect was found for the rest of the herbivores (Table D6).

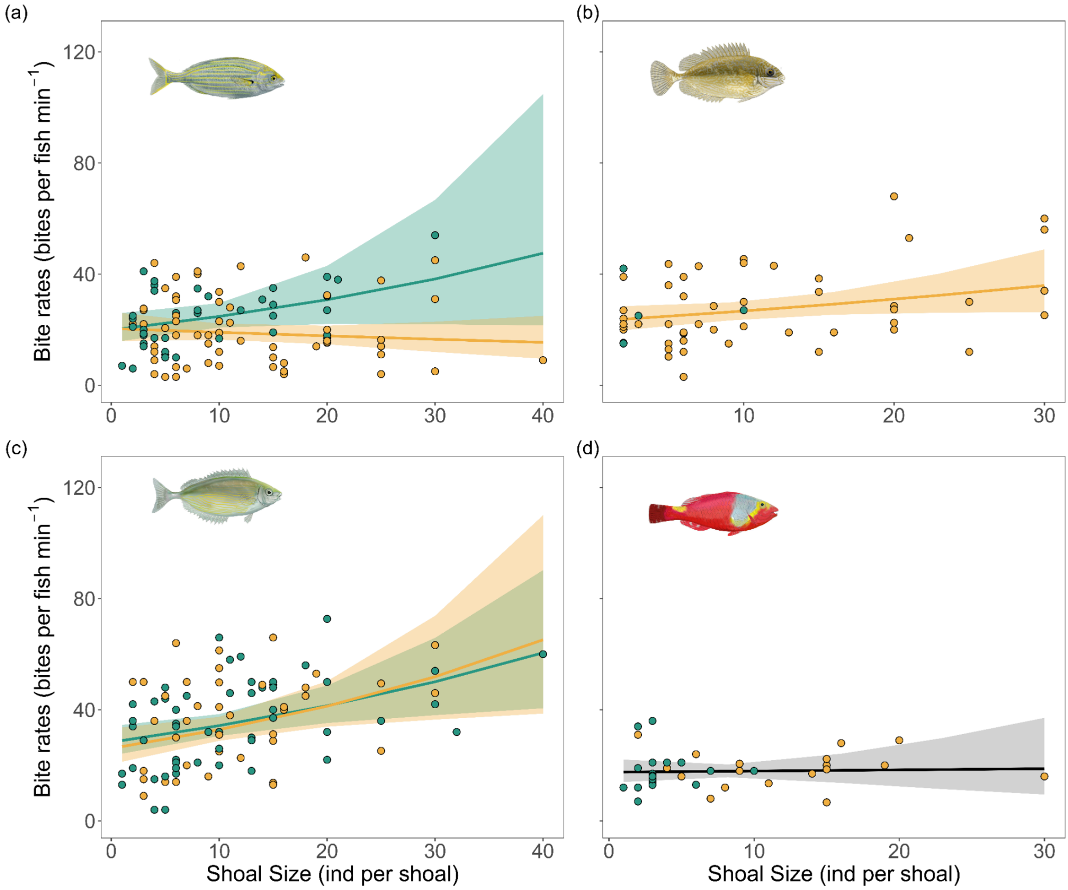


Figure 6.3. Relationships between bite rates (bites per fish min^{-1}) and shoal type, along a gradient of shoal size for: (a) *S. salpa*, (b) *S. luridus*, (c) *S. rivulatus* and (d) *S. cretense*. Circles represent field collected data (mono- and multi-specific shoals in green and yellow, respectively) and they are shown with fitted GLM (gamma distribution) smooths and 95% confidence intervals. Unlike colored smooths, gray ones represent no statistical relationship between these variables.

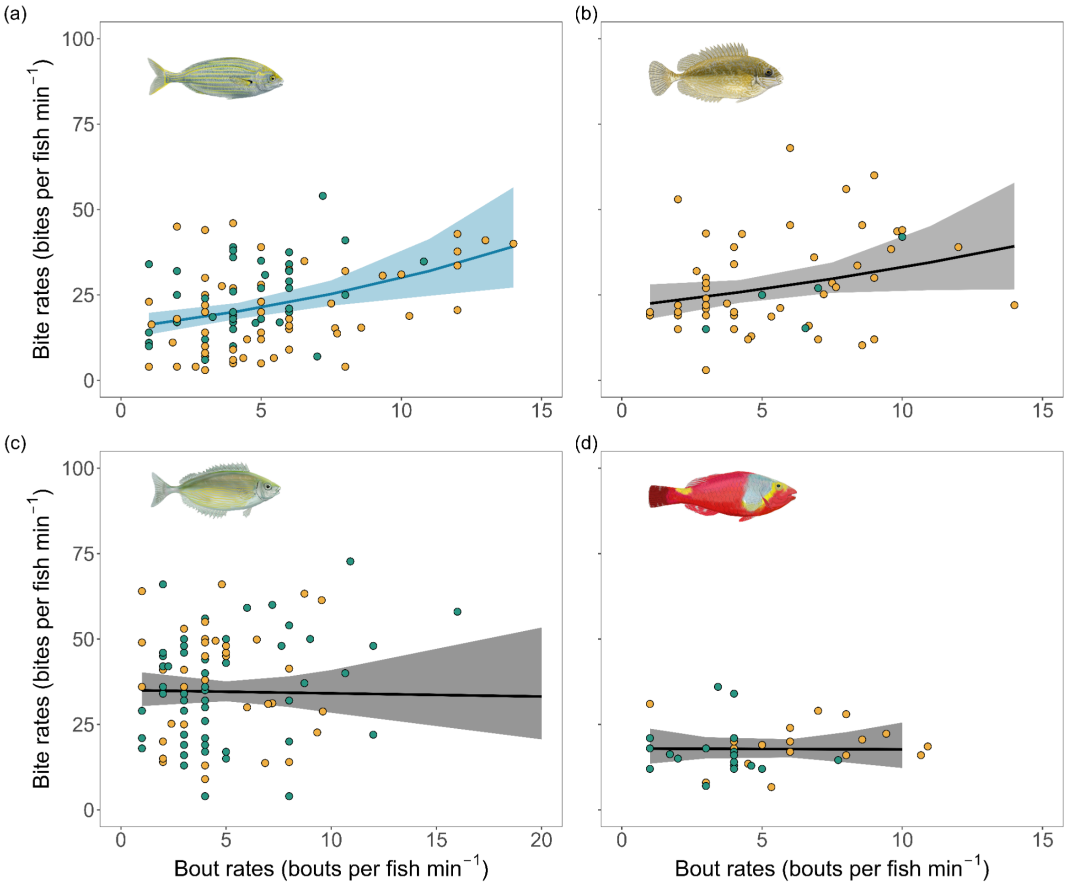
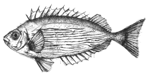


Figure 6.4. Relationships between bite rates (bites per fish min^{-1}) and bouts rates (bouts per fish min^{-1}) for: (a) *S. salpa*; (b) *S. luridus*; (c) *S. rivulatus*; and (d) *S. cretense*. Circles represent field collected data (mono- and multi-specific shoals in green and yellow, respectively) and they are shown with fitted GLM (gamma distribution) smooths and 95% confidence intervals. Blue and gray smooths represent a significant and non- significant relationship, respectively, between these variables.

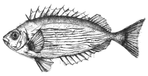


6.4. Discussion

The novel assemblages of tropicalized seas force unfamiliar species to interact. The outcomes of these evolutionarily novel interactions could influence the success of range-extending species in temperate ecosystems worldwide, with attendant consequences for their native communities (Vergés et al., 2014a, Zarzyczny et al., 2023). This study shows that range-extending species (i.e., *S. rivulatus* and *S. luridus*) benefited from facilitative associations with native herbivores (i.e., *S. salpa* and *S. cretense*) by foraging collectively in mixed-species shoals. In the tropicalized reefs of Crete, multi-specific shoals involving rabbitfishes were relatively common, either formed just by range-extending species (14% of all shoals observed in this study) or by fishes from both origins (27%). Native species, in clear contrast, were hardly observed forming mixed-species shoals among them (less than 3% of our observations). Our results suggest that rabbitfish have introduced a novel function in the Mediterranean Sea: mixed-species shoaling. This generalist shoaling strategy allowed tropical rabbitfishes to enlarge their shoal sizes and increase their feeding activity (i.e., bite rates), resulting in improved foraging efficiencies. While *S. rivulatus* formed positive or neutral associations with all other species and *S. luridus* preferred to associate with its congener to obtain similar foraging benefits, mixed-species shoaling did not confer such benefits to native species. *S. salpa*, the most widespread herbivorous fish in the Mediterranean, showed lower bite rates which, moreover, did not increase with shoal size when foraging in mixed-species shoals. Therefore, *S. salpa* only improved their bite rates when shoaling with conspecifics and when their bout rates were high. These results suggest lower foraging efficiencies of *S. salpa*, regardless of the close shoaling association formed with *S. rivulatus*. Meanwhile, the native parrotfish *S. cretense* did not change its foraging activity when shoaling in mono- or multi-specific groups, reinforcing its largely unsocial behaviour. Altogether, our results emphasize that shoaling strategies are highly species-specific and depend on the species origin (i.e., native Mediterranean vs. tropical), leading to asymmetric foraging benefits in favour of tropical rabbitfishes.

6.4.1. Mixed-species shoaling in the eastern Mediterranean Sea

Mixed-species foraging is behaviourally complex, requiring accurate information-sharing between species to coordinate the formation of shoals, determine their movement patterns, identify feeding areas, and respond effectively to perceived threats (Sridhar & Guttal, 2018; Paijmans et al., 2019). In this study, we found that rabbitfishes tended to associate more and form larger groups when shoaling with others, compared to native Mediterranean herbivorous fishes. Mixed-shoaling strategies were virtually absent in the Mediterranean prior to the arrival of tropical rabbitfish, where their two only native herbivores fishes rarely interact. The shoaling associative interaction between rabbitfishes and the ubiquitous Mediterranean species *S. salpa* appears to be particularly intense and may be highly linked to morphological similarity (Azzurro et al., 2014). These species are well matched in shape, size, colour, swimming style, and other life history features, which might help them override potential “oddity effects” (Mathis & Chivers, 2003). In addition, tropical rabbitfish species seem to inherently have the experiential competence required to forage in mixed-species groups, likely mediated by their evolutive origins in ecosystems with higher richness and functional diversity of herbivorous fishes (Vergés et al., 2014a; Steneck et al., 2017; Zarzyczny et al., 2023). Indeed, in the Red Sea, where both rabbitfish originate, they represent less than two percent of the total abundance of coral reef herbivores (Bouchon-Navarro & Harmelin-Vivien, 1981; Giakoumi, 2014). In sharp contrast, the shoal-forming bream *S. salpa* (Buñuel et al., 2020) may be at an evolutive disadvantage here since it has been the only dominant herbivore fish throughout the entire Mediterranean basin (Verlaque, 1990; Bariche et al., 2004). Hence, having evolved in a more functionally redundant environment, rabbitfish may be better equipped in terms of behaviour to interact with unfamiliar species in their adoptive communities (Steneck et al., 2017; Zarzyczny et al., 2023). In a similar vein, *S. cretense*, the only native parrotfish in the Mediterranean, emerged as the least sociable species within the herbivore assemblage, foraging in small mono-specific groups or as a sub-dominant member of large multi-specific shoals. *S.*



cretense occupies a slightly separate feeding niche, with a beak-like jaw modified to scrape coralline algae and turfs (Azzurro et al., 2007), which makes it the least morphologically similar species, likely contributing to its lower association strength with others (Azzurro et al., 2014; Paijmans et al., 2019). The morphological and functional distinctiveness, along with the unsocial behaviour of this native parrotfish might help explain, at least in part, why many shoaling tropical species with few similar native counterparts to associate with (like the parrotfish *Scarus ghobban* or several acanthurids), have not become abundant unlike rabbitfishes (Azzurro et al., 2014; Smith et al., 2018; Miller et al., 2023). In fact, despite range-extending species are growing from a trickle to a stream with tropicalization, not all establish successfully, and even fewer become abundant (Sakai et al., 2001; Azzurro et al., 2014).

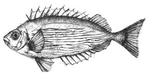
6.4.2. Asymmetric foraging benefits resulting from mixed-species shoaling

Social species can profit from group-living strategies and facilitative associations with others they encounter by foraging collectively in mixed-species groups (Sridhar & Guttal, 2018; Paijmans et al., 2019). Our study revealed that the feeding activity of all herbivore species, here reported as bite rates, scaled with group size when shoaling in mono-specific groups, except for *S. cretense*. Interestingly, rabbitfish species foraging in multi-specific groups also increased their feeding activity with shoal size. This mixed-species foraging is known to help species bulk up shoal sizes or gain social cohesion, reaping the benefits of feeding in larger groups (Smith et al., 2018; Coni et al., 2022). However, *S. salpa* exhibited a clear contrasting pattern. Despite increasing numbers in multi-specific shoals or standing as the most abundant species within many shoals (see Fig. D3), it did not improve its feeding activity when foraging with others. Why *S. salpa* continues to associate with *S. rivulatus* has not been evaluated here but may be potentially due to non-foraging benefits of mixed-species shoaling, including increased joint vigilance or predator confusion, among other factors (Paijmans et al., 2019). Alternatively, given the high densities of *S. rivulatus* across

Cretan waters (see Appendix D: Section D1), *S. salpa* may have had little choice. Our results point to this interaction as a one-way relationship, with *S. rivulatus* seeking out *S. salpa* shoals, which the latter endures because the costs of avoidance (e.g., relinquishing feeding grounds) may be considerably greater than shoaling together. Eventually, although range-extending species could be unfamiliar with resources and predators in their new environments, those exhibiting more generalist (behavioural) strategies can benefit from previously unoccupied functional niches (Monaco et al., 2020; Stuart-Smith et al., 2021; Coni et al., 2022). In contrast, native temperate herbivores, less diverse and specialized than their tropical counterparts, may be limited in their range of ecological functions as biotic interactors (Vergés et al., 2014b; Zarco-Perello et al., 2020; Zarzyczny et al., 2023). In fact, a large part of the unprecedented success of rabbitfishes (in the Mediterranean as in other temperate areas) lies in their natural history and specific traits, including their highly plastic ecophysiology that allows them to settle in such increasingly hospitable environments and their generalist foraging and behavioural strategies (Hassan et al., 2003; Vergés et al., 2014b; Zarco-Perello et al., 2022). This behavioural plasticity, common in rabbitfish and other successful range-extending species, helps explain the asymmetry found in shoaling interactions and foraging benefits between temperate and tropical herbivorous species (Zarco-Perello et al., 2017; Smith et al., 2018).

6.5. Conclusion

How much range-extending herbivorous species succeed and whether they prevail as dominant on their novel assemblages will largely depend on species-specific traits, ecosystem compositions, and the ecological context of each tropicalized environment (Azzurro et al., 2014; Zarzyczny et al., 2023). The success of range-extending species appears to have much to do with generalist social behaviours, which help tropical fishes improve their foraging and feeding strategies in temperate environments (Monaco et al., 2020; Stuart-Smith et al., 2021; Coni et al., 2022). In the tropicalized rocky reefs of the eastern Mediterranean Sea, rabbitfish species showed a greater ability to forage in mixed-species shoals compared to native herbivores. This



behavioural generalism might help explain the overwhelming herbivory pressures experienced by macrophyte communities in this transitional area since the arrival of these voracious herbivores (Sala et al., 2011; Vergés et al., 2014b). While the functional consequences of these novel herbivore interactions are quickly redefining normality in the world's most invaded sea, the intrusion of tropical species is drastically influencing herbivory dynamics across temperate communities globally (Vergés et al., 2014a; Zarco-Perello et al., 2020). This new normality in temperate environments is seriously jeopardizing ecosystem functioning and services provided by marine vegetated habitats and will have severe socio-economic repercussions for these regions (Vergés et al., 2019; Zarzyczny et al., 2023).

7. General discussion

Marine macrophyte-dominated habitats are among the world's most threatened ecosystems due to unprecedented anthropogenic pressures that drive global change (Unsworth et al., 2015; Filbee-Dexter & Wernberg, 2018; Wernberg et al., 2023; Zarzyczny et al., 2023). These ecosystems are approaching dangerous tipping points, challenging the scientific community to more fully understand their tolerance limits (see, for example, Armstrong McKay et al., 2022). A better understanding of the mechanisms and processes triggering these undesired shifts could provide ecosystem managers with crucial information to act before these changes cascade beyond control. Although the imprint of global change extends across continents and ecosystems, its impacts and responses vary vastly with the local ecological context (Strain et al., 2014; Krumhansl et al., 2016; de los Santos et al., 2019; Dunic et al., 2021). In this thesis, I have explored these context-specific conditions in benthic ecosystems dominated by marine vegetation and unpacked some of the underlying mechanisms that control their responses.

I addressed some of the principal pressures posed by global change that marine macrophyte-dominated ecosystems face today (Wernberg et al., 2023). These anthropogenic stressors include the degradation of water quality that affects light penetration; sea urchin overgrazing dynamics as a result of human-induced alterations in abiotic and biotic factors (e.g., overfishing, nutrient enrichments, rising temperatures, etc.) that shape ecological contexts; and the novel interactions among herbivorous fishes as a result of range-extensions driven by tropicalization. This research identified some of the essential ecological mechanisms severely altering the functioning of marine vegetated ecosystems under varying scenarios of anthropogenic stress, with a special focus on the Mediterranean Sea. Using a diversity of approaches, this thesis (i) synthesized some of the linear and nonlinear mechanistic responses that shape the tolerance of seagrass species to light limitation, (ii) the influence of ecological contexts on the vulnerability of macroalgal forests against herbivory, and (iii) the ability of novel tropical fish herbivores to associate with Mediterranean native species (Fig 7.1). The findings of this thesis reveal significant variations in species responses, contingent upon their identity and often associated with species traits (i.e., physiological, morphological, structural, behavioural, etc.), their interactions with others, and the broader ecosystem context in which these species thrive. These results contribute to establishing more accurate and context-specific baseline management strategies in response to global anthropogenic pressures. In the subsequent general discussion, I aim to synthesize my key findings and implications from the chapters of this thesis, encompassing:

i. The species-specific tolerance of seagrasses to light limitation and its influence on their resilience.

ii. The importance of ecological contexts to understand the vulnerability of vegetated ecosystems to overgrazing.

iii. The drivers of tropicalization in Mediterranean herbivore assemblages within ecosystems dominated by marine vegetation.

iv. Future directions.

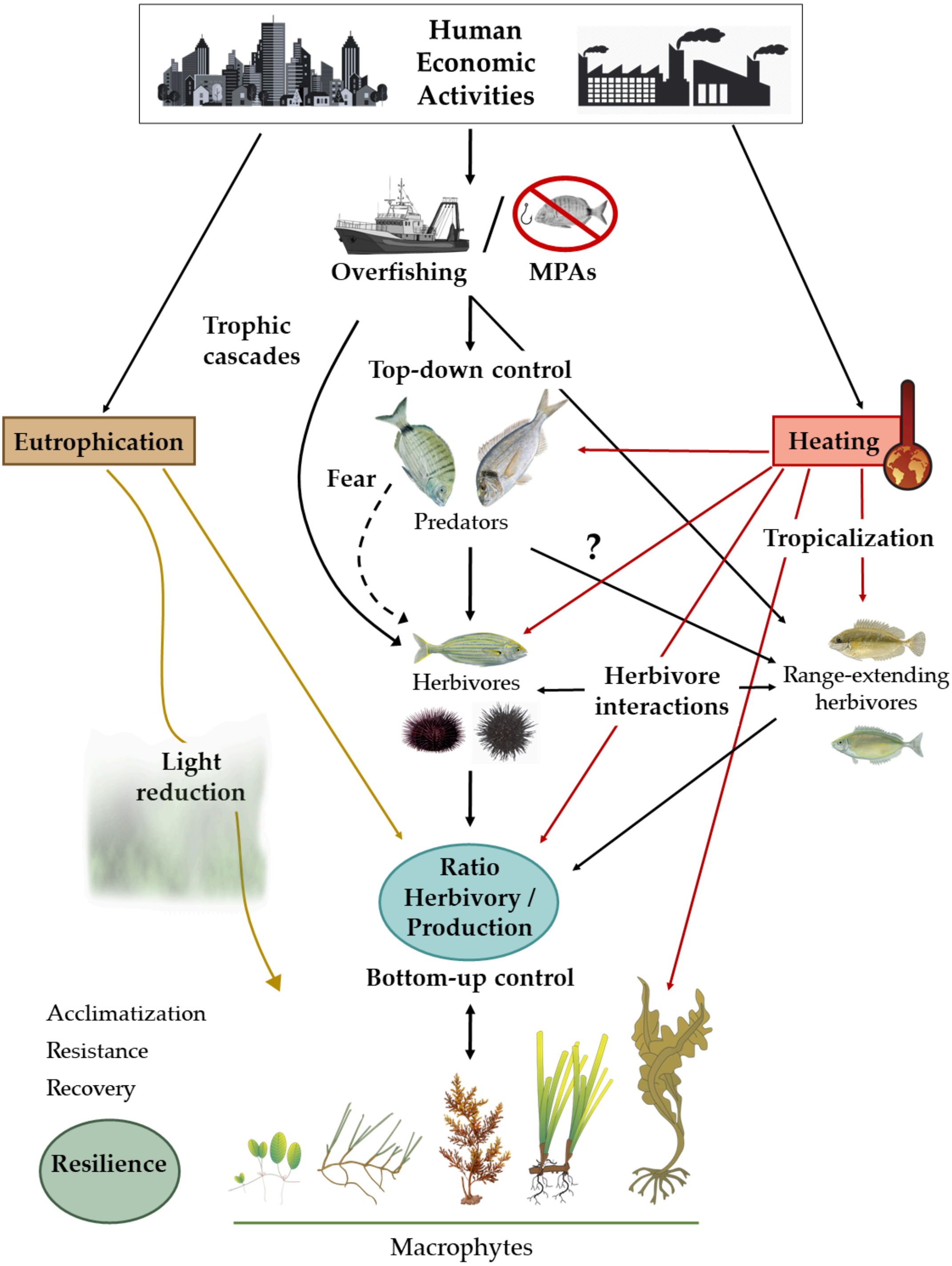

Human
Economic
Activities
Overfishing
MPAs
Trophic
cascades
Top-down control
Eutrophication
Heating
Fear
Predators
?
Tropicalization
Herbivores
Herbivore
interactions
Range-extending
herbivores
Light
reduction
Ratio
Herbivory /
Production
Bottom-up control
Acclimatization
Resistance
Recovery
Resilience
Macrophytes

Figure 7.1. Global change stressors affecting macrophyte ecosystems investigated in this thesis. Human activities drive the processes of eutrophication, overfishing, and anthropogenic heating, while ecosystem management can help reverse some of these effects. These interventions cascade through trophic webs and influence top-down and bottom-up control. Eutrophication affects light penetration through the water column causing species-specific effects on the resilience of marine macrophytes. While light limitation can reduce productivity, nutrient enrichments can stimulate primary production. Anthropogenic heating drives the range-extension of tropical herbivores within temperate ecosystems resulting in novel herbivore interactions which could intensify macrophyte consumption. Overfishing directly reduces predator populations and indirectly reduces fear triggering trophic cascades that allows herbivores to feed uncontrolled on marine vegetation. In contrast, MPAs can alleviate these detrimental effects on marine vegetated habitats. These factors together influence the ratio between primary production and herbivore consumption, which is a vital indicator of macrophyte ecosystem resilience.

7.1. Species-specific responses of seagrasses to light limitation

Light is one of the main factors driving the growth and distribution of marine macrophytes in shallow benthic ecosystems (Dennison, 1987; Duarte, 1991; Krause-Jensen et al., 2007). How macrophytes cope with light reduction is highly species-specific, driven by inherent life history traits, which determine the minimum light requirements (MLR) for each species and, in turn, establish their specific depth limits (Dennison et al., 1993; Lee et al., 2007; Park et al., 2021; Sant & Ballesteros 2021). Results in **Chapters 3** and **4** of this thesis show that MLR and, eventually, the vertical distributions of seagrasses largely depend on species-specific physiological, morphological, and structural traits related to their acclimatization potential. As a direct consequence, not all species colonize identical depth ranges, nor are equally susceptible to human-induced degradation of water transparency. Indeed, it is likely that these specific traits have facilitated the natural colonization of diverse depth ranges by seagrasses, with species that inhabit narrower and shallower ranges (i.e., species with stricter light requirements) being particularly vulnerable to light limitation. Given that the 72 species of seagrasses included within the order Alismatales (Short et al., 2011) exhibit a heterogeneous array of strategies for coping with disturbances (Kilminster et al., 2015; Unsworth et al., 2015), I focused on this group of macrophytes to unravel which specific set of traits, at different scales, most strongly mediate their capacity to acclimatize and persist in light-deprived waters (**Chapters 3** and **4**).

In **Chapter 3**, I provided evidence of how species-specific physiological photo-acclimatization strategies can significantly modify seagrass resistance to light deprivation and thus contribute to reducing their MLR. Our results demonstrate that the nonlinear acclimatization pattern of photosynthesis-irradiance (*P-I*) parameters (i.e., P_{max}, R, and I_k) of the seagrass *Cymodocea nodosa* approximately halved its MLR compared to a non-acclimatization strategy. This capacity of *C. nodosa* to enhance its light use efficiency and boost its carbon balance relied, in part, on its ability to decrease I_k, regardless of the decline in maximum photosynthesis (Olivé et al., 2013; Silva et al., 2013). However, the physiological photo-acclimatization capacity of *C. nodosa* extends beyond the reduction of I_k. By reducing its above-ground respiration rates (R), this species can further decrease its MLR in response to declines in light availability, which is consistent with prior ecophysiological studies conducted on other species (Fourqurean & Zieman, 1991; Masini et al., 1995). Notably, I demonstrate in **Chapter 4** that these findings related to the ecophysiological strategy of *C. nodosa* exhibit remarkable qualitative consistency when extrapolated to a broader spectrum of seagrass species (13 species studied, comprising approximately 18% of seagrasses). Seagrass species with a greater physiological photo-acclimatization capacity, indicated by the reduction in saturation irradiance (I_k or E_k), tend to colonize greater depth ranges. Altogether, the additive effects of these physiological mechanisms give *C. nodosa*, as well as many other seagrass species, an increased ability to photo-acclimatize, which enhances its resistance against light deprivation. In line with the fact that physiological photo-acclimatization is the first resistance mechanism of seagrasses against light limitation (Waycott et al., 2005;

Collier et al., 2012; Marín-Guirao et al., 2022), the findings in this thesis suggest that seagrasses with larger capacities to photo-acclimatize, pre-adapted to thrive across larger depth ranges (i.e., low-light environments in deep waters), will exhibit a higher tolerance to the on-going global declines in water quality and transparency. Nevertheless, species with larger acclimatization capacities also occupy larger ranges and, as a result, can potentially lose more extensive areas.

Chapters 3 and **4** highlight the importance of recognizing the co-occurrence of diverse photo-acclimatization mechanisms to cope with low-light conditions and explore how they contribute to explaining maximum seagrass vertical distributions worldwide. Although physiological photo-acclimatization emerged as a fast-response mechanism to acclimatize to light reduction (**Chapters 3** and **4**), we have found that photo-acclimatization strategies based on morphological or structural mechanisms also play a fundamental role for survival in low-light environments (**Chapter 4**). In this latter study, other acclimatization mechanisms mostly linked to the alteration in the number of leaves per shoot and above-ground biomass were identified as essential parameters to predict species' acclimatization abilities to cope with light reduction at depth. While physiological photo-acclimatization strategies contribute to harvesting light more efficiently under conditions of light limitation (e.g., Silva et al., 2013), morphological and structural photo-acclimatization appear to cumulatively contribute to macrophyte persistence in impoverished light environments. Above-ground biomass reduction facilitates light penetration through the canopy by employing so-called "canopy-opening" strategies that mitigate self-shading effects and by increasing light capture through the loss of less viable shoots, which subsequently helps alleviate seagrass mortality rates (Alcoverro et al., 1999; Ruiz & Romero, 2001; Enríquez et al., 2019). This reduction in the number of leaves per shoot also diminishes the excessive costs of leaf respiration, promoting the loss of older, less photosynthetically efficient seagrass leaves (Alcoverro et al., 1998; Mackey et al., 2007; Collier et al., 2012). What emerges from this thesis is that the ability of certain seagrass species (e.g., *Posidonia oceanica*, *Halophila stipulcaea*, *Cymodocea nodosa*, *Amphibolis grifithii*) to colonize deeper areas is conferred not by a single adaptive strategy but by a combination of species-specific physiological, morphological, and/or structural mechanisms. Indeed, these analyses revealed that specific vulnerabilities to light limitation are not linked (as previously thought) to simple indicators such as seagrass size or to functional groups enveloping seagrasses as a function of their strategies to face disturbances (Kilminster et al., 2015; Unsworth et al., 2015).

The results obtained through **Chapters 3** and **4** of this thesis, highlight the role of key macrophyte traits (including physiological, morphological, and structural traits) as proxies explaining their relative resistance capacity in the face of light reduction in coastal ecosystems worldwide (Orth et al., 2006; Waycott et al., 2009; Unsworth et al., 2015). While the loss of vast meadows may be detectable in shallower waters, seagrass losses in deeper waters could be more challenging to ascertain (Short & Neckles, 1999). These losses could result in the depletion of intangible natural resources and their associated biodiversity but also in a deficit of highly-valuable ecosystem services (Fourqurean et al., 2012; Unsworth et al., 2019).

7.2. Resilience of marine vegetation to light limitation

Anthropogenic pressures are pushing seagrasses and marine macroalgae to their resistance limits (O'Brien et al., 2018; Wernberg et al., 2023). Model outcomes in **Chapter 3** describe how, as the gradient of available benthic light declines, the maximum levels of a healthy vegetated seagrass state slowly diminish up to a threshold where the available light is not enough to achieve a positive carbon balance. This type of nonlinear behaviour means that the degradation of the vegetated ecosystem state often remains hidden from managers and researchers, and once such thresholds are exceeded, ecosystems abruptly shift to unvegetated states that are poorer in structure, functioning, and services (Fourqurean et al., 2012; Bennet et al., 2016; Unsworth et al., 2019). However, the reduction observed in *C. nodosa's* MLR, which directly results from its photo-acclimatization strategy, indicates that the larger the acclimatization in *P-I* parameters, the higher the likelihood of macrophytes returning to their optimal state. The mathematical approaches I used in **Chapter 3** helped demonstrate that physiological photo-acclimatization not only increases resistance (i.e., the reduction in MLR) but can also improve *C. nodosa*'s overall resilience (i.e., increases the basin of attraction of the vegetated state; sensu Scheffer et al., 2001) (Fig. 4.3). Species that have these enhanced photo-acclimatization strategies show greater resilience to light deprivation events compared to those that are less flexible in the acclimatization of their *P-I* parameters.

Despite the nonlinear photo-acclimatization response of *C. nodosa* to light limitation, this mechanism alone did not yield bistable behaviours of seagrass meadows. For bistability to emerge in our models, it required the inclusion of a self-facilitation mechanism associated with plant abundance. The very presence of plants can alter the abiotic conditions within the meadow (Maxwell et al., 2017), exerting strong self-reinforcing feedbacks (e.g., reduced mortality due to increased clonal integration) that stabilize an undisturbed seagrass state (Nielsen & Pedersen, 2000; Mayol et al., 2022). Indeed, this self-facilitating feedback mechanism, apart from contributing to reducing the MLR of *C. nodosa*, led to the emergence of bistable behaviours. Such bistability emerged as a result of the influence of this on seagrass mortality rates and not because of its physiological photo-acclimatization strategy (Fig. 3.3b). Depending on specific seagrass traits, these self-facilitating mechanisms may manifest with varying intensities that define the properties of seagrass meadows (Kilminster et al., 2015; O'Brien et al., 2018). What this means is that once a threshold of collapse has been surpassed, these self-facilitating mechanisms can influence the hysteretic behaviour of the system and thus determine (i) whether the recovery of the target seagrass meadow is possible by slightly alleviating the source of stress, (ii) if it is highly unlikely, or (iii) even totally prevented because of the feedbacks governing alternative stable states (van der Heide et al., 2007; Nyström et al., 2012).

In summary, the findings in this thesis highlight how different nonlinear mechanisms (i.e., physiological photo-acclimatization and self-facilitation mechanisms) together define and enhance seagrass resilience to light limitation (**Chapter 3**). However, it is essential to note that these nonlinearities do not always lead to the emergence of alternative stable states (Scheffer et al., 2001; McGlathery et al., 2013). Regarding the management and conservation of macrophyte ecosystems facing light deprivation, it has to be emphasized that while the emergence of bistability and hysteretic behaviours (i.e., recovery dynamics) only occurred in models altering seagrass mortality as a function of self-facilitation, the nonlinear photosynthetic patterns described for *C. nodosa* may have similar implications for the occurrence of nonlinear transitions and threshold behaviours (i.e., resistance dynamics). These results underscore how species-specific macrophyte traits shape resistance dynamics and the occurrence of abrupt shifts. These factors need to be taken into consideration when implementing guidelines to protect specific meadows from reductions in water transparency, as well as from other potential stressors rising with global change. Further, to understand the overall resilience, an extra evaluation should recognize the post-collapse recovery potential based on such specific seagrass traits (O'Brien et al., 2018). This includes assessing specific recovery mechanisms related to the presence of seed banks, colonization rates, the frequency of sexual reproduction, etc. (Kilminster et al., 2015).

7.3. Anthropogenic pressures and ecological contexts: Their effects on plant-herbivore interactions shape ecosystem vulnerability

Herbivory is a central process in the structuring and functioning of natural communities (Hairston et al., 1960). The ability of herbivores to regulate communities of primary producers is substantially stronger in aquatic systems where they can remove up to ten times more plant biomass than their counterparts on land (Bakker et al., 2016). In the marine realm, herbivores can reduce macrophyte abundance by 68% on average (Poore et al., 2012). Although herbivory is a natural force structuring the abundance of marine vegetation from tropical to subarctic rocky reefs and soft bottoms, environmental contexts also play an intrinsic role in determining primary production and, therefore, the abundance and distribution of marine macrophytes

(Dayton, 1985; Steneck et al., 2017; Duarte et al., 2022). Across environments and latitudes, key abiotic factors (e.g., nutrient or light availability, seawater temperatures or acidification, etc.) control bottom-up processes, which are coupled with biotic mechanisms of top-down control (i.e., herbivory and predation) that together regulate ecosystem dynamics (Burkepile & Hay, 2006; Borer et al., 2006). Depending on how all these processes interact, they could yield a vast array of ecosystem configurations, each with its own intrinsic vulnerability to overgrazing (Bakker et al., 2016; Wood et al., 2017; Campbell et al., 2024). Much of this natural variability depends on how macrophytes and herbivores interact, influenced by their own endogenous factors (e.g., species traits, primary production) and those exogenous ones that shape local biotic and abiotic contexts, making ecosystem dynamics complex to predict (Conversi et al., 2015). Beyond the top-down or bottom-up debate, the challenge remains to integrate all these ecological mechanisms into simple, comprehensive measures across ecosystems and environmental contexts (Wood et al., 2017; Verdura et al., 2023).

In **Chapter 5**, I explored the effect of a relevant set of context-specific factors that strongly influenced the vulnerability of macroalgal communities to herbivory. The novelty of this work lies in the possibility of integrating the effect of all these factors into a simple and comparable indicator: individually-produced sea urchin grazing halos. This integrative index offers a convenient proxy for assessing the interplay between habitat production and herbivore consumption, which allowed conducting more than 1200 individual measurements to estimate relative vulnerabilities to overgrazing across distinct biotic and abiotic contexts in the Mediterranean Sea. Using grazing halos, I evaluated the inherent variability within macroalgae-herbivore interactions as abiotic and biotic conditions change. These drivers include endogenous factors associated with both biotic agents involved (i.e., species identity, herbivore size, habitat type) or site-specific conditions and large-scale factors (i.e., seawater temperature, nutrient levels, depth, and predator-induced fear) that together shape the strength of macrophyte-herbivore interactions and set the ecological context contributing to structuring ecological communities (Burkepile & Hay, 2006; Hereu et al., 2008; Pessarrodona et al., 2019; Campbell et al., 2024).

7.3.1. Endogenous factors influencing plant-herbivore interactions

A critical finding of **Chapter 5** is that multiple co-acting factors interact unequally to determine the strength of plant-herbivore interactions (i.e., halo size). The most influential factors explaining halo sizes and, therefore, ecosystem vulnerability to overgrazing were herbivore identity and its individual size. What this means is that herbivore species traits make a large difference in explaining herbivory impacts. These results suggest that biomass values or population size-structures of sea urchins, rather than overall density, is a much more reliable indicator of herbivory impact, as halo sizes increased nonlinearly with sea urchin size. Further, when monitoring sea urchin dynamics and their herbivory impacts, these biomass values must also be considered for each species separately, as we found that the halos of the urchin species *Arbacia lixula* were, in general, more than twice as large as those of the urchin species *Paracentrotus lividus*. These findings indicate that relative abundances within herbivore communities can give rise to very different vulnerabilities for (Mediterranean) habitats dominated by marine vegetation. Broadly extrapolating from our data, solely influenced by their traits, *A. lixula* could potentially require less than half the abundance of *P. lividus* of a given size and under similar conditions to trigger abrupt transitions from macroalgal forests to impoverished barren states (Bulleri et al., 1999; Boada et al., 2017). Species identity and its demography can, therefore, shape herbivory dynamics confirming patterns suggested by previous field and laboratory manipulations (Bulleri, 2013; Agnetta et al., 2013; Agnetta et al., 2015; Pessarrodona et al., 2019).

Beyond species identity, the type of macroalgal assemblage (here turfs, shrubs, and canopy-forming dominated by Fucales) also played a pivotal role in determining habitat vulnerability to overgrazing. While larger halos were consistently observed in macroalgal forests of Fucales (which is likely due to the fact that the larger sea urchins were found in these forests), our model predicted increased herbivory effects (i.e., larger halos) of *P. lividus* in turf grounds. These model predictions could be explained by the intense consumption rates on turf-forming species derived from their higher nutritional contents and lower anti-herbivore defenses (Pessarrodona et al., 2022b). However, these findings varied with species identity, as the herbivory impact of *A. lixula* did not change within distinct habitat types. These results are consistent with those of Agnetta et al. (2013), who reported similar gut contents of *A. lixula* individuals in barrens and macroalgal forests, as this species showed a preference for encrusting corallines and feeds substantially on sessile animal prey (Wangensteen et al., 2011). A possible explanation for this pattern could be related to the fact that *A. lixula* forages like a bulldozer, removing algal biomass without necessarily consuming it (Bulleri, 2013; Agnetta et al., 2015). This could explain why, despite its increased total impact, *A. lixula* halos were not affected by habitat type. Indeed, these specific foraging strategies have been proposed as a functional facilitation mechanism, wherein *P. lividus* contributes to the deforestation of marine vegetated habitats, expanding the niche where *A. lixula* can easily move and feed, which later prevents the recolonization of canopy-forming species (Bonaviri et al., 2011; Agnetta et al., 2013; Bulleri, 2013). By using individually-produced grazing halos as an index of overgrazing, we can explore the relative importance of these putative feedback mechanisms, and help understand recent trends in the miniaturization of these vegetated ecosystems (Filbee-Dexter & Wernberg, 2018; Pessarrodona et al., 2021).

7.3.2. Exogenous factors influencing plant-herbivore interactions

Across the global ocean, marine ecosystems have experienced decades of decimation of their predator populations due to overfishing (Pauly et al., 1998; Myers & Worm, 2003). This has led to powerful cascading effects on marine vegetation (Estes et al., 1998; Shurin et al., 2002; Steneck, 2002), including catastrophic shifts to ecosystem states devoid of vegetation (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015; Christianen et al., 2023). While most studies have concentrated on the direct trophic effects of predators on herbivore abundance, subtler indirect effects such as the landscape of fear imposed by predators have also emerged as important factors influencing herbivore foraging patterns and, therefore, their impacts on (marine) vegetation (Laundré et al., 2001; Catano et al., 2016; Pessarrodona et al., 2019; Pagès et al., 2021). Although, in general, smaller halos were found within marine protected areas compared to unprotected sites, this effect was only true for halos of *P. lividus* and not *A. lixula* (**Chapter 5**). This suggests that species traits can mediate specific anti-predator responses, influencing species resistance and perception of predation risk as a result of, for instance, the different lengths of their spines or their attachment tenacity (Guidetti & Mori, 2005; Guidetti, 2006; Guidetti & Dulčić, 2007; Pagès et al., 2021). This potential effect of reduced fear influences sea urchin mobility, regardless of their dietary preferences or ability to move in specific habitats (Gianguzza et al., 2010; Agnetta et al., 2013). Hence, more fearful species such as *P. lividus*, which move less within MPAs due to higher predator abundances (Hereu et al., 2005; Pessarrodona et al., 2019), exhibit reduced herbivory impacts in comparison to species better able to cope with fear (**Chapter 5**). Again, species-specific traits matter in explaining herbivory impacts on macrophyte communities, not only as a result of direct effects but also as a consequence of how they respond to exogenous factors like predator presence.

Abiotic conditions, including nutrient availability, seawater temperature, and light conditions, can also influence the interaction strength between marine macrophytes and herbivores (O'Connor, 2009; Kordas et al., 2011; Boada et al., 2017; Hernán et al., 2017; Pagès et al., 2018; Buñuel et al., 2021; Nikolaou et al., 2023). Indeed, our study revealed a negative effect of nutrients (estimated as the annual maximum levels of chlorophyll *a*) on halo size, indicating that vegetated habitats in oligotrophic areas are more prone to overgrazing. The main mechanism explaining this vulnerability can be associated with the nutrient limitation of primary productivity in oligotrophic areas and the compensatory feeding displayed by herbivores derived from the lower nutritional quality of algae growing in these areas (Dayton, 1985; Burkepile & Hay, 2006; Boada et al., 2017; Kriegisch et al., 2019). However, while high-nutrient environments could reduce herbivory pressures as a result of increased macrophyte growth, there may exist other complexities. For instance, in areas characterized by strengthened nutrient supplies, interactions with other stressors, such as light reduction and/or increased turbidity could diminish macrophyte growth (Burkholder et al., 2007; Ralph et al., 2007; Bakker et al., 2016) or stimulate sea urchin recruitment, thus influencing herbivory pressure on these habitats (Prado et al., 2012; Cardona et al., 2013).

Unlike nutrient conditions, depth had a positive effect on halo size, regardless of the sea urchin species. Grazing impacts increased likely due to the lower primary production at deeper environments of reduced light, making these deeper environments much more vulnerable (Nikolaou et al., 2023). However, the highly impactful *A. lixula* is rarely encountered below 10 - 15 m depth (see Kempf, 1962; Chelazzi et al., 1997), meaning that deeper macroalgal forests may be generally protected from its increased herbivory impacts. In addition, our analyses revealed that rising temperatures strengthen producer-consumer interactions, once again showing highly species-specific responses. While *P. lividus* exhibited increased herbivory impacts at locations with higher temperatures (evaluated here as annual maximum SSTs), no effect was detected for *A. lixula*, indicating the high specificity of environmental effects on macrophyte-herbivore interactions (Pagès et al., 2018). This specific effect on temperature is further discussed in Section 7.4.2.

To conclude this section, although both sea urchin biomass or density are commonly used as primary predictors of macrophytes vulnerability to abrupt overgrazing collapses (Steneck et al., 2002; Eklöf et al., 2008; Filbee-Dexter & Scheibling, 2014), we identified a broad range of biotic and abiotic factors that can directly influence the fundamental interaction between macrophytes and herbivores. Marine vegetated ecosystems exhibit a broad spectrum of context-specific configurations that determine their differential vulnerabilities to overgrazing and shape their maximum tolerance thresholds against herbivore stress (Conversi et al., 2015). When assessing ecosystem vulnerability to the impacts of herbivory, it is critical therefore to consider the ecological context and specific population dynamics within herbivore guilds. In general, macroalgal forests will be more vulnerable when subjected to higher oligotrophic conditions, seawater temperatures, and depths, as well as in areas with lower biomass of predators.

7.4. The tropicalization of Mediterranean ecosystems dominated by marine vegetation

As the Earth warms up and (bio)geographical barriers are removed by human actions, species move pole-ward, yielding a global redistribution of biodiversity (Pecl et al., 2017). These range shifts occur faster and more intensely throughout the oceans (Sorte et al., 2010; Burrows et al., 2011; Lenoir et al., 2020), contributing to the tropicalization of once-temperate environments (Vergés et al., 2014a; Zarzyczny et al., 2023). Range extensions of tropical intruders occur faster than range contractions of temperate species, promoting areas of transition in temperate seas with richer species diversity (Kumagai et al., 2018; Zarco-Perello et al., 2020; Smith et al., 2021). In these areas, completely unprecedented community assemblages emerge, offering the opportunity to understand how such novel species interactions are established and shape the structure and functioning of temperate communities (Vergés et al., 2019; Stuart-Smith et al., 2021; Pessarrodona et al., 2022b; Miller et al., 2023; Nagelkerken et al., 2023). The arrival of range-extending herbivorous species intensifies herbivory pressures on temperate macrophytes ecosystems they colonize, which can cause regime shifts to degraded ecosystem states (see e.g., Ling et al., 2009; Sala et al., 2011; Vergés et al., 2014b; Vergés et al., 2016; Wernberg et al., 2016; Rodriguez et al., 2022; Zarzyczny et al., 2023). In fact, it is these biotic interactions arising from global change, rather than, for instance, rising temperatures alone, which ultimately impact biodiversity and play a fundamental part in the current degradation of the world’s ecosystems (Tylianakis et al., 2008; Ockendon et al., 2014; Vergés et al., 2019; Pessarrodona et al., 2021).

In this context, two chapters of this thesis directly or indirectly explored the effect of this tropicalization and redistribution of marine species. In **Chapter 6**, I investigated the yet poorly understood social interactions (i.e., mixed-species shoaling behaviour) between two range-extending rabbitfishes *Siganus rivulatus* and *S. luridus* and the two native Mediterranean herbivore species, *Sarpa salpa* and *Sparisoma cretense*, in the world's most invaded basin, the eastern Mediterranean Sea (Lejeusne et al., 2010; Cramer et al., 2018). Gaining an ecological understanding of these interactions could contribute to predicting future tropicalization scenarios in still uninvaded areas. It could help us predict, for example, if native species facilitate or impose a resistance to such range shifts (Smith et al., 2018; Santamaría et al., 2022). In addition, in **Chapter 5**, I investigated the differential impact of two Mediterranean sea urchin species: a thermophilic species with tropical affinities *A. lixula* and the more temperate *P. lividus* (Wangensteen et al., 2013a,b). In the last few decades, seawater warming has allowed local increases in the abundance of *A. lixula* (Francour et al., 1994; Gianguzza, 2020), while *P. lividus* have shown signals of population collapse at the warm edges of their range in the eastern basin (Yeruham et al., 2015; Yeruham et al., 2020). As shown in **Chapter 5**, these species can exert differential impacts on marine vegetation, and by sampling across the east-west Mediterranean gradient, we also assessed the effect of temperature on sea urchins' herbivory impact.

7.4.1. The intrusion of fish tropical herbivores in the Mediterranean

Although the intrusion of tropical herbivores into temperate transition zones remains one of the most concerning and widely studied ecological consequences of tropicalization (Vergés et al., 2014a; Zarzyczny et al., 2023), once in a new environment, not all tropical herbivores succeed (Azzurro et al., 2014). Besides abiotic conditions, several factors make some range-extending species more successful than others in expanding their range towards temperate systems (Smith et al., 2018; Bennet et al., 2021; Stuart-Smith et al., 2021; Monaco et al., 2020; Miller et al., 2023). For instance, factors related to enlarged thermotolerance, swimming abilities, and reproduction capacities have demonstrated an advantageous effect at leading edges of range extensions (Sunday et al., 2012; Sunday et al., 2015; Schickele et al., 2021). However, behavioural interactions with native species (e.g., mixed-species shoaling and foraging) can also mediate their relative success (Smith et al., 2018; Paijmans et al., 2020; Coni et al., 2022; Nagelkerken et al., 2023). Results in **Chapter 6** describe how the two tropical rabbitfish species (i.e., *S. rivulatus* and *S. luridus*), widely distributed along the shallow waters of the island of Crete (see Fig. D1 in Appendix D), were more likely than native species to associate with others (either native or tropical species) in mixed-species shoals. Given the large imbalance between multi-specific shoals consisting of just range-extending species (~14% of all observations) compared to those formed just by native species (less than 3%) and, together with the fact that *S. rivulatus* induced most of these shoaling interactions (**Chapter 6**), it is clear that tropical rabbitfish species have introduced a novel function in the Mediterranean Sea: mixed-species shoaling.

This generalist behavioural strategy exhibited by rabbitfishes can be particularly useful at initial stages of range extensions (Stuart-Smith et al., 2021). By shoaling with others, they can learn from native temperate counterparts about the distribution and palatability of local resources, reduce their overall predation risk and vigilance requirements, or increase their shoal cohesion and swimming efficiency, among many other benefits (Paijmans et al., 2019). Indeed, rabbitfishes improved their foraging efficiency in large shoals, regardless of who they shoal with (**Chapter 6**). Nevertheless, the native bream *S. salpa* only increased its bite rates with shoal size when foraging in mono-specific shoals. These results suggest that high behavioural generalism is required to take advantage of mixed-species shoaling (Smith et al., 2018). It includes, for instance, a large dietary generalism that helps to profit from novel diets while shoaling with temperate counterparts (Monaco et al., 2020; Coni et al., 2022). However, while behavioural and dietary flexibility could help explain why generalist species like rabbitfishes are succeeding within a changing ocean (Stuart-Smith et al., 2021; Smith et al., 2018), much of their potential success also relies on the degree of similarity that range-shifters have with temperate species (Azzurro et al., 2014; Miller et al., 2023). The results in **Chapter 6** align with other studies, which have found that functional niche similarity between tropical and temperate species facilitates the spread of the former due to its pre-adaptation to the functioning in temperate ecosystems (Smith et al., 2021; Miller et al., 2023). While this clearly seems to be the case between rabbitfish species and *S. salpa*, this lack of functional similarity could also be the reason why the native parrotfish *S. cretense* was rarely observed forming mono- or mixed-species shoals in field samplings. Other studies have found that these relationships vary depending on the environmental context and the availability of food resources. For instance, competition between species, including aggression and territorial behaviours, have been related to both the density of vagrants or resource availability (Sala et al., 2011; Vergés et al., 2014b; Taylor & Figueira, 2021; Coni et al., 2021). Thus, mechanisms that reduce competition in scenarios of low food resources (such as those observed in the eastern Mediterranean Sea), including diet partitioning and niche segregation, could promote the co-existence of range-extending and native fishes along the world's temperate environments (Azzurro et al., 2007; Kingsbury et al., 2020; Zarco-Perello et al., 2020).

7.4.2. Anthropogenic heating and species reconfigurations across the Mediterranean Sea

Apart from the intrusion of tropical herbivores, another critical aspect of global warming is the extension of thermophilic, warm-affiliated species and the decline of less thermotolerant species in historically temperate ecosystems (Smale et al., 2022; Wernberg et al., 2023). This trend is especially true in the warm-temperate Mediterranean Sea, where no north expansion is possible, and increasing temperature reduces the growth and distribution of cool-water species, causing severe mass mortality events (Coll et al., 2010; Milazzo et al., 2013; Garrabou et al., 2022). Given the fundamental role of species interactions (including herbivory and competition) in regulating the functioning of ecological communities, the effect of anthropogenic heating on species density and dominance within ecosystems remains (likely) underestimated (Tylianakis et al., 2008; Gilman et al., 2010). How this will affect the composition of herbivore communities across the cooler edges of the Mediterranean Sea and, consequently, their herbivory impact on macrophyte ecosystems is not yet fully clear. Regardless of whether these reconfigurations are mediated by physiological processes affecting the metabolism of consumers, by the effect of temperature on marine macrophytes, or by changes in macrophyte-herbivory interactions, alterations in herbivory community composition may substantially promote herbivory impacts and ecosystem vulnerabilities across future Mediterranean contexts (Kordas et al., 2011; Yeruham et al., 2015; Pagès et al., 2018; Buñuel et al., 2021).

In the western Mediterranean Sea, the warm-adapted *A. lixula* is showing signs of population increase with increasing sea surface temperatures (Francour et al., 1994; Wangensteen et al., 2013a,b; Medrano et al., 2019; Gianguzza et al., 2020). For instance, a ten-fold population increase was reported between 1983 and 1992 in Corsica (Francour et al., 1994), while in 2016, it reached an unprecedented abundance in Catalonia (Medrano et al., 2019). These values in Catalonia occurred even though their numbers had remained stable at one-tenth the population of *P. lividus* for 19 years from 1991 to 2010 within and outside a well-established marine reserve. Given that the herbivory impact of *A. lixula* is more than twice the impact (i.e., halo size) of *P. lividus* (**Chapter 5**), this case shows how species redistributions related to global change could put marine vegetation under severely increased risk. On the other hand, although *P. lividus* does show increased grazing with sea surface temperatures (**Chapter 5**), its impacts could reach a limit that may reduce overall herbivory pressures on marine vegetation. The excessively high temperatures observed in the far-eastern Mediterranean Sea define such limits, which could exceed *P. lividus* thermotolerant thresholds and lead to massive population collapses (Yeruham et al., 2015). Moreover, global change impacts interact in complex ways, leading to a tendency toward oligotrophication as temperatures increase (Agusti et al., 2017). This effect could curb primary production and promote compensatory feeding behaviours across herbivore communities (Boada et al., 2017). Compensatory feeding could feed back to continue reducing macrophytes growth, leading to miniaturized habitats more suitable for *A. lixula*, which can entirely remove marine vegetation and prevent their recolonization (Agnetta et al., 2013; Bulleri, 2013).

Taken together, these trends indicate that temperature-mediated reconfigurations of herbivore communities and their consequently novel interactions with producers and counterparts can produce severe imbalances of the production-herbivory ratio, drastically altering ecosystem dynamics (Yeruham et al., 2020; Santana-Garcon et al., 2023; Nikolaou et al., 2023). Sampling across environmental gradients that capture those patterns observed in the eastern basin can help us understand how Mediterranean ecosystems in their cooler environments will look under the projected scenarios of anthropogenic climate change.

7.5. Future perspectives

7.5.1. Can we effectively generalize ecological knowledge across species and functional groups? Exploring underrepresented seagrasses

In this thesis, I used a combination of approaches to describe the wide variety of strategies that marine macrophytes and, in particular, seagrass species exhibit to cope with light limitation. The use of natural environmental gradients or field manipulative experiments provides critical data that helps model macrophyte responses to stress (here light limitation; see next section). These approaches can be employed to establish comparative metrics that help explain specific acclimatization capacities and overall resilience of marine macrophytes under this or other global change stressors (see **Chapter 3**). However, biases in the research of seagrass strategies to withstand light limitation toward certain species became evident while conducting **Chapter 4**. Whatever the causes of these biases, including natural species abundance and distribution, or geographical and socioeconomic reasons, these gaps must be addressed. Although I have addressed how seagrasses with deeper vertical distribution ranges exhibit greater acclimatization capacities in key physiological, morphological, and structural traits, expanding the number of traits studied and including such underrepresented species is a clear research priority. According to Short et al. (2011), 24 seagrass species (i.e., 33% of all 72 seagrass species) grow in vertical ranges equal to or lower than 10 meters depth and 41 (i.e., 57%) in ranges within the first 20 meters depth, which make the vast majority of seagrasses particularly vulnerable to light limitation. A future inclusion of understudied species will contribute to establishing more accurate baselines in each local context and improve predictions of seagrass losses in the face of business-as-usual global change scenarios (Waycott et al., 2009; de los Santos et al., 2019). To secure the entire suite of critical ecosystem services that seagrasses provide, scientists will need to evaluate life history traits of poorly studied seagrasses so that managers can use these to protect real-world ecosystems.

7.5.2. How do marine macrophytes respond to cumulative stressors?

Deterministic models in **Chapter 3** are useful in understanding nonlinear dynamics and tracking the erosion of macrophyte ecosystem resilience in response to light limitation gradients. While these approaches need to be tested in other species to describe accurate physiological responses that help compare responses and resilience within functional groups (see previous section), other potential stressors must also be incorporated to address the complex reality marine macrophytes are experiencing under global change (Strain et al., 2014; Adams et al., 2020). The use of process-based models helps to provide a mechanistic understanding of the ecological responses to the cumulative and interacting stressors that influence ecosystem dynamics (see **Chapter 3**; Adams et al., 2020; Turschwell et al., 2022). Nutrient enrichment, increasing temperatures, altered herbivory dynamics, or acidification (among others) are some of these fundamental drivers that accumulate and interact to shape the net carbon balances of macrophytes (Moreno-Marin et al., 2018). This is of particular interest in the severely anthropized Mediterranean Sea, where endemic species (e.g., *Posidonia oceanica*) are confined and have no spatial or latitudinal escape from rising anthropogenic stress (Coll et al., 2010; Lejeusne et al., 2010).

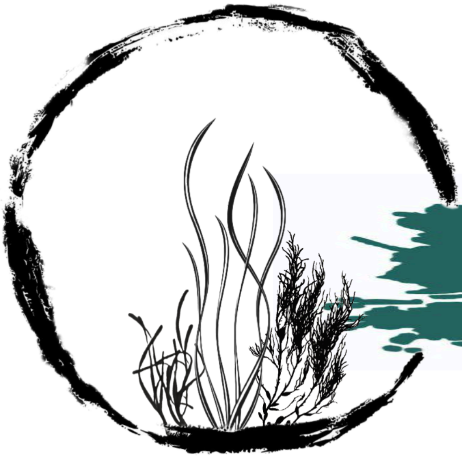
Furthermore, although seagrass net carbon balances could be severely influenced by below-ground tissues and their ratio with above-ground biomass (**Chapter 3**), few studies have parameterized carbon balance models accounting for below-ground respiratory rates (Collier et al., 2017). Although it is widely recognized that this ratio can vary considerably with site-specific conditions, seasonality, or other driver of stress; below-ground tissues usually report larger respiration rates than seagrass leaves, which can additionally be substantially affected by environmental conditions such as nutrient enrichments or temperature (Pérez et al., 1994; Staehr & Borum, 2011). Future studies should, therefore, seek to incorporate below-ground respiration rates into the carbon balance of macrophytes and add cumulative sources of stress to provide better estimates of macrophytes resilience in a world subjected to multiple interacting stressors (Adams et al., 2020; Turschwell et al., 2021).

7.5.3. Integrating sea urchin population dynamics with environmental factors shaping plant-herbivore interactions

In this thesis, I have addressed the interaction between primary production and herbivory consumption along the broad biogeographical gradients of the Mediterranean Sea. This investigation offers an integrative view of how biotic and abiotic factors mediate the strength of these interactions under distinct ecological contexts. The findings in **Chapter 5** are of interest in understanding nonlinear ecosystem behaviours. The theory of alternative stable states predicts that once critical thresholds of stress (e.g., herbivore biomass) are exceeded, they often trigger regime shifts resulting in the collapse of macrophyte habitats (Scheffer et al., 2001; Filbee-Dexter & Scheibling, 2014). Most models of ecosystem dynamics typically rely on biomass values of consumers and resources. However, they do not take into account the complex species-specific dynamics of each population, which underlie their trajectories and often vary from location to location and with the environmental context (Hereu et al., 2012). As I have shown in **Chapter 5**, consumption impacts can critically vary with urchin size and between species, and every consumer may be differently affected by fear, temperature conditions, or the type of habitat. Future models of ecosystem dynamics should incorporate elements of species identity, interaction strengths, and population structure to make them more representative of real-world conditions (Hereu et al., 2008; Ling et al., 2009b). The struggle in model building is always to find the right balance between ecological reality and model complexity, but if we acknowledge that all models are wrong but some are useful, we can create future models that help managers protect real ecosystems.

7.5.4. Managing the future Mediterranean Sea

The Mediterranean Sea represents a natural laboratory to study the ecological consequences of global change, where both abiotic and biotic conditions are being severely influenced by anthropogenic heating and pressures derived from high population and urbanization levels (Lejeusne et al., 2010; Cramer et al., 2018). Besides affecting plant-herbivore interactions, rising seawater temperatures are reshaping herbivore communities by creating suitable thermal niches for tropical herbivores (Vergés et al., 2014b), and increasing the prevalence of warm-affiliated temperate species (Milazzo et al., 2013). In the world's largest confined water body, there is no escape to northern latitudes. This poses a significant threat to future Mediterranean vegetated habitats, increasing risks of ecosystem collapses and driving the homogenization and miniaturization of their macrophyte communities (Vergés et al., 2014a; Pessarrodona et al., 2021). Given the natural environmental gradients along the Mediterranean Sea, understanding the novel ecological interactions mediated by warming that are emerging in its eastern basin can help foresee which species will become more frequent under a business-as-usual scenario (Verdura et al., 2023) and, if possible, prevent or manage their undesired effects on marine temperate ecosystems. Regarding management, rabbitfish species could be promoted as a legitimate fishing target that could help restrict their establishment in novel territories (El-Haweet, 2001). However, this could be more difficult in the case of species of low commercial interest such as the thermophilic and high-impact *A. lixula* (**Chapter 5**). These alternatives need to be evaluated against standard management approaches like MPAs. Given the extent of climate impacts and invasive species, it is still unclear whether MPAs reliably enhance ecosystem resilience by ensuring the stability of fish communities under global warming (Benedetti-Cecchi et al., 2024) or whether they will be effective in halting the growing pressures resulting from the range extension of tropical herbivores by safeguarding fundamental trophic relationships such as predation (see e.g., Dimitriadis et al., 2024; Ling & Keane, 2024). Such uncertainties challenge us to evolve new, innovative, and site-specific strategies to secure temperate macrophyte ecosystems of the future.



8. General conclusions

- Physiological photo-acclimatization and self-facilitation mechanisms were essential drivers of seagrass resilience to light deprivation. Physiological photo-acclimatization approximately halved the minimum light requirements (MLR) in our seagrass model *Cymodocea nodosa*, improving its resistance compared to a non-acclimatization seagrass model. Self-facilitation mechanisms associated with density-dependence also reduced the MLR and contributed to the emergence of bistable behaviours through its influence on mortality rates.

- Seagrass species exhibit specific tolerances to light reduction. Their species-specific capacity to acclimatize key traits to light reduction strongly influenced their ability to colonize depth. Among them, reducing the saturation irradiance, the number of leaves per shoot, and the above-ground biomass effectively predicted specific seagrass maximum depth ranges worldwide.

- The relationship between primary production and sea urchin herbivore consumption was influenced by a range of endogenous and exogenous factors of biotic and abiotic nature that cumulate and interact in complex ways. Endogenous factors such as the herbivore identity, its individual size, and the type of macrophytes community determine context-specific ecosystem vulnerabilities to overgrazing. Exogenous factors, including nutrient availability, seawater temperature, depth, or predator-induced fear, also shaped this vulnerability.

- Tropical herbivorous fishes *Siganus rivulatus* and *Siganus luridus* have introduced the mixed-species shoaling strategy as a novel herbivory function in the Mediterranean Sea. These range-extending species shoaled among them and with native species (i.e., *Sarpa salpa* and *Sparisoma cretense*) improving their foraging efficiency with shoal size and benefiting from shoaling in mixed-species groups. In contrast, *S. salpa* reduced its foraging efficiency when shoaling with other species. This generalist strategy of range-extending rabbitfish might boost herbivory pressures in tropicalized environments dominated by marine vegetation.

- Global change impacts place severe pressure on marine vegetated ecosystems worldwide that can interact in complex ways at local and/or regional scales. Embracing this context-specific (ecological) variability, which includes the macrophytes' species-specific tolerance and vulnerability to stress, will help ensure the resilience of marine vegetated habitats in the face of impacts influencing light limitation, overgrazing, or species redistributions. For macrophyte ecosystem management policies to be effective, nonlinear dynamics, bistable or not, must be considered.

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10. Supporting information

Appendix A

Supplementary Text A1: Justification of parameter values

The full list of model parameters used in this paper and their references are shown in Table 3.1. Here, we provide a deeper justification of the parameter values, from those obtained through field experiments to those adapted from literature.

Photosynthetic – Irradiance (*P-I*) parameters against light reduction

Marín-Guirao et al. (2022) found, after two months of experimental shading in the field, the pattern of physiological photo-acclimatization represented by dots in Fig. 3.2. Authors measured the maximum gross photosynthetic rates (P_{max}, in units of μmol 0_2 g^{-1} ABG FW h^{-1}); above-ground respiration (R, in units of μmol 0_2 ABG g^{-1} FW h^{-1}); saturation irradiance (I_k, in units of μmol quanta m^{-2} s^{-1}) and compensation irradiance (I_c, in units of μmol quanta m^{-2} s^{-1}). To do so, they tested 9 values of light reduction with respect to the natural incoming light: 0%, 18%, 43%, 56%, 64%, 66%, 78%, 87% and 94% of subsurface irradiance (SI). That experiment yielded a control value (no light reduction) of 74% SI, which after conversions to instantaneous irradiance resulted in 634.96 μmol quanta m^{-2} s^{-1}. This implies a maximum value of instantaneous irradiance (100% SI) that is equivalent to 858.04 μmol quanta m^{-2} s^{-1}. Thus, the shade screens produced an 8-level light reduction gradient corresponding to 60, 42, 32, 26, 25, 16, 10, 4% SI, which are equivalent to 514.82, 360.42, 274.54, 223.14, 214.58, 137.26, 85.88, 34.26 μmol quanta m^{-2} s^{-1}, respectively.

In this work, we created two models of carbon balance, to quantitatively evaluate the contribution of physiological photo-acclimatization on seagrass response when facing such levels of light reduction. One of these models assumed the pattern obtained in Marín-Guirao et al. (2022) for *Cymodocea nodosa.* In the other and for comparison, it was assumed that plants cannot photo-acclimatize. To do this so, values of P_{max} and R found in Marín-Guirao et al. (2022) needed to be converted from units of μmol 0_2 g^{-1} ABG FW h^{-1} to units of mg 0_2 ABG DW h^{-1}. Therefore, we made the conversions from mol to mg with 32 g 0_2 corresponding to 1 mol 0_2 (Pérez & Romero, 1992) and from FW to DW with 3.37 g FW corresponding to 1 g DW (Marco-Méndez, 2015). I_k and I_c maintained the same units (μmol quanta m^{-2} s^{-1}).

Once the values were transformed (Table A1), we applied a nonlinear fitting procedure to determine the nonlinear least-squares estimates of the model parameters presented in equations (3)-(5) in **Chapter 3**. We used a robust and efficient implementation of the Levenberg-Marquardt algorithm (via the R package *minpack.lm*). The estimated values of model parameters estimated from this fitting procedure were used in subsequent model simulations; the full list of these model parameters is shown in Table A2.

Below-ground parameters

To set the value of below-ground respiration (roots-rhizomes respiration [*RRR*]) we used the ratio obtained for *Zostera marina* by Staehr & Borum (2011) as follows. They found that root and rhizome respiration rates were nearly 10-fold lower than above-ground respiration rates (leaves), analogous to ten-fold differences in turnover rate observed between above-ground and below-ground biomass compartments (Vonk et al., 2015). This respiration ratio between photosynthetic and non-photosynthetic tissues was independent of seasonal and temperature changes (Staehr & Borum, 2011). Therefore, we set a value of the *RRR* parameter to be equal to 1/10 of R_{max} (maximum leaf respiration).

The ratio [*BAR*] between below-ground biomass and above-ground biomass was set to one, following the findings on Pérez et al. (1994). This ratio is ~1 for high and medium nutrient-mediated seagrass beds of *C. nodosa*. While this ratio is largely dependent on the seasonality and local context of seagrass beds, a below-ground to above-ground biomass ratio of ~1 has also been found for some seagrass beds of its congener species *Cymodocea serrulata* (Collier et al., 2017 and references therein).

Biomass and growth parameters

Given that our carbon balance model was written in units of mg 0_2 g^{-1} ABG DW h^{-1}, we had to include a conversion factor (*K*; in units of g total DW mg^{-1} 0_2) to obtain the growth rates (in units of h^{-1}) for *Cymodocea nodosa*. To parameterize the value of *K*, we considered the maximum values of above-ground growth rates (μ_{max}) known for *C. nodosa* (Zharova et al., 2008; Nielsen & Pedersen, 2000) and solved our model for maximum net carbon production of *C. nodosa*:

$$\mu_{max} \approx K \frac{1}{1 + BAR}\left(\frac{1}{2}P_{gmax} - \ (R_{max} + RRR * BAR)\right),$$

$$\therefore K \approx \ \frac{\mu_{max}(1 + BAR)}{{}^{1}/_{2}\,P_{gmax} - \ (R_{max} + RRR * BAR)}.$$

Thus, since our fitted P_{gmax} = 11.64 mg 0_2 g^{-1} ABG DW h^{-1}, R_{max} = 1.987 mg 0_2 g^{-1} ABG DW h^{-1}, the roots and rhizomes respiration [*RRR*] = R_{max}/10, the below-ground to above-ground biomass ratio [*BAR*] was set to 1 and the greatest value of μ_{max} we found in the literature was 0.001958333 h^{-1} (Nielsen & Pedersen, 2000; Zharova et al., 2008), the calculated value for *K* was set to 0.001075 g total DW mg^{-1} O_2.

Mortality parameters

For *C. nodosa* mortality rates we considered two potential processes: one where clonal integration is absent (no self-facilitation); and a second where this mechanism is present, producing a self-facilitation that decreases the mortality rates of the seagrass (Mayol et al., 2022). These two processes, together with the choice of including the presence or absence of photo-acclimatization, results in the four models tested in the present work.

For meadows where self-facilitation is absent, we assumed the values reported by Mascaró et al. (2014). In that study, they reported the values of mortality per month, as well as an integrated mortality rate for one year in two seagrass meadows of *C. nodosa*. We used the mortality rate values from the oligotrophic meadow to avoid the interaction with algal overgrowth (increased mortality). We selected the values of July since Marín-Guirao et al. (2022) obtained the photosynthetic measures in that month. Therefore, we set d_0 = 0.000116 h^{-1}, as the constant for the mortality rate which is always proportional to the current biomass of seagrass, for meadows where self-facilitation is absent.

For meadows where self-facilitation is present, we assumed an increased mortality (δ) for low levels of biomass and a nonlinear relationship that reduces δ as biomass levels increase. We modelled this self-facilitation as a sigmoidal function that yields an increased mortality rate for low levels of biomass. However, as biomass in the system increases, mortality rates start to decrease with a slope λ_B after crossing a threshold (B_0 = 10), leading to very low values of seagrass mortality when biomass levels are high (Mayol et al., 2022).

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Table A1. Values and standard errors (SE) for the photo-physiological response of *Cymodocea nodosa* after two months of experimental field shading (light reduction values as instantaneous irradiance in µmol quanta m^{-2} s^{-1} and in percentage of surface irradiance). Photosynthetic-Irradiance (*P-I*) parameters: maximum gross photosynthesis (P_{max}) and above-ground respiration (*R*) are shown after conversion from µmol O_2 g^{-1} ABG FW h^{-1} to mg O_2 ABG DW h^{-1}; and saturation irradiance (I_k) is shown in units of µmol quanta m^{-2} s^{-1}.

Ins. irradiance (µmol quanta m^{-2} s^{-1})	*Surface irradiance (% SI)*	P_{max}	P_{max} *(SE)*	*R*	*R (SE)*	I_k	I_k *(SE)*
634,96	74	11,2110684	0,44938581	1,97954554	0,0451396	67,6174237	7,12340965
514,82	60	12,0879902	0,60707836	1,93366887	0,01490785	71,5354374	8,4700463
360,42	42	11,1221678	0,63719271	2,04638972	0,00388821	54,3873511	7,30750426
274,54	32	11,9533882	0,56001197	1,9710401	0,0907847	70,075462	9,88600491
223,14	26	9,35382663	0,81513649	1,3734172	0,05134231	47,6515868	4,36793889
214,58	25	10,9309355	1,09412616	1,67061898	0,13280724	43,9724649	3,88216705
137,26	16	10,8572891	0,61362881	1,58959835	0,05436356	46,8406129	9,25578237
85,88	10	8,91133928	1,53433285	1,43301247	0,13259262	38,5555954	6,81642059
34,26	4	8,5697564	0,72797163	1,47591874	0,21613532	34,3856763	3,06302302

Table A2. Summary of nonlinear fits of the physiological photo-acclimatization models (left panels in Fig. 3.1) of *Cymodocea nodosa* against light reduction. The values of each estimated parameter are shown in Table 3.1.

Non-linear fitting of P_{gross} (I)

	Estimate	*Std. Error*	*t value*	*Pr (> |t|)*	*(*)*
P_{gmax}	11.64	0.8837	13.174	4.5 e^{-05}	***
P_{gmin}	2.096	>> Estimate	0.028	0.979	
λ_p	0.008524	0.0195	0.435	0.681	
y_{cP}	-49.1	>> Estimate	-0.032	0.975	

Residual standard error: 0.9227 on 5 degrees of freedom
Number of iterations to convergence = 17
Achieved convergence tolerance: 1.49 e^{-08}

Non-linear fitting of R (I)

	Estimate	*Std. Error*	*t value*	*Pr (> |t|)*	*(*)*
R_{max}	1.987	0.06547	30.34	7.29 e^{-07}	***
R_{min}	1.509	0.05670	26.61	1.40 e^{-06}	***
λ_R	0.4567	>> Estimate	0.00	1	
y_{cR}	267.1	>> Estimate	0.00	1	

Residual standard error: 0.1134 on 5 degrees of freedom
Number of iterations to convergence = 35
Achieved convergence tolerance: 1.49 e^{-08}

Non-linear fitting of I_k (I)

	Estimate	*Std. Error*	*t value*	*Pr (> |t|)*	*(*)*
I_{kmax}	70.04809	10.53706	6.648	0.00116	**
I_{kmin}	24.54396	49.72699	0.494	0.64252	
λ_K	0.00863	0.01362	0.634	0.55417	
y_{cK}	177.45783	259.00230	0.685	0.52371	

Residual standard error: 8.315 on 5 degrees of freedom
Number of iterations to convergence = 19
Achieved convergence tolerance: 1.49 e^{-08}

Appendix B

Supplementary Text B2: Systematic review and meta-analyses: selection of key traits that acclimatize to extreme low-light

Inclusion criteria

From the lists generated with our search term, we selected i) manipulative shading experiments in the field, where traits were measured under control (natural light) and severe light reduction treatments for each species, and ii) studies comparing the species-specific traits between shallower and deeper zones (deep limit or close to) of the same meadow. We excluded from our analyses traits with data available from less than seven species and/or coming from less than 15 studies.

To be included in our study, the publication had to provide information on seagrass trait responses to light reduction at different organizational levels: i) physiological (saturation irradiance [grouping data from I_k and E_k], maximum photosynthetic rate [grouping data from P_{max} and ETR_{max}] or photosynthetic efficiency [α]), ii) morphological (leaf length, leaf width or leaves per shoot), iii) structural (shoot density or above-ground biomass), or iv) growth (shoot growth). Our final list did not include 11 relevant publications that we manually included in the list of selected studies (see Table B1), as well as one publication conducted with collaborators for which we had data prior to publication. When comparative investigations reported more than one meadow and/or years, we included data as different studies in our meta-analyses. Therefore, one publication can add more than one study in our meta-analyses and we will hereafter refer to all these investigations as scientific studies. After scrutinizing all the selected manuscripts and rejecting those not accomplishing the selection criteria, we ended up with a total of 78 scientific studies (Table B1; Fig. B1), that included 19 strictly physiological [24%], 3 morphological [4%], 3 structural [4%], 8 growth [10%] and 45 mixed [58%]) that measured seagrass response to light deprivation. These 78 studies were obtained from 54 scientific publications (15 strictly physiological [27%], 3 morphological [6%], 3 structural [6%], 3 growth [6%] and 30 mixed [55%]) and grouped by the type of seagrass traits studied in each of them.

In shading experiments, we only selected data from the most extreme treatments (avoiding medium treatments), for experimental durations equal to or longer than 11 days. In these cases, we assumed the light decline imposed by experimental manipulation to be sufficient to cause changes in trait performance (McMahon et al., 2013; Léger-Daigle et al., 2015; Roca et al., 2016, see references below). Whenever shading manipulative experiments were conducted at different depths, we extracted data from shallower treatments to avoid interferences of other factors varying with depth and maximize the differences in incoming light between control and shading treatments. In addition, where repeated measures were taken, we only extracted data from the last one to capture the maximum level of acclimatization to low-light conditions. When studies looked for differences in trait performance according to seasonality, we selected data from spring or summer treatments, where differences in performance and light conditions are maximized. Since our aim was to evaluate the species-specific acclimatization capacity of seagrasses to light limitation, we excluded those treatments whose objective was to evaluate the time to seagrass mortality and only included data from those treatments where seagrasses survived.

The final list summarizing the number of publications, studies and species, grouped by trait that remained after screening the initial lists with the above-mentioned inclusion criteria is shown in Table 4.1. Fig. B1 shows the species for which data meeting the criteria were available and the traits that were evaluated for each of them.

Data extraction

We extracted trait data from controls and from treatments with the maximum level of light reduction in shading experiments, only if plants survived. In the case of depth-based experiments, we extracted data from the shallowest and the deepest observations, which were assigned to 'control' and 'treatment' levels respectively, in our meta-analyses. Whenever a study met all of our selection criteria, we then extracted the mean, the standard deviation (SD), and the sample size values from controls (natural light) and low-light treatment groups, for experimental shading; and the minimum and maximum depth groups, for comparative depth-based studies. Given that not all scientific publications presented their data in a numerical format, we used the WebPlotDigitizer 4.5 software (https://apps.automeris.io/wpd/), to manually extract seagrass traits results from plots.

Calculation of effect sizes

We quantified the *log transformed ratio of means* (ROM) as the effect size of each seagrass trait gathered from shading experiments and depth-based investigations (Hedges et al., 1999). This calculation was conducted with the *escalc()* function of the 'metafor' R package (Viechtbauer, 2010):

$$ROM = \ln\left(\frac{\bar{X}_T}{\bar{X}_C}\right) \tag{1}$$

where ROM is the natural logarithm of proportional change in the means of the treatment ($\bar{X}_T$) and control ($\bar{X}_C$) groups. The ROMs of each trait from different publications and species were pooled in our meta-analyses with an inverse-variance method (Hedges & Olkin, 1985). We then assigned a weight to each study based on its sampling variance $\hat{\sigma}^2$:

$$\hat{\sigma}^2(ROM) = \frac{(SD_C)^2}{N_C\bar{X}^2{}_C} + \frac{(SD_T)^2}{N_T\bar{X}^2{}_T} \tag{2}$$

where SD_C = SD of control groups, SD_T = SD of treatment groups, N_C = sample size of control groups and N_T = sample size of treatment groups considered (Hedges & Olkin, 1985).

Meta-analyses

To explore the acclimatization potential of seagrass species traits, we conducted separate meta-analyses for each trait. This allowed us to estimate an overall mean effect with 95% confidence intervals (corresponding to the species-specific trait acclimatization potential to severe light reduction for each trait). We included 'Article' and 'Species' as random factors in mixed-effects models. However, the added complexity of introducing such random factors was not supported by AIC and log-likelihood ratio tests (Zuur et al., 2009) for most of the response variables. We only fitted mixed-effects models for two traits, leaves per shoot and above-ground biomass, while the rest of the response variables were modelled using a random-effects framework. All modelling was done in R, using the package 'metafor' (Viechtbauer, 2010). Variance heterogeneity (τ^2) was calculated using a restricted maximum likelihood estimator (REML) (Harrer et al., 2021). The Knapp-Hartung test was used in the random-effects models to estimate the confidence interval related to the overall effect (Knapp & Hartung, 2003). Forest plots for each seagrass trait resulting from our meta-analyses are shown in Fig. S2 of this Appendix. Additionally, publication bias was evaluated both visually with funnel plots and by applying Egger's test (Viechtbauer, 2010) (Table B7). In the case of random effects models, we also performed sensitivity analyses to test the robustness of the overall effect sizes (as this cannot be implemented for mixed-effects models (Viechtbauer, 2010). We used trim and fill methods (Table B8), to estimate the number of missing studies using an iterative procedure (Koricheva et al., 2013). Sensitivity analyses were also performed using the *omit one* procedure (Koricheva et al., 2013). As trim and fill methods cannot be applied to mixed-effects models, after appreciating some evidences of publication bias, we proceeded to assess the importance of this bias with a random-effects model, which only slightly changed the estimates of model fits. We then ran Egger's tests and adjusted coefficient values using trim and fill methods. This also allowed us to run the sensitivity analysis and detect potential influential studies on models that while were not the best-selected ones according to AIC and log-likelihood ratio, had very similar coefficients, giving almost identical results (even after correcting for publication bias, and in any case, values far from crossing 0, hence, with very high evidence for an effect).

Egger's tests indicated a publication bias for some physiological (I_k; $P = 0.0038$ and α; $P < 0.0001$), structural (sh. density; $P = 0.0027$ and above-ground biomass; $P < 0.0001$) and growth traits (sh. growth; $P = 0.0197$). We found little or no evidence for publication bias associated with the remaining seagrass variables (Table B7). Trim and fill methods indicated that publication bias may have only slightly affected the estimation of overall effect sizes, except for leaf length, where it influenced the significance of its p-value ($P = 0.0063$) (Table B8). Besides, sensitivity analyses following the omit one procedure did not show influential observations changing the magnitude or direction of overall effect sizes.

Table B1. List of publications included in our meta-analyses. 78 scientific studies, from 54 publications (including grey literature), were evaluated.

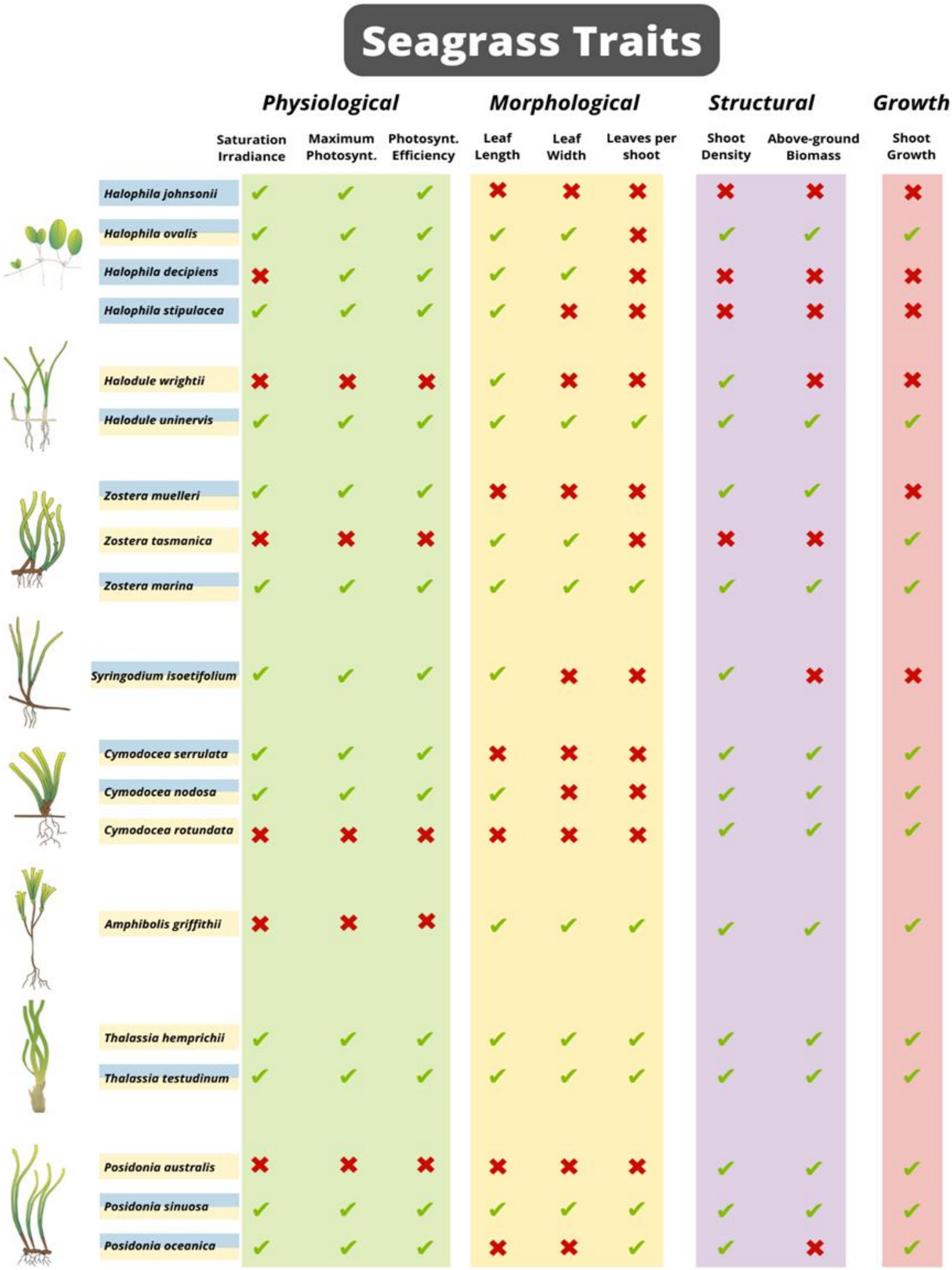
Study	ID	Article	Study Type	Seagrass Traits	Year	Title
1	1**	Marín-Guirao *et al.,* 2022	Shading	Physiological	2022	Photo-acclimatory thresholds anticipate sudden shifts in seagrass ecosystem state under reduced light conditions.
2	2	Wong *et al.,* 2020	Shading	Morphological	2020	Seasonal Response and Recovery of Eelgrass (*Zostera marina*) to Short-Term Reductions in Light Availability
3	3	Kong *et al.,* 2020	Shading	Mix	2020	Effects of shading on seagrass morphology and thermal optimal of productivity
4	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
5	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
6	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
7	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
8	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
9	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
10	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
11	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
12	4	Tuya *et al.,* 2019	Shading	Mix	2019	Biogeographical scenarios modulate seagrass resistance to small-scale perturbations
13	5	Barry *et al.,* 2018	Shading	Mix	2018	Resilience to shading influenced by differential allocation of biomass in *Thalassia testudinum*
14	5	Barry *et al.,* 2018	Shading	Mix	2018	Resilience to shading influenced by differential allocation of biomass in *Thalassia testudinum*
15	5	Barry *et al.,* 2018	Shading	Mix	2018	Resilience to shading influenced by differential allocation of biomass in *Thalassia testudinum*
16	6*	Lyimo *et al.,* 2018	Shading	Structural	2018	Shading and simulated grazing increase the sulphide pool and methane emission in a tropical seagrass meadow
17	7	Deyanova *et al.,* 2017	Shading	Mix	2017	Contribution of seagrass plants to CO_2 capture in a tropical seagrass meadow under experimental disturbance
18	8	Evans *et al.,* 2017	Shading	Growth	2017	Genotypic Diversity and Short-term Response to Shading Stress in a Threatened Seagrass: Does Low Diversity Mean Low Resilience?
19	8	Evans *et al.,* 2017	Shading	Growth	2017	Genotypic Diversity and Short-term Response to Shading Stress in a Threatened Seagrass: Does Low Diversity Mean Low Resilience?
20	8	Evans *et al.,* 2017	Shading	Growth	2017	Genotypic Diversity and Short-term Response to Shading Stress in a Threatened Seagrass: Does Low Diversity Mean Low Resilience?

21	8	Evans *et al.,* 2017	Shading	Growth	2017	Genotypic Diversity and Short-term Response to Shading Stress in a Threatened Seagrass: Does Low Diversity Mean Low Resilience?
22	8	Evans *et al.,* 2017	Shading	Growth	2017	Genotypic Diversity and Short-term Response to Shading Stress in a Threatened Seagrass: Does Low Diversity Mean Low Resilience?
23	8	Evans *et al.,* 2017	Shading	Growth	2017	Genotypic Diversity and Short-term Response to Shading Stress in a Threatened Seagrass: Does Low Diversity Mean Low Resilience?
24	9	Chartrand *et al.,* 2016	Shading	Structural	2016	Light Thresholds to prevent dredging impacts on the great barrier reef seagrass, *Zostera muelleri ssp. Capricorni*
25	10	Salo *et al.,* 2015	Shading	Mix	2015	Genotype-specific responses to light stress in eelgrass *Zostera marina*, a marine foundation plant
26	11*	Kim *et al.,* 2015	Shading	Mix	2015	Seasonal Growth Responses of the Seagrass *Zostera marina* under Severely Diminished Light Conditions
27	12*	McMahon & Lavery, 2014	Shading	Mix	2014	Canopy-scale modifications of the seagrass *Amphibolis griffithii* in response to and recovery from light reduction
28	13	Yaakub *et al.,* 2014	Shading	Mix	2014	Chronic light reduction reduces overall resilience to additional shading stress in the seagrass *Halophila ovalis*
29	13	Yaakub *et al.,* 2014	Shading	Mix	2014	Chronic light reduction reduces overall resilience to additional shading stress in the seagrass *Halophila ovalis*
30	14	Silva *et al.,* 2013	Shading	Physiological	2013	Physiological Responses of *Zostera marina* and *Cymodocea nodosa* to Light-Limitation Stress
31	15	LaNafie *et al.,* 2013	Shading	Morphological	2013	Biomechanical response of two fast-growing tropical seagrass species subjected to in situ shading and sediment fertilization
32	16	Serrano *et al.,* 2011	Shading	Mix	2011	Seasonal response of *Posidonia oceanica* to light disturbances
33	17*	Mateo *et al.,* 2010	Shading	Growth	2010	Long-term stability in the production of a NW Mediterranean *Posidonia oceanica* (L.) Delile meadow
34	18	Gartner *et al.,* 2010	Shading	Structural	2010	Light reductions drive macroinvertebrate changes in *Amphibolis griffithii* seagrass habitat
35	19	Collier *et al.,* 2009	Shading	Mix	2009	Shade-induced response and recovery of the seagrass *Posidonia sinuosa*
36	20	Lavery *et al.,* 2009	Shading	Mix	2009	Interactive effects of timing, intensity and duration of experimental shading on *Amphibolis griffithii*
37	21	Bité *et al.,* 2007	Shading	Physiological	2007	Chlorophyll fluorescence measures of seagrasses *Halophila ovalis* and *Zostera capricorni* reveal differences in response to experimental shading
38	21	Bité *et al.,* 2007	Shading	Physiological	2007	Chlorophyll fluorescence measures of seagrasses *Halophila ovalis* and *Zostera capricorni* reveal differences in response to experimental shading
39	22	Mackey *et al.,* 2007	Shading	Mix	2007	Effects of experimental reduction of light availability on the seagrass *Amphibolis griffithii*
40	23*	Fokeera-Wahedally & Bhikajee, 2005	Shading	Mix	2005	The effects of in situ shading on the growth of a seagrass, *Syringodium isoetifolium*
41	24*	Ibarra-Obando *etal.,* 2005	Shading	Mix	2005	Response of Turtlegrass to Natural and Reduced Light Regimes Under Conditions of Rhizome Isolation

42	25	Ruiz & Romero, 2001	Shading	Mix	2001	Effects of in situ experimental shading on the Mediterranean seagrass *Posidonia oceanica*
43	26*	Uy *et al.,* 2001	Shading	Mix	2001	Functioning of philippine seagrass species under deteriorating light conditions
44	26*	Uy *et al.,* 2001	Shading	Mix	2001	Functioning of philippine seagrass species under deteriorating light conditions
45	27	Longstaff *et al.,* 1999	Shading	Mix	1999	Effects of light deprivation on the survival and recovery of the seagrass *Halophila ovalis* (R.Br.) Hook
46	28*	Neely 2000	Shading	Mix	1999	Somatic, respiratory, and photosynthetic responses of the seagrass *Halodule wrightii* to light reduction in Tampa Bay, Florida including a whole plant carbon budget
47	29*	Bach *et al.,* 1998	Shading	Mix	1998	Species composition and plant performance of mixed seagrass beds along a siltation gradient at Cape Bolinao, The Philippines
48	30	Lee & Dunton, 1997	Shading	Mix	1997	Effects of in situ light reduction on the maintenance, growth and partitioning of carbon resources in *Thalassia testudinum* Banks ex Kijnig
49	31	Goodman *et al.,* 1995	Shading	Physiological	1995	Photosynthetic Responses of Eelgrass (*Zostera marina* L) to Light and Sediment Sulfide in a Shallow Barrier Island Lagoon
50	32*	Czerny & Dunton, 1995	Shading	Growth	1995	The Effects of in Situ Light Reduction on the Growth of Two Subtropical Seagrasses, *Thalassia testudinum* and *Halodule wrightit*
51	33	Fitzpatrick & Kirkman 1995	Shading	Mix	1995	Effects of prolonged shading stress on growth and survival of seagrass *Posidonia australis* in Jervis Bay, New South Wales, Australia
52	34*	Gordon *et al.,* 1994	Shading	Mix	1994	Changes to the structure and productivity of a *Posidonia sinuosa* meadow during and after imposed shading
53	35	Bulthius, 1983	Shading	Morphological	1983	Effects of in situ light reduction on density and growth of the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) Den Hartog in western port, Victoria, Australia
54	36	Sharon *et al.,* 2011	Depth	Physiological	2011	Photoacclimation of the seagrass *Halophila stipulacea* to the dim irradiance at its 48-meter depth limit
55	37	Campbell *et al.,* 2007	Depth	Physiological	2007	Patterns in tropical seagrass photosynthesis in relation to light, depth and habitat
56	38	Schubert & Demes, 2017	Depth	Mix	2017	Phenotypic plasticity in the marine angiosperm *Halophila decipiens* (Hydrocharitaceae, Streptophyta)
57	39	Schwarz and Hellblom, 2002	Depth	Mix	2002	The photosynthetic light response of *Halophila stipulacea* growing along a depth gradient in the Gulf of Aqaba, the Red Sea
58	40	Park *et al.,* 2016	Depth	Mix	2016	Photoacclimatory Responses of *Zostera marina* in the Intertidal and Subtidal Zones
59	40	Park *et al.,* 2016	Depth	Mix	2016	Photoacclimatory Responses of *Zostera marina* in the Intertidal and Subtidal Zones
60	41	Olesen *et al.,* 2002	Depth	Mix	2002	Depth-acclimation of photosynthesis, morphology and demography of *Posidonia oceanica* and *Cymodocea nodosa* in the Spanish Mediterranean Sea
61	41	Olesen *et al.,* 2002	Depth	Mix	2002	Depth-acclimation of photosynthesis, morphology and demography of *Posidonia oceanica* and *Cymodocea nodosa* in the Spanish Mediterranean Sea

62	42	Collier *et al.*, 2008	Depth	Physiological	2008	Physiological characteristics of the seagrass *Posidonia sinuosa* along a depth-related gradient of light availability
63	42	Collier *et al.*, 2008	Depth	Physiological	2008	Physiological characteristics of the seagrass *Posidonia sinuosa* along a depth-related gradient of light availability
64	43	Dattolo *et al.*, 2014	Depth	Physiological	2014	Response of the seagrass *Posidonia oceanica* to different light environments: Insights from a combined molecular and photo-physiological study
65	44	Schwarz *et al.*, 2004	Depth	Physiological	2004	Contribution of photosynthetic gains during tidal emersion to production of *Zostera capricorni* in a North Island, New Zealand estuary
66	45	Massini & Manning, 1997	Depth	Physiological	1997	The photosynthetic responses to irradiance and temperature of four meadow-forming seagrasses
67	46	Tuya *et al.*, 2016	Depth	Physiological	2016	Photo-physiological performance and short-term acclimation of two coexisting macrophytes (*Cymodocea nodosa* and *Caulerpa prolifera*) with depth
68	47	Schwarz *et al.*, 2000	Depth	Physiological	2000	Photosynthetic utilisation of carbon and light by two tropical seagrass species as measured in situ
69	48	Enríquez *et al.*, 2019	Depth	Mix	2019	Structural complexity governs seagrass acclimatization to depth with relevant consequences for meadow production, macrophyte diversity and habitat carbon storage capacity
70	49	Bité *et al.*, 2007	Depth	Physiological	2007	Chlorophyll fluorescence measures of seagrasses *Halophila ovalis* and *Zostera capricorni* reveal differences in response to experimental shading
71	49	Bité *et al.*, 2007	Depth	Physiological	2007	Chlorophyll fluorescence measures of seagrasses *Halophila ovalis* and *Zostera capricorni* reveal differences in response to experimental shading
72	50	Durako *et al.*, 2003	Depth	Physiological	2003	Depth-related variability in the photobiology of two populations of *Halophila johnsonii* and *Halophila decipiens*
73	50	Durako *et al.*, 2003	Depth	Physiological	2003	Depth-related variability in the photobiology of two populations of *Halophila johnsonii* and *Halophila decipiens*
74	51	Dawes, 1998	Depth	Mix	1998	Biomass and photosynthetic responses to irradiance by a shallow and a deep water population of thalassia testudinum on the west coast of florida
75	52	Collier *et al.*, 2007	Depth	Mix	2007	Morphological, growth and meadow characteristics of the seagrass *Posidonia sinuosa* along a depth related gradient of light availability
76	52	Collier *et al.*, 2007	Depth	Mix	2007	Morphological, growth and meadow characteristics of the seagrass *Posidonia sinuosa* along a depth related gradient of light availability
77	53	Sharon *et al.*, 2009	Depth	Physiological	2009	Photosynthetic responses of *Halophila stipulacea* to a light gradient. II. Acclimations following transplantation
78	54	Olesen *et al.*, 2017	Depth	Mix	2017	Depth-Related Changes in Reproductive Strategy of a Cold-Temperate *Zostera marina* Meadow

* Publications marked with an asterisk were added to the full list of scientific studies included in our meta-analyses as the search terms failed to capture them. The publication marked with 2 asterisks (**) was included, since we had data prior to publication.



Seagrass Traits

	Physiological			Morphological			Structural		Growth
	Saturation Irradiance	Maximum Photosynt.	Photosynt. Efficiency	Leaf Length	Leaf Width	Leaves per shoot	Shoot Density	Above-ground Biomass	Shoot Growth
Halophila johnsonii	✓	✓	✓	✗	✗	✗	✗	✗	✗
Halophila ovalis	✓	✓	✓	✓	✓	✗	✓	✓	✓
Halophila decipiens	✗	✓	✓	✓	✓	✗	✗	✗	✗
Halophila stipulacea	✓	✓	✓	✓	✗	✗	✗	✗	✗
Halodule wrightii	✗	✗	✗	✓	✗	✗	✓	✗	✗
Halodule uninervis	✓	✓	✓	✓	✓	✓	✓	✓	✓
Zostera muelleri	✓	✓	✓	✗	✗	✗	✓	✓	✗
Zostera tasmanica	✗	✗	✗	✓	✓	✗	✗	✗	✓
Zostera marina	✓	✓	✓	✓	✓	✓	✓	✓	✓
Syringodium isoetifolium	✓	✓	✓	✓	✗	✗	✓	✗	✗
Cymodocea serrulata	✓	✓	✓	✗	✗	✗	✓	✓	✓
Cymodocea nodosa	✓	✓	✓	✓	✗	✗	✓	✓	✓
Cymodocea rotundata	✗	✗	✗	✗	✗	✗	✓	✓	✓
Amphibolis griffithii	✗	✗	✗	✓	✓	✓	✓	✓	✓
Thalassia hemprichii	✓	✓	✓	✓	✓	✓	✓	✓	✓
Thalassia testudinum	✓	✓	✓	✓	✓	✓	✓	✓	✓
Posidonia australis	✗	✗	✗	✗	✗	✗	✓	✓	✓
Posidonia sinuosa	✓	✓	✓	✓	✓	✓	✓	✓	✓
Posidonia oceanica	✓	✓	✓	✗	✗	✓	✓	✗	✓

Figure B1. Seagrass traits found grouped by organizational level (colours) and species. Species are grouped by genus, from smallest sizes (upper panel) to largest (lower panel). Seagrass traits studied in at least one scientific publication were denoted with a green tick, while those with a red cross were not studied in any of them. Boxes enclosing species names are shown in yellow and blue shades depending on publication type (shading and depth-based, respectively).

Table B2. Linear model fitting using the logarithmic transformation of vertical distribution as response variable and rhizome diameter as predictor.

Coefficients	*Estimate*	*Std. Error*	*t value*	*P-value*	
Intercept	2.75	0.25	10.80	**< 0.001**	***
Rhizome diameter	-0.01	0.06	-0.22	0.82	
Multiple R Squared:	0.001				
Adjusted R Squared:	-0.03				
ANOVA Table					
	Sum sq	*Df*	*F value*	*P-value*	
Rhizome diameter	0.047	1	0.051	0.823	
Residuals	32.526	35			

Table B3. Linear model fitting using the square-root transformation of vertical distribution as response variable and seagrass growth/reproductive strategy as categorical predictor.

	Sum Sq	*Mean Sq*	*Df*	*F value*	*P-value*
Growth/Reproductive Strategy	22.35	5.59	4	1.63	0.178
Residuals	194.89	3.42	57		

Table B4. Meta-analytic models and values of significance

Fitted Model	*Trait*	*Est.*	*se*	*tval*	*df*	*ci.lb*	*ci.ub*	*P-value*
Random-Effects Model	Saturation Irradiance	-0.711	0.15	-4.85	34	-1.009	-0.413	**<0.0001*** **
Random-Effects Model	Maximum Photosynthesis	-0.329	0.09	-3.47	44	-0.520	-0.138	**0.0012** **
Random-Effects Model	Photosynthetic Efficiency	0.289	0.08	3.41	39	0.118	0.460	**0.0015** **
Random-Effects Model	Leaf Length	0.134	0.11	1.18	25	-0.100	0.368	0.2490
Random-Effects Model	Leaf Width	-0.008	0.05	-0.16	23	-0.115	0.098	0.8739
Mixed-Effects Model	Leaves per shoot	-0.212	0.09	-2.39	15	-0.384	-0.038	**0.0165***
Random-Effects Model	Shoot Density	-0.972	0.15	-6.63	48	-1.266	-0.677	**<0.0001*** **
Mixed-Effects Model	Above-ground Biomass	-1.213	0.26	-4.73	26	-1.724	-0.714	**<0.0001*** **
Random-Effects Model	Shoot Growth	-0.419	0.10	-4.16	41	-0.622	-0.215	**0.0002*** **

Table B5. Analysis of variance (type II) from linear mixed models (LMMs). The logarithmic transformation of the specific seagrass vertical distribution (m) was set as the response variable and trait acclimatization potential (i.e., weighted effect sizes) and type of study as predictors. Article was set as a random factor in LMMs. Likelihood ratio tests were applied.

Trait	*Predictors*	*Chisq*	*Df*	*P - value*
Saturation Irradiance	Effect Size	8.21	1	**0.004****
	Type of Study	0.49	1	0.485
	Effect Size*Type of study	0.73	1	0.394
Maximum Photosynthesis	Effect Size	0.49	1	0.482
	Type of Study	1.17	1	0.280
Photosynthetic Efficiency	Effect Size	0.15	1	0.696
	Type of Study	2.47	1	0.116
	Effect Size*Type of study	0.70	1	0.402
Shoot Density	Effect Size	0.01	1	0.940
Shoot Growth	Effect Size	1.52	1	0.217

Table B6. Analysis of variance (type II) from linear models (LMs). The logarithmic transformation of the specific seagrass vertical distribution (m) was set as the response variable and trait acclimatization potential (i.e., weighted effect sizes) as the predictor. F-tests were applied.

Trait	*Predictors*	*Sum sq*	*Df*	*F-value*	*P - value*
Leaves per shoot	Effect Size	15.63	1	59.23	**< 0.001*****
	Residuals	3.69	14		
Above-ground Biomass	Effect Size	3.16	1	5.39	**0.0288***
	Residuals	14.65	25		

Table B7. Egger's tests for publication bias.

Trait	*b*	*tval*	*df*	*ci.lb*	*ci.ub*	*P-value*	
Saturation Irradiance	-1.8178	3.1163	33	-2.3316	-1.3041	**0.0038**	**
Maximum Photosynthesis	-0.8000	1.7370	43	-1.1645	-0.4355	0.0895	
Photosynthetic Efficiency	-0.2961	5.7979	38	-0.3293	-0.2628	**<0.0001**	***
Leaf Length	0.1430	0.5448	24	-0.0735	0.3595	0.5909	
Leaf Width	-0.0935	0.9474	22	-0.2450	0.0580	0.3537	
Leaves per shoot	0.1068	-1.9687	14	-0.1240	0.3377	0.0691	
Shoot Density	-0.1008	-3.1702	47	-0.4350	0.2334	**0.0027**	**
Above-ground Biomass	0.0432	-5.1798	25	-0.0960	0.1823	**<0.0001**	***
Shoot Growth	-0.0605	-2.4294	40	-0.1966	0.0755	**0.0197**	*

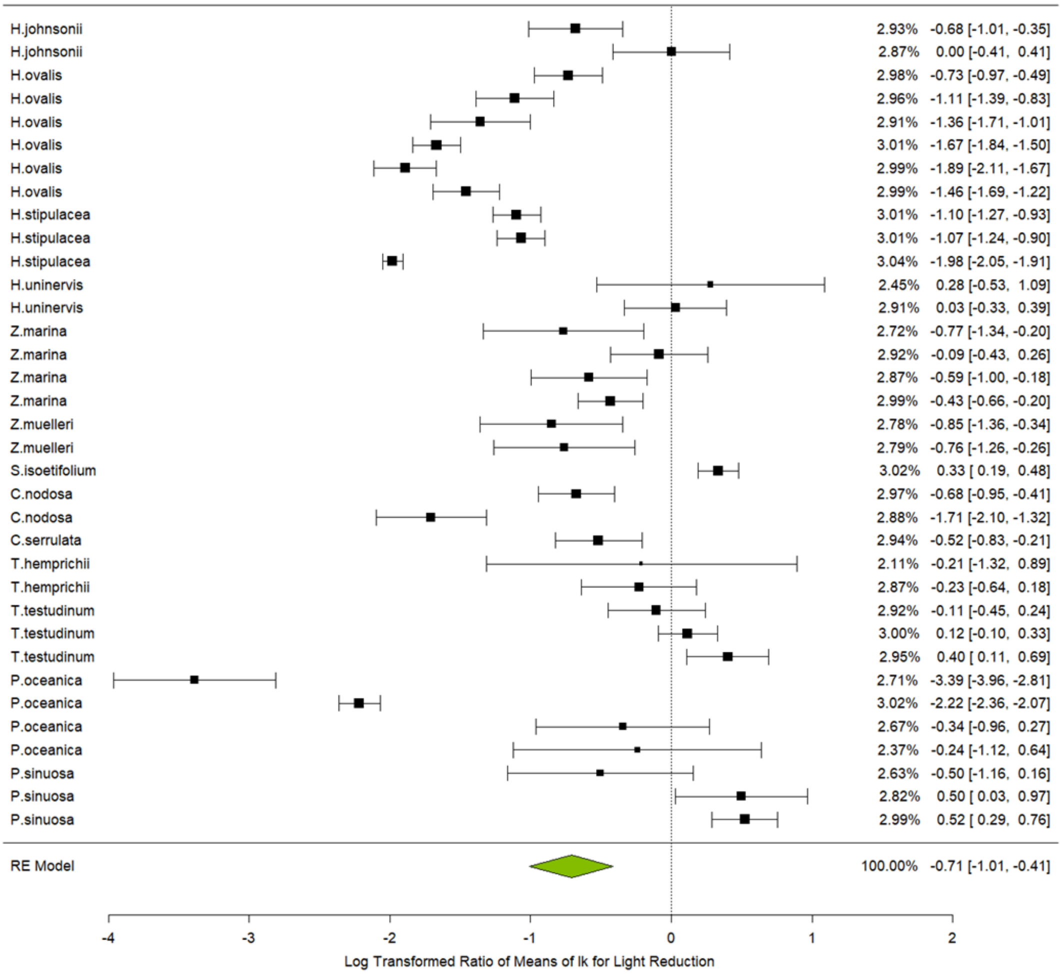
Table B8. Results of trim-and-fill method for estimating and adjusting for the number and outcomes of missing studies for each separate meta-analysis related to each trait.

Trait	*Est.*	*se*	*tval*	*df*	*ci.lb*	*ci.ub*	*P-value*	
Saturation Irradiance	-1.005	0.15	-6.57	42	-1.304	-0.704	**< 0.0001**	***
Maximum Photosynthesis	-0.603	0.10	-5.77	56	-0.808	-0.398	**< 0.0001**	***
Photosynthetic Efficiency	0.289	0.08	3.41	39	0.118	0.460	**0.0015**	**
Leaf Length	0.342	0.13	2.73	31	0.096	0.587	**0.0063**	**
Leaf Width	0.081	0.05	1.55	30	-0.021	0.183	**0.1202**	
Leaves per shoot	-0.185	0.06	-2.95	15	-0.319	-0.051	**0.0099**	**
Shoot Density	-0.972	0.145	-6.63	48	-1.266	-0.677	**< 0.0001**	***
Above-ground Biomass	-1.127	0.18	-6.41	27	-1.472	-0.782	**< 0.0001**	***
Shoot Growth	-0.419	0.10	-4.16	41	-0.622	-0.215	**0.0002**	***

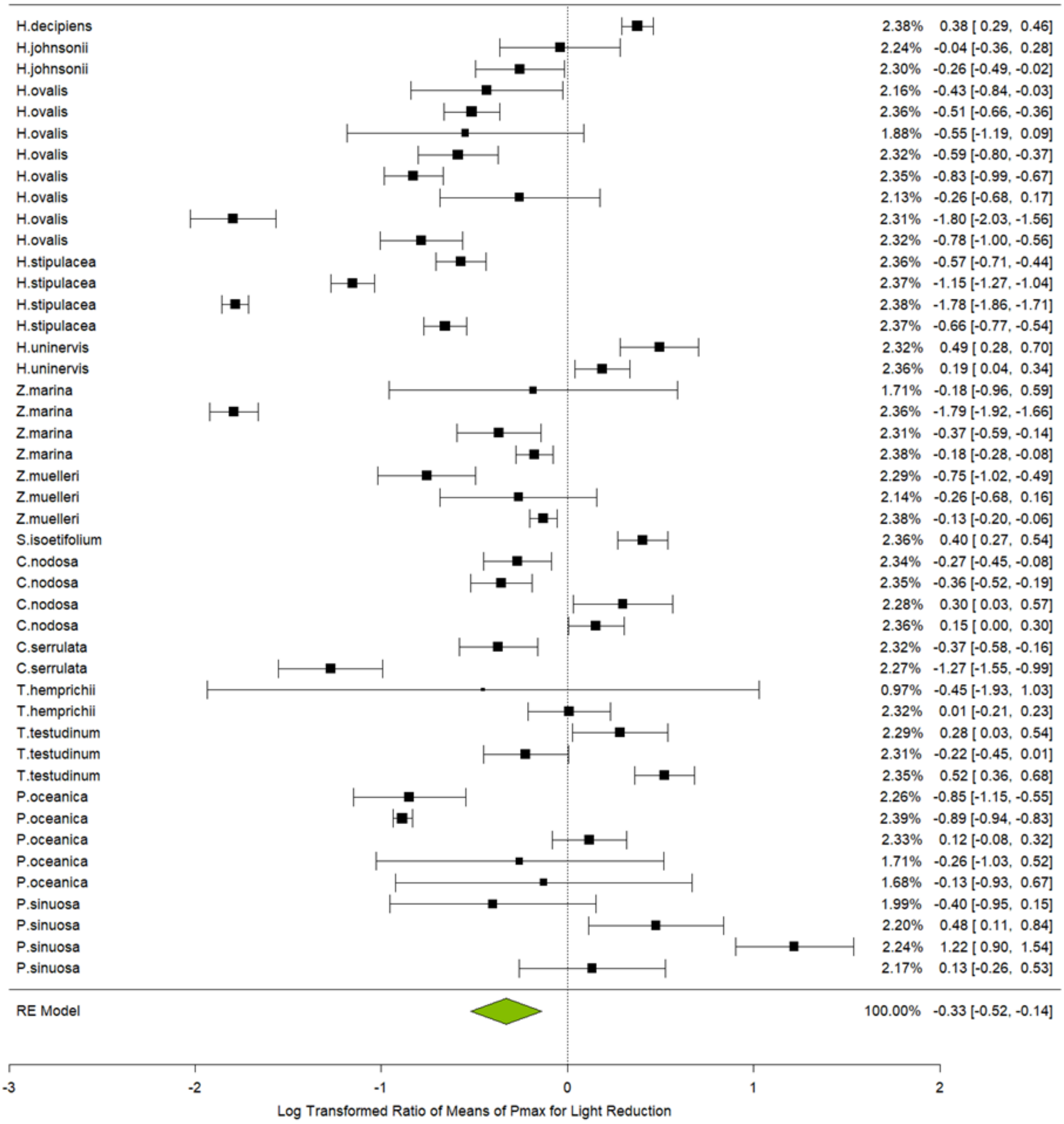
Red color indicates the traits that change their significance value when adjusted for publication bias.

Figure B2. Forest plots for all the response variables tested.

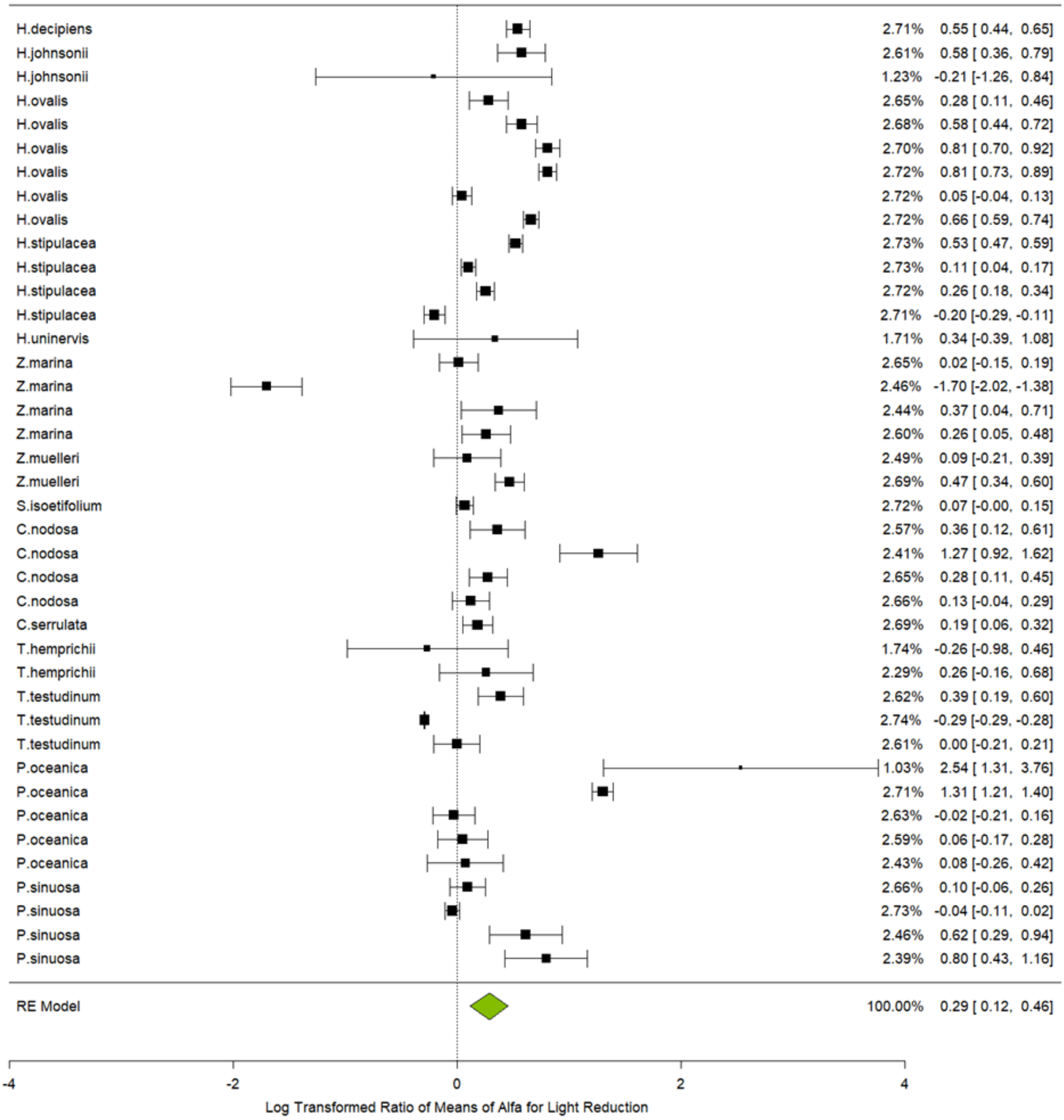
a) Saturation irradiance (I_k)



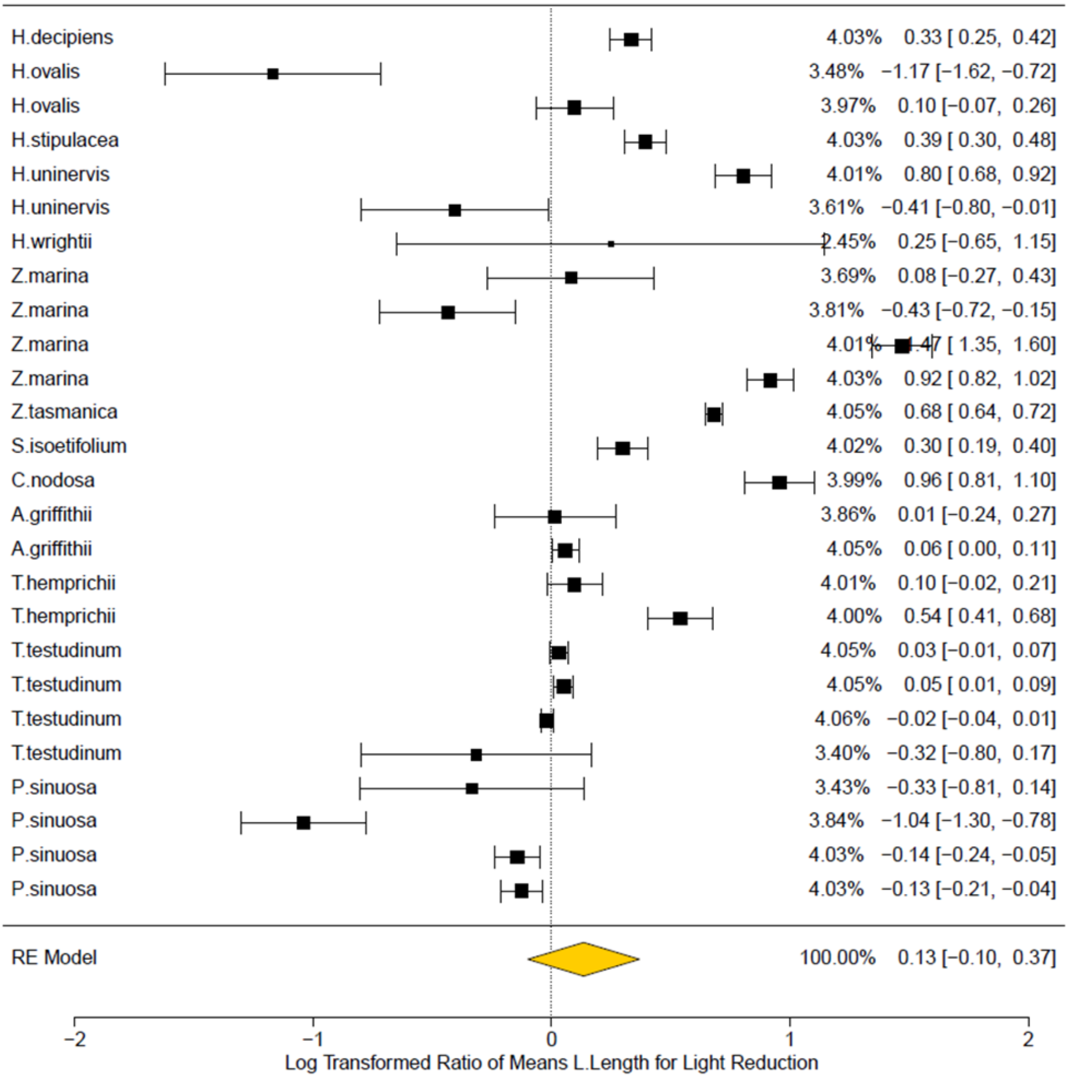
b) Maximum photosynthesis (P_{max})



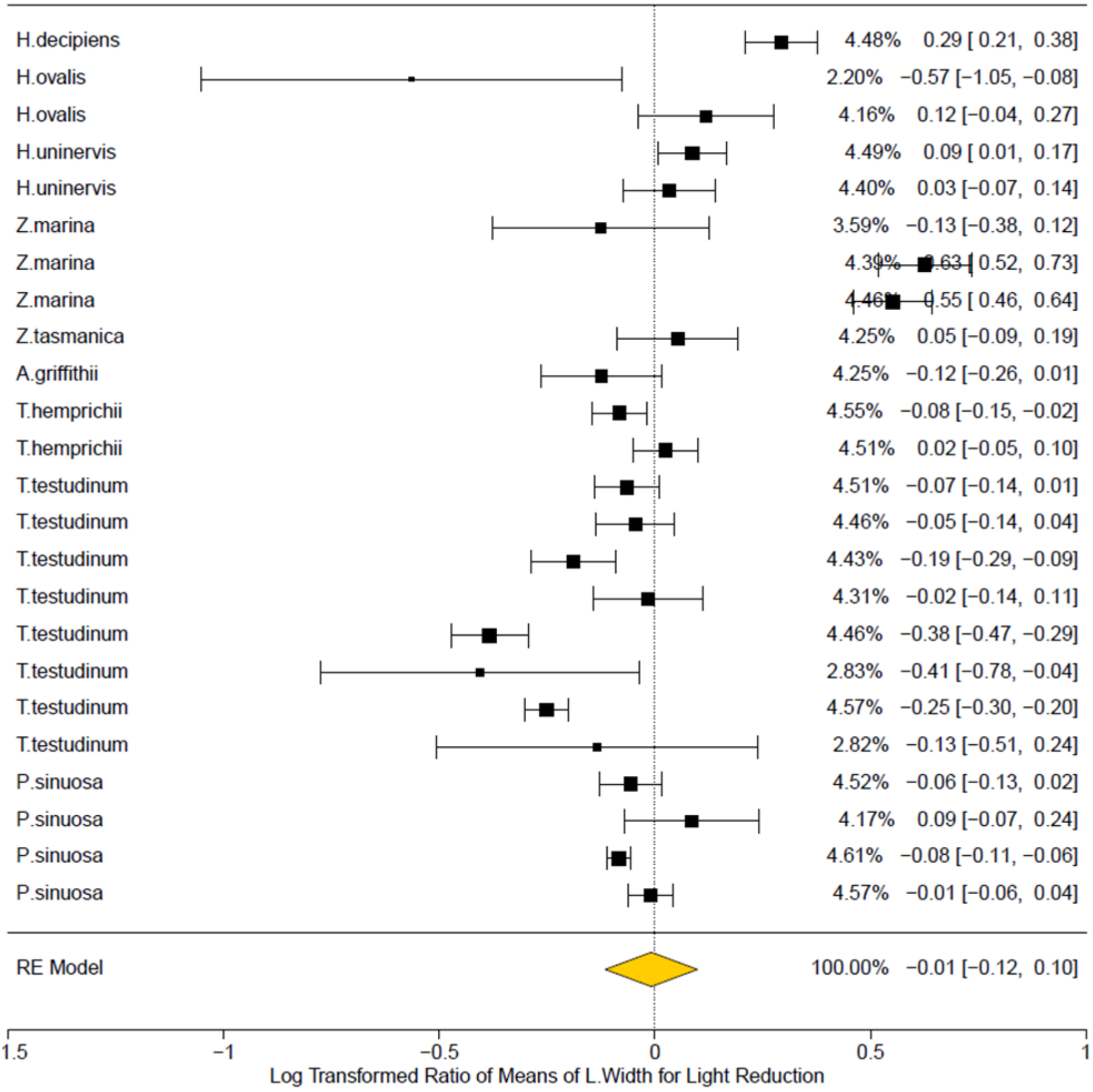
c) Photosynthetic efficiency (α)



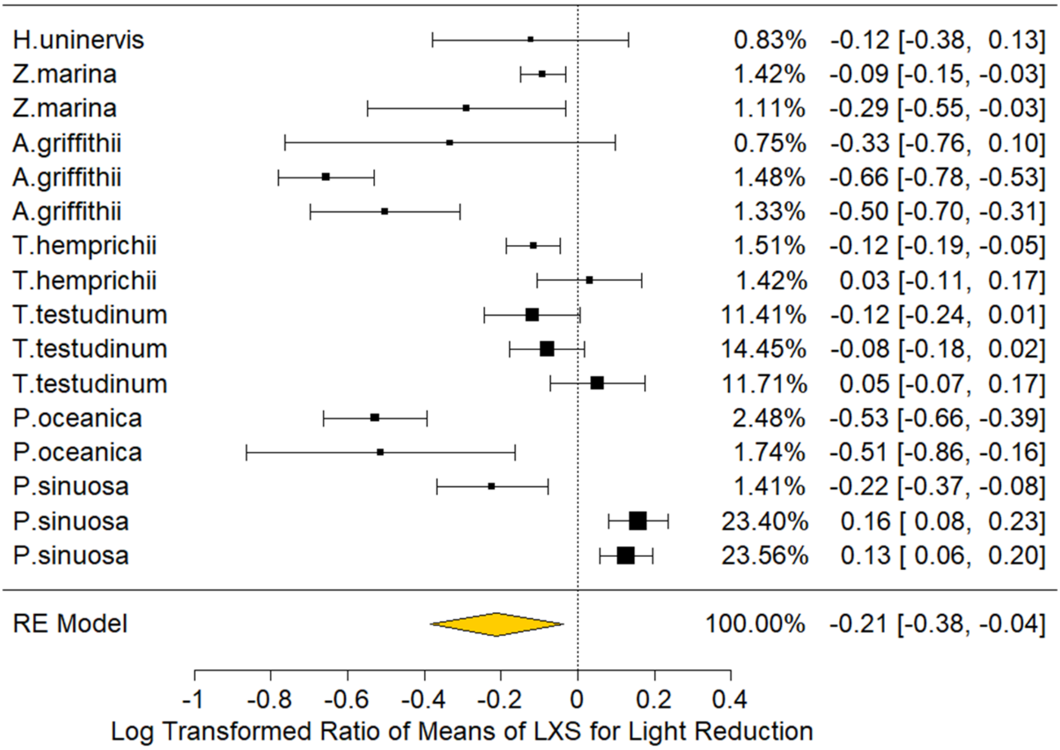
d) Leaf length (L.Length)



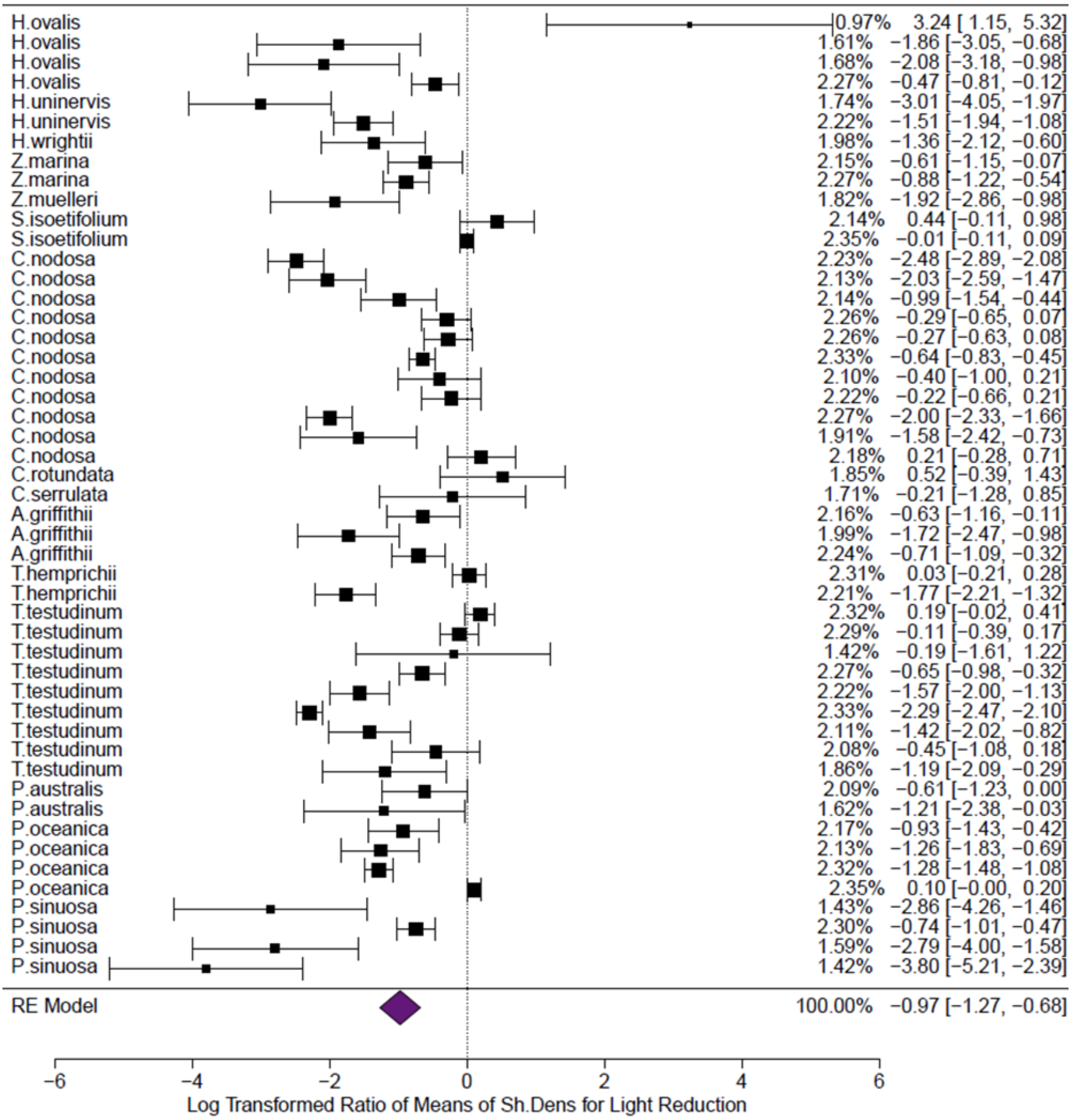
e) Leaf width (L.Width)



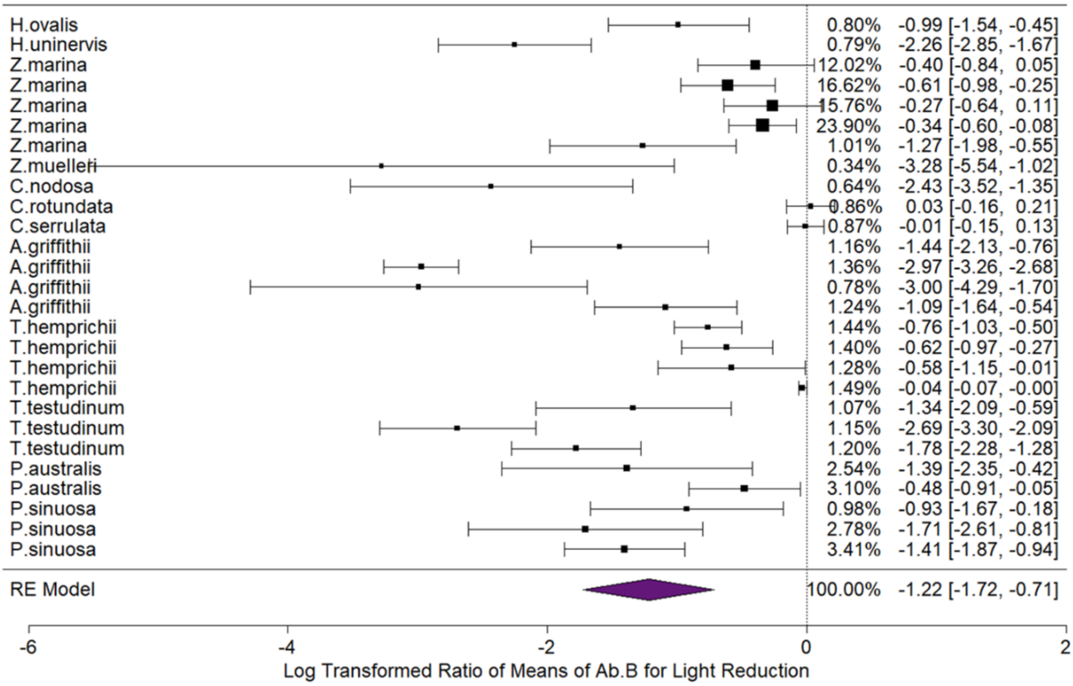
f) Leaves per shoot (LXS)



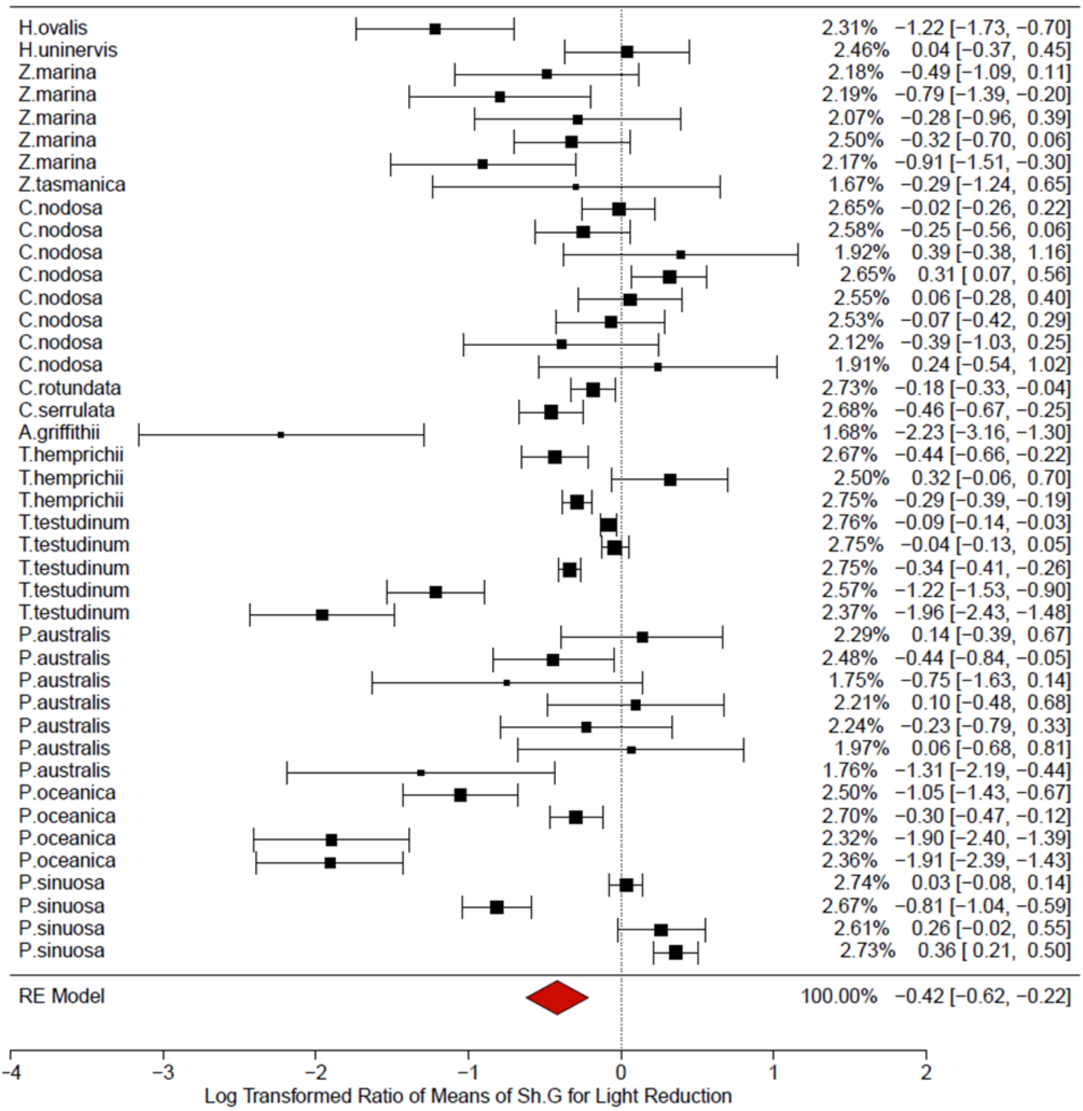
g) Shoot density (Sh. Dens)



h) Above-ground Biomass (Ab.B)



i) Shoot Growth (Sh.G)



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Appendix C

Table C1. Goodness-of-fit statistics and criteria for selecting the distribution of the response variable ‘Halo size’.

Goodness-of-fit statistics			
	Gamma	*Log-normal*	*Weibull*
Kolmogorov-Smirnov	0.123	**0.073·**	0.131
Cramer-Von Mises	3.651	0.933	4.829
Anderson-Darling	20.232	5.219	29.299
Goodness-of-fit criteria			
AIC	8839.015	**8676.955**	8963.809
BIC	8849.225	**8687.165**	8947.019

Table C2. Summary of general LMM models (i.e., including halos of *Arbacia lixula* and *Paracentrotus lividus*) evaluated with multi-model inference that yielded delta values lower than two, to assess the vulnerability of marine forests to sea urchin overgrazing. The finally selected model, based on AICc and likelihood ratio tests, is shown in bold.

(Intercept)	Annual max Chl. a	Depth	Habitat type	Protect. level	Size	Species	Annual max SST	Size * Chl. a	Species * Chl. a	Species * Habitat	df	logLik	AICc	delta	weight
1.404	0.025	0.051	+	+	0.276	+		-0.019	+	+	17	-688.7	1401.98	0	0.53
-2.409	**0.033**	**0.049**	**+**	**+**	**0.276**	**+**	**0.139**	**-0.019**	**+**	**+**	**18**	**-682.8**	**1402.19**	**0.21**	**0.47**

Table C3. Analysis of variance (type III) from the general LMM (i.e., including halos of *Arbacia lixula* and *Paracentrotus lividus*) explaining halo size (halo diameter in cm) as a function of all predictor variables. The likelihood ratio test was applied.

Predictors	*LR Chisq*	*Df*	*P - value*
Intercept	1.573	1	0.210
Species	57.401	1	**< 0.001*****
Sea urchin size	246.745	1	**< 0.001*****
Protection level	9.463	1	**0.002****
Habitat type	10.027	2	**0.007****
Annual max. chlorophyll *a*	0.633	1	0.426
Annual max. SST	3.687	1	0.055·
Depth	32.222	1	**< 0.001*****
Species * Annual max. chlorophyll *a*	6.626	1	**0.010***
Sea urchin Size * Annual max. chlorophyll *a*	17.381	1	**< 0.001*****
Species * Habitat type	11.175	2	**0.004****

Table C4. Analysis of variance (type III) from species-specific LMMs explaining the size of the halos produced by *A. lixula* and *P. lividus* as a function of all predictor variables. The likelihood ratio test was applied.

Predictors	*LR Chisq*	*df*	*P – value*
Arbacia lixula			
Intercept	0.144	1	0.705
Sea urchin size	18.869	1	**< 0.001*****
Protection level	1.142	1	0.285
Habitat type	3.688	2	0.158
Annual max. chlorophyll *a*	0.754	1	0.385
Annual max. SST	0.060	1	0.807
Depth	4.355	1	**0.037***
Sea urchin size * Annual max. chlorophyll *a*	4.398	1	**0.036***
Paracentrotus lividus			
Intercept	3.478	1	0.062·
Sea urchin size	265.337	1	**< 0.001*****
Protection level	8.836	1	**0.003****
Habitat type	7.826	2	**0.020***
Annual max. chlorophyll *a*	4.063	1	**0.044***
Annual max. SST	4.928	1	**0.026***
Depth	28.916	1	**< 0.001*****
Sea urchin size * Annual max. chlorophyll *a*	13.215	1	**< 0.001*****

Table C5. Significant multiple comparisons of means: Tukey contrasts for the effect of habitat type (i.e., turf, shrub-forming algae or Fucales) on the halos produced by *P. lividus.*

Predictor	*Tukey Contrast*	*Est.*	*Std. Errors*	*Df*	*Stat.*	*Adj. p-value*
Hab. type	Shrub-forming – Fucales	-0.108	0.05	1	-2.132	0.099·
Hab. type	Turf – Fucales	0.028	0.06	1	0.449	0.894
Hab. type	Turf - Shrub-forming	0.137	0.06	1	2.44	**0.039***

Appendix D

Supplementary Text D3: Abundance of herbivorous fishes in the study site

Materials and Methods

Study area

The study was conducted in the island of Crete (Greece) in September 2021. Crete, in the eastern Mediterranean, has an herbivorous fish assemblage of four ubiquitous species, the natives, *Sarpa salpa* and *Sparisoma cretense*, and two invasive rabbitfish, *Siganus rivulatus*, first reported in Cretan waters in 2010 (Poursanidis & Zenetos, 2013) and *S. luridus*, first reported in Dodecanese waters in the late 1950s (Stergiou, 1988). The study was designed to characterize the herbivore fish assemblage across the island, to determine pairwise association strength between species, and to evaluate individual bite rates (our proxy of foraging activity) of species, in mono- and multi-specific groups, and along a gradient of shoal size. We sampled four locations along the north coast (in the Cretan Sea): Agia Pelagia, Psaromoura, Hersonissos, Elounda; and three locations along the south coast (in the Libyan Sea): Agios Ioannis, Vathi and Krassas (see caption in Fig. S1 of this Appendix). At each location, fish surveys were conducted around noon (between 11:00 am and 2:00 pm) to minimize diurnal variations in fish assemblages (Willis et al., 2006; Myers et al., 2016). All surveys were carried out by snorkeling over shallow rocky reef habitats (depth range 0 – 6 m). Most reefs were dominated by photophilic turf algae typical of early colonization stages, or with canopy-forming species of fucales, composed mostly of *Cystoseira spp*. (*sensu lato)*, close to the surface. At all sites, reefs were adjacent to (or mixed with) sandy areas, with patches of *Posidonia oceanica* and *Cymodocea nodosa* completing the mosaic of these highly variable coastal areas.

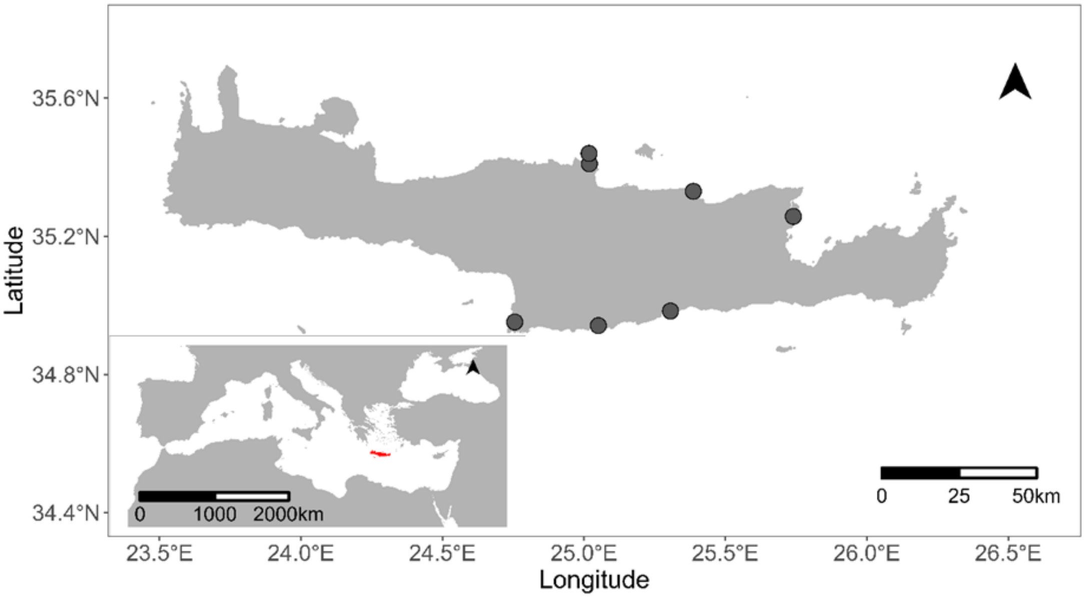

Figure D1. Sampling locations on the north coast (Cretan Sea), Psaromoura, Agia Pelagia, Hersonissos and Elounda (from west to east, respectively); and on the south coast of Crete (Libyan Sea), Vathi, Agios Ioannis and Krassas (from west to east, respectively). In the lower left corner, Crete's location in the Mediterranean Sea is highlighted in red.

Characterizing abundances of herbivore shoals

We quantified the abundance of native and invasive herbivorous fish species using visual transects of 50 m x 5 m (n = 3 per location) at six locations of Crete's shallow rocky reefs (Agia Pelagia, Psaromoura, Elounda, Agios Ioannis, Vathi and Krassas). Replicate transects were separated by at least 10 m (Schramm et al., 2020). Along the transect, the observer (TA) recorded the type (mono- and multi-specific) and size of each shoal (number of individuals), as well as the number of individuals of each species and their average individual sizes (cm).

Data Analysis

Abundances of herbivore shoals: We examined differences in fish abundance per species and shoal type with a linear mixed model (LMM). In this LMM, we set 'Abundance' (fish individuals transect^{-1}) as the response variable, and 'Species' (four levels: *S. salpa*, *S. luridus*, *S. rivulatus* and *S. cretense*), and 'Shoal Type' (two levels: mono- and multi-specific shoals) as fixed predictor variables. 'Location' (six levels: Agia Pelagia, Psaromoura, Elounda, Agios Ioannis, Vathy and Krassas) was included as a random factor to control for site-level variance. All the assumptions of linear models were met after logarithmic transformation of the response variable. We evaluated model assumptions with visual and statistical examination of residuals using the R packages, *performance* (Lüdecke et al., 2021) and DHARMa (Hartig, 2022).

Results

Abundances of herbivore shoals

Most species in the herbivore fish assemblage in Crete were found predominantly in shoals. Along the transects, individuals were encountered in shoals 89% of the time for *Sarpa salpa*, 75% of the time for *Siganus rivulatus*, and 60% of the time for *Siganus luridus*. Only the native parrotfish *Sparisoma cretense* was observed almost equally in shoals (49%) as alone. However, herbivore abundance did not vary between mono- and multi-specific shoals (*P = 0.479*), and there was no evidence of an interactive effect of shoal type and species (*P = 0.515*) (see Table D1; Fig. D2). In contrast, herbivorous fish abundance varied strongly across species (*P < 0.001*) (see Table D1; Fig. D2). The invasive *S. rivulatus* was by far the most abundant in Crete's herbivorous fish assemblage (mean ± SE = 33 ± 4.48 individuals per transect), with abundances nearly 3 times higher than the native *S. salpa* (mean ± SE = 11.5 ± 3.48 individuals per transect), and eight times greater than its congener *S. luridus* (4.10 ± 0.87 individuals per transect) (Table D1). The abundance of the native *S. salpa* was significantly higher than *S. cretense*, which was the least abundant herbivore (mean ± SE = 2.67 ± 0.51 individuals per transect).

Table D1. Analysis of variance (type III) from LMMs explaining fish abundance (fish per transect^{-1}) as a function of species and shoal type. Location was set as a random factor. The likelihood ratio test was applied.

Predictors	*Chisq*	*Df*	*P - value*
(Intercept)	27.16	1	**< 0.001*****
Species	70.76	3	**< 0.001*****
Shoal type	0.50	1	0.479
Species * Shoal type	2.29	3	0.515

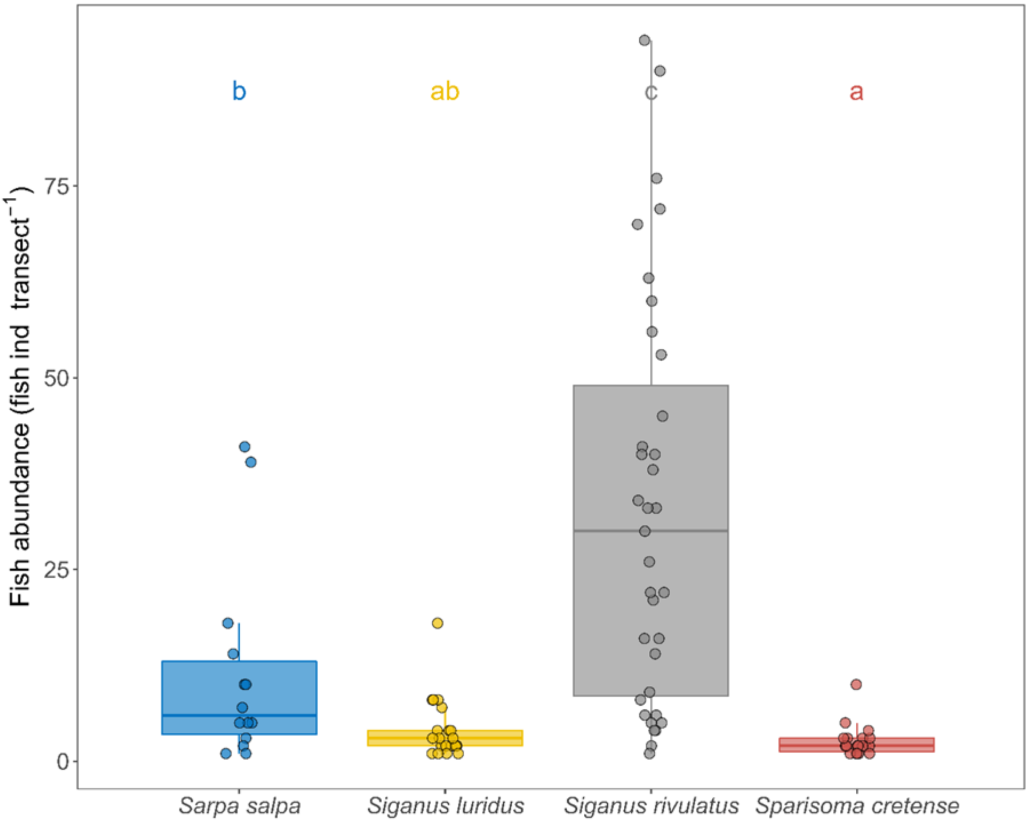

Figure D2. Relationships between fish abundance (fish individuals transect^{-1}) and the predictor 'Species'. Data points represent field observations of bite rates per individual measured of the four fish herbivorous species. Results of Tukey test are shown with letters.

Section D2: Statistical analyses on shoal size, shoaling strategy and fish foraging activity

Table D2. Goodness-of-fit statistics and criteria for selecting the distribution of the response variables ‘Shoal size’, ‘Bite rates’ and ‘Bout rates’.

Goodness-of-fit statistics for shoal size				
	Gamma	*Log-normal*	*Weibull*	*Neg. Binomial*
Kolmogorov-Smirnov	0.1238	**0.0783**	0.1273	0.1056
Cramer-Von Mises	0.5689	0.2110	0.6956	0.4959
Anderson-Darling	3.3554	1.4684	4.2907	4.2437
Goodness-of-fit criteria for shoal size				
AIC	1595.306	1575.442	1611.792	1611.128
BIC	1602.412	1582.547	1618.898	1618.234
Goodness-of-fit statistics for bite rates				
	Gamma	*Log-normal*	*Weibull*	
Kolmogorov-Smirnov	**0.0507·**	0.0603·	0.0777·	
Cramer-Von Mises	0.1412	0.2738	0.2373	
Anderson-Darling	0.9359	2.3740	1.2052	
Goodness-of-fit criteria for bite rates				
AIC	2374.23	2401.19	2372.15	
BIC	2381.600	2408.56	2380.27	
Goodness-of-fit statistics for bout rates				
	Gamma	*Log-normal*	*Weibull*	
Kolmogorov-Smirnov	**0.1047**	0.1239	0.1230	
Cramer-Von Mises	0.4229	0.4971	0.6007	
Anderson-Darling	2.4086	3.4406	3.1602	
Goodness-of-fit criteria for bout rates				
AIC	1377.88	1389.84	1387.74	
BIC	385.25	397.21	395.11	

Table D3. Analysis of variance (type III) from general and species-specific GLMs models (log-normal distribution) explaining shoal sizes (fish per shoal) as a function of species origin. The F test was applied.

Predictors	*Sum Sq*	*Df*	*F-value*	*P - value*
Intercept	960.95	1	2041.23	**< 0.001*****
Species origin	6.83	2	7.25	**< 0.001*****
Residuals	120.05	255		

Table D4. Analysis of variance (type III) from general GLMs models (gamma distribution) explaining fish foraging activity (bites per fish min^{-1} and bouts per fish min^{-1}) as a function of species, shoal type, shoal size, individual length and bouts (only in the model of bite rates). The likelihood ratio test was applied.

Predictors	*Chisq*	*Df*	*P - value*
Bites per minute			
Species	84.74	3	**< 0.001*****
Shoal type	0.64	1	0.424
Shoal size	8.60	1	**0.003***
Individual length	13.35	1	**<0.001*****
Bouts rates	13.43	1	**< 0.001*****
Shoal type * Shoal size	4.21	1	**0.040***
Bouts per minute			
Species	0.70	3	0.873
Shoal type	1.12	1	0.289
Shoal size	6.30	1	**0.012***
Individual length	4.41	1	**0.036***
Shoal type * Shoal size	0.19	1	0.664

Table D5. Significant multiple comparisons of means: Tukey contrasts for bite rates (measured as bite per fish min^{-1}) between species.

Predictor	*Tukey Contrast*	*Estimates*	*Std. Errors*	*Statistics*	*Adj. p-value*
Species	*S. luridus – S. salpa*	0.280	0.08	3.58	**0.002****
Species	*S. rivulatus – S. salpa*	0.535	0.07	7.93	**< 0.001*****
Species	*S. rivulatus – S. luridus*	0.255	0.08	3.04	**0.012***
Species	*S. cretense – S. luridus*	-0.401	0.10	-4.03	**< 0.001*****
Species	*S. cretense – S. rivulatus*	-0.656	0.09	-7.14	**< 0.001*****

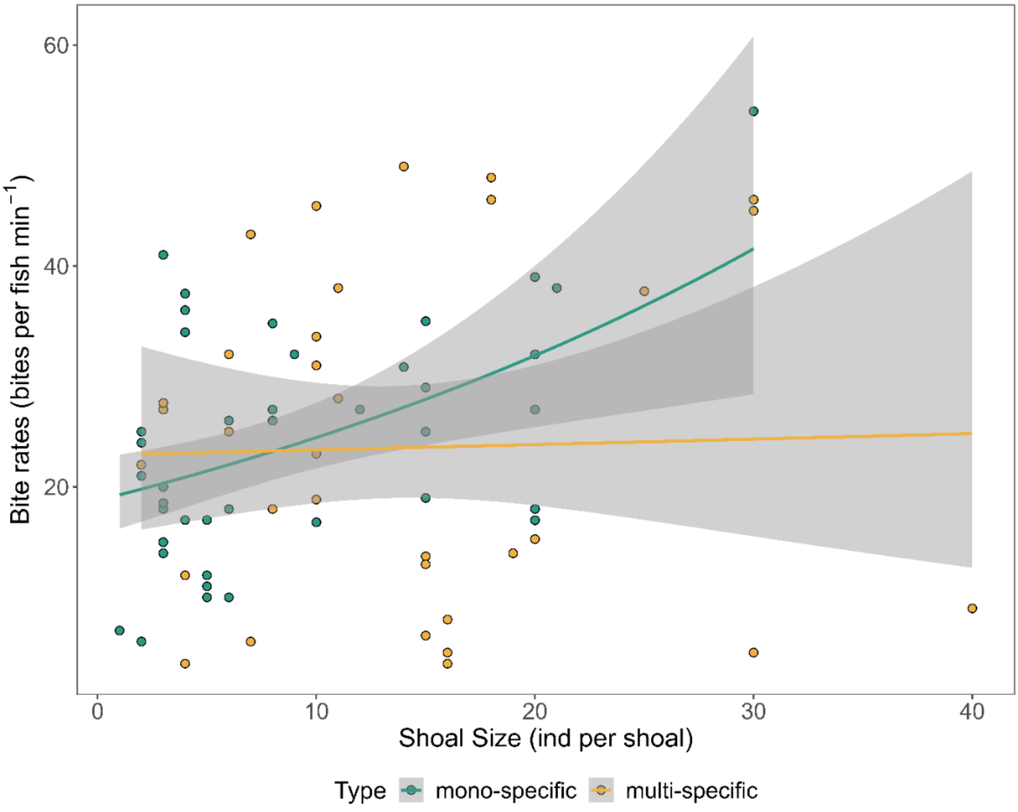

Figure D3. Relationship between the bite rates (measured in bites per fish min^{-1}) of the native herbivore *Sarpa salpa* and shoal type, along a gradient of shoal size, when it was the most abundant species within the shoal.

Table D6. Analysis of variance (type III) from GLMs explaining bites per fish min^{-1} as a function of shoal size, shoal type, individual length and bouts for each species studied. We dropped shoal type and/or the interaction between shoal type and shoal size from the model in those cases where there was insufficient data either because mono-specific shoals were not present (*S. luridus*), or large shoals were not represented in mono-specific shoals (*S. cretense*). The likelihood ratio test was applied.

	Sarpa salpa			***Siganus luridus***			***Siganus rivulatus***			***Sparisoma cretense***		
Predictors	*LR Chisq*	*Df*	*P - value*	*LR Chisq*	*Df*	*P - value*	*LR Chisq*	*Df*	*P - value*	*LR Chisq*	*Df*	*P - value*
Shoal size	0.96	1	0.328	**3.89**	1	**0.049***	13.63	1	**<0.001*** **	0.02	1	0.876
Shoal type	0.02	1	0.891				0.26	1	0.609	0.26	1	0.614
Individual length	0.19	1	0.665	0.08	1	0.774	26.19	1	**<0.001*** **	0.03	1	0.865
Bouts rates	13.30	1	**<0.001*** **	3.73	1	0.053·	0.03	1	0.855	0.00	1	0.964
Sh. size * Sh. type	4.16	1	**0.041***				0.12	1	0.733			

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Quantifying the role of photoacclimation and self-facilitation for seagrass resilience to light deprivation

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Introduction: Light gradients are ubiquitous in marine systems as light reduces exponentially with depth. Seagrasses have a set of mechanisms that help them to cope with light stress gradients. Physiological photoacclimation and clonal integration help to maximize light capture and minimize carbon losses. These mechanisms can shape plants minimum light requirements (MLR), which establish critical thresholds for seagrass survival and help us predict ecosystem responses to the alarming reduction in light availability.

Methods: Using the seagrass *Cymodocea nodosa* as a case study, we compare the MLR under different carbon model scenarios, which include photoacclimation and/or self-facilitation (based on clonal integration) and that where parameterized with values from field experiments.

Results: Physiological photoacclimation conferred plants with increased tolerance to reducing light, approximately halving their MLR from 5-6% surface irradiance (SI) to ≈ 3% SI. In oligotrophic waters, this change in MLR could translate to an increase of several meters in their depth colonization limit. In addition, we show that reduced mortality rates derived from self-facilitation mechanisms (promoted by high biomass) induce bistability of seagrass meadows along the light stress gradient, leading to abrupt shifts and hysteretic behaviors at their deep limit.

Discussion: The results from our models point to (i) the critical role of physiological photoacclimation in conferring greater resistance and ability to recover (i.e., resilience), to seagrasses facing light deprivation and (ii) the importance of self-facilitating reinforcing mechanisms in driving the resilience and recovery of seagrass systems exposed to severe light reduction events.

KEYWORDS

minimum light requirements, physiological photoacclimation, bistability, resilience, *Cymodocea nodosa*

1 Introduction

Seagrasses provide multiple goods and services to humans, such as nursery habitat for fish species, coastal protection against erosion, water quality improvement, carbon sequestration, and buffering capacity against ocean acidification (Duarte et al., 2013; Unsworth et al., 2019a; Ricart et al., 2021). One of the main reasons for the global decline of seagrasses is coastal eutrophication and the subsequent reduction of light availability, which contracts the space where seagrasses can thrive (Cloern, 2001; Orth et al., 2006; Burkholder et al., 2007; Waycott et al., 2009). Light limitation reduces photosynthetic rates of seagrasses, altering their overall carbon balance (Ralph et al., 2007; McMahon et al., 2013), and subsequently leading to net carbon losses which is likely a primary control of seagrass decline (Moreno-Marín et al., 2018; Adams et al., 2020). Indeed, seagrass ecosystems shift to a bare sand state when light availability drops below critical tolerance thresholds, with entire seagrass meadows collapsing after major light limitation events (Walker and McComb, 1992; Preen et al., 1995; van der Heide et al., 2007). For long-term changes in light availability, these thresholds are commonly known as minimum light requirements (MLR). MLR therefore determine the critical light availability for survival of seagrasses over ecologically-relevant time frames and are calculated with light values at maximum colonization depth (Collier et al., 2016). Because of their relevance to sustain meadow persistence, MLR have been identified for numerous seagrass species distributed worldwide (e.g., Erftemeijer and Robin Lewis, 2006; Lee et al., 2007).

Understanding the processes conferring seagrasses with increased resistance to disturbances becomes essential to forecast and prevent the loss of these habitat-forming species. Since light plays the most pivotal role in modulating plant growth and depth limits (Dennison, 1987; Duarte, 1991), changes in seagrass responses to light reduction are a likely pathway by which resistance is conferred to them. Seagrasses respond to light deprivation with a well-defined sequence of changes, the first of which is physiological photoacclimation (Waycott et al., 2005). Physiological photoacclimation refers to the ability of plant leaves to increase their efficiency of converting light into photosynthate and/or decrease respiration demand. The presence or absence of physiological photoacclimation can be identified by measuring changes in both the maximum photosynthetic rates and photochemical efficiency of seagrass leaves in response to changes in their local light environment (Cayabyab and Enríquez, 2007). Under light limitation, plants physiologically acclimate, through two strategies: enhancing light harvesting efficiency (e.g., adjusting metabolic demand of leaf tissues, increasing total chlorophyll, reducing the chlorophyll a:b ratio, etc.), and/or minimizing carbon losses (i.e., carbon allocation strategies) (Olivé et al., 2013; Silva et al., 2013). For instance, the higher content of total chlorophyll (as well as other altered pigments) in the seagrass *Cymodocea nodosa*, together with its carbon allocation strategy, have been argued as the underlying reasons for its superior ability to cope with light deprivation compared to *Zostera marina* (Silva et al., 2013). In addition, seagrasses can also acclimate to low light by increasing shoot size and reducing shoot density (i.e., self-thinning) in order to optimize light capture by the canopy (Enríquez et al., 2019). These strategies are critical for maintaining a positive carbon balance and reducing MLR (Campbell et al., 2007; Silva et al., 2013). However, seagrass species are not all equal and a greater ability to acclimate certain traits can confer plants an improved carbon balance and reduced MLR, allowing seagrasses to survive in environments with lower light availability (Ruiz and Romero, 2001; Minguito-Frutos et al., 2023). Hence the MLR for different seagrass species may depend substantially on the magnitude of its photoacclimation capacity, which itself can be mediated by the contextual conditions where that population resides (Erftemeijer and Robin Lewis, 2006; Cayabyab and Enríquez, 2007). Local contexts, referring to light but also to thermal natural histories, have influenced the strategies of marine macrophytes in responding to abiotic impacts such as light reduction (Ruiz and Romero, 2003; Robledo and Freile-Pelegrín, 2005; Yaakub et al., 2014) or marine heatwaves (Nguyen et al., 2020; Schubert et al., 2021). In particular, seagrasses growing in suboptimal light environments have their MLR altered and show different photosynthetic performance compared to those growing in optimal conditions (Ruiz and Romero, 2003; Yaakub et al., 2014).

In addition to these well-defined acclimation responses (Waycott et al., 2005), seagrass ecosystems may also be characterized by the occurrence of feedbacks leading to the emergence of nonlinear dynamics (van der Heide et al., 2007; McGlathery et al., 2013). When sufficiently strong, feedbacks can push seagrass meadows to express bistable behaviors with two possible stable states (seagrass and bare sand) for the same level of external stress (Maxwell et al., 2017; Adams et al., 2018). Bistable behaviors may arise as a consequence of increased light stress provoking abrupt transitions at the deep edge of seagrass meadows (Mayol et al., 2022). For example, if reinforcing mechanisms driven by plant presence exists, and if such mechanisms act to reduce the mortality rates of a stressed seagrass bed (i.e., self-facilitation mechanisms), they can lead to bistability as explored in Mayol et al. (2022) (see Figure 1). In that recent work, it was found that bistable behaviors could potentially arise due to clonal integration, which refers to the ability of seagrass species to translocate resources between connected ramets (Terrados et al., 1997; Nielsen and Pedersen, 2000). However, under light stress gradients, mortality increases resulting in shoot density decrease and this lower biomass could significantly modify the local environment by reducing sediment trapping, increasing damage from erosion, reducing physical integration, reducing anchoring and amplifying toxicity from eutrophication (Duarte and Sand-Jensen, 1990; Olesen and Sand-Jensen, 1994; Vidondo et al., 1997; van der Heide et al., 2007; van der Heide et al., 2008; Collier et al., 2009). Overall, seagrasses will display a set of responses to cope with light stress gradients linked to changes in biomass that eventually affect mortality rates, but it is so far unclear whether photoacclimation itself is a nonlinear process able to cause bistability.

Mechanistic models provide a useful tool to explore and untangle the effects of causal processes on ecosystem behavior (Burd and Dunton, 2001). Such models may help to elucidate the effects of physiological photoacclimation and self-facilitation mechanisms (e.g., mechanisms related to a reduction in mortality associated with large biomasses) on identifying MLR and bistability behaviors in seagrass beds. In addition, models incorporating data-calibrated seagrass responses to light reduction can predict seagrass carbon balance (Adams et al., 2020) and quantify their resilience to light limitation (Adams et al., 2018). Hence, predictions of suitably-designed mechanistic models can indicate how plants respond to light reduction (Burd and Dunton, 2001). If seagrasses represented by such models exhibit nonlinear responses and/or alternative stable states, these predictions are critical to inform management actions that could alleviate the light pressure in time before an abrupt change in seagrass ecosystem state, which may be potentially irreversible.

The aim of this study is thus to assess seagrass biomass responses and resilience to four different conditions: the presence (or absence) of physiological photoacclimation as light reduces, and the presence (or absence) of self-facilitation mechanisms (represented here by clonal integration) as biomass reduces. To achieve the study's aim, we built and parameterized deterministic models of carbon balance using data for the Mediterranean seagrass *Cymodocea nodosa* gathered in field experiments (Marín-Guirao et al., 2022) and field light gradients (Mayol et al., 2022) where both mechanisms have been described. These models do not aim to incorporate all mechanisms influencing seagrass dynamics; rather, the presented models focus on a few relevant mechanisms with the aim of uncovering gaps in scientific knowledge (Burd and Dunton, 2001 and references there in). Our predictions demonstrate how the MLR and potential bistability of seagrass ecosystems is dependent on each of the four proposed models, and thus yield guidance for what new information should be sought if one or more of these ecosystem properties (MLR and bistability) is of interest for decision-making in environmental management.

2 Materials and methods

2.1 Study system

Cymodocea nodosa (Ucria) Ascherson 1869 is a subtidal seagrass species native and widely distributed throughout the

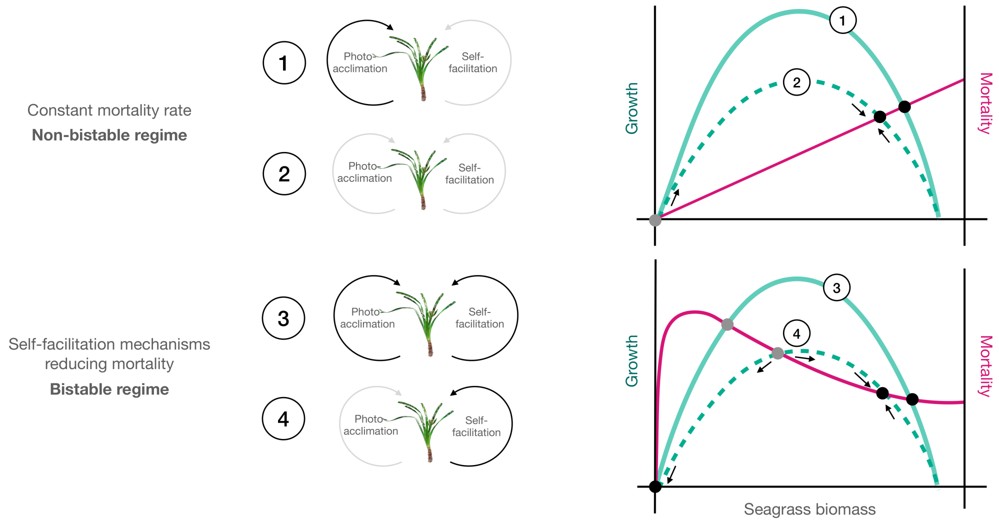

FIGURE 1
Conceptual diagram describing the different models explored. Green curves represent seagrass growth rates as a function of biomass up to a certain maximum carrying capacity. Red lines represent seagrass mortality rates. Equilibrium points are represented by grey (unstable) and black (stable) dots at the intersection between growth and mortality curves. In the absence of self-facilitation (1 and 2 upper panel), mortality increases with biomass and intersects growth curves forming stable equilibria. In contrast, self-facilitation mechanisms (3 and 4 lower panel) reduce seagrass mortality as biomass increases, promoting the emergence of unstable equilibria leading to bistability (two stable equilibria separated by an unstable equilibrium point). Moreover, plants able to photoacclimate (solid lines) both in non-bistable (1) and in bistable regimes (3) are expected to use light more efficiently and increase their growth, compared to those that cannot (dashed lines 2 and 4).

Mediterranean, extending in the East Atlantic coasts including the Canary Islands (Garrido et al., 2013). It is considered a fast-growing, medium-size opportunistic species with remarkable phenotypic plasticity that inhabits a broad range of environments, including those with more fluctuating environmental conditions (Olesen et al., 2002; Olivé et al., 2013; Silva et al., 2013; Peralta et al., 2021). *C. nodosa* forms dense monospecific meadows between the water surface and 40 m depth (Terrados and Ros, 1992; Short et al., 2011), exhibiting often abrupt declines in shoot density at their depth limits compatible with alternative stable states caused by self-facilitation mechanisms (Mayol et al., 2022). This plastic seagrass species is characterized by a strong photoacclimation potential, altering its photosynthetic-irradiance (*P-I*) parameters as light is reduced, to optimize its light use efficiency (Olivé et al., 2013; Silva et al., 2013; Marín-Guirao et al., 2022).

2.2 Model description

To quantitatively assess the influence of physiological photoacclimation on seagrass ecosystem properties, we examined four models of plant responses to light reduction (Figure 1; Table 1). In two of the four models, it was assumed that plants photoacclimate (Figure 1; scenarios 1 and 3) to changes in light availability by adjusting their photosynthetic-irradiance (*P-I*) parameters (for physiological mechanisms which potentially cause these parameter adjustments see e.g., Marín-Guirao et al., 2022). In the other two models (Figure 1; scenarios 2 and 4) and for comparison, it was assumed that plants cannot photoacclimate.

In the models without photoacclimation, carbon balance is based on the following three *P-I* parameters: maximum gross photosynthetic rate P_{max} (in units of mg O_2 g^{-1} above-ground [ABG] dry weight [DW] h^{-1}), saturation irradiance I_k (µmol quanta m^{-2} s^{-1}) and above-ground respiration R (mg O_2 g^{-1} ABG DW h^{-1}). In the models that include photoacclimation, each of these three parameters P_{max}, I_k and R possess a nonlinear dependence on the benthic irradiance I (µmol quanta m^{-2} s^{-1}) as detailed later in this section. We parameterized our models in terms of the saturation irradiance parameter I_k instead of the (also commonly used) photosynthetic efficiency α due to our recent finding that the species-specific ability of seagrasses to acclimatize the parameter I_k better explains these species' ability to cope with light reduction and colonize depth ranges (Minguito-Frutos et al., 2023). Below-ground respiration by roots and rhizomes (Fourqurean and Zieman, 1991; Burd and Dunton, 2001) was also included in the carbon balance of all four models. Specifically, it was assumed that the rate of below-ground respiration per unit below-ground biomass was 1/10 of the maximum rate of above-ground respiration per unit above-ground biomass (Staehr and Borum, 2011), analogous to ten-fold differences in turnover rate observed between above-ground and below-ground biomass compartments (Vonk et al., 2015). This assumption was mathematically characterized by the constant parameter $[RRR] = R_{max}/10$ (where $[RRR]$ denotes root/rhizome respiration in units of mg O_2 g^{-1} below-ground [BG] DW h^{-1}). The ratio of below-ground biomass to above-ground biomass, required here, was denoted by $[BAR]$. $[BAR]$ can be highly variable in the field but typically its order of magnitude is one (see e.g., Pérez et al., 1994; Collier et al., 2017), so for simplicity its default value was set to one in all four models. However, we also explored the effect of increasing $[BAR]$ above one in later simulations.

The difference between each of the two models that included photoacclimation and those that excluded photoacclimation was the absence or presence (Figure 1; upper and lower panel, respectively) of self-facilitation (clonal integration) reducing mortality rates as biomass increases (see Mayol et al., 2022). We included self-facilitation in our analysis since it may be crucial in favoring natural or induced recovery of seagrasses (van Katwijk et al., 2016; Moksnes et al., 2018). In the models where this self-facilitation was absent, the seagrass mortality rate (δ) was set to a constant equal to d_0 (in units of h^{-1}) so that the biomass lost due to mortality is always proportional to the current biomass of seagrass. In contrast, when self-facilitation was present, this mortality rate (δ) depended nonlinearly on the current total biomass of the seagrass state (mortality is reduced at high biomass), as detailed later, in the next section.

All four models used an ordinary differential equation to track the total seagrass biomass B (in units of g total DW m^{-2}). Models

TABLE 1 Equations used in the physiological photoacclimation models.

Eqn.	Model equations	Which scenarios used in?
(1)	$\frac{dB}{dt} = K\frac{1}{1+[BAR]}\Big(\frac{1}{2}P - (R + [RRR][BAR])\Big)B \quad (1 - \frac{B}{N}) - \delta(B)$	①,②,③,④
(2)	$P = \frac{P_{max}I}{I + I_k}$	①,②,③,④
(3)	$P_{max}(I) = P_{gmax} + \frac{P_{gmin} - P_{gmax}}{1 + e^{\lambda_P(I - y_{cP})}}$	①,③
(4)	$I_k(I) = I_{kmax} + \frac{I_{kmin} - I_{kmax}}{1 + e^{\lambda_K(I - y_{cK})}}$	①,③
(5)	$R(I) = R_{max} + \frac{R_{min} - R_{max}}{1 + e^{\lambda_R(I - y_{cR})}}$	①,③
(6)	$\delta(B) = d_0B$	①,②
(7)	$\delta(B) = \Big(\frac{1 + e^{-\lambda_B B_0}}{1 + e^{\lambda_B(B - B_0)}}\Big)d_0B$	③,④

employed the common logistic growth assumption that biomass can accumulate up to some maximum carrying capacity (g total DW m^{-2}). The carrying capacity N represents, therefore, the maximum population that a system can sustain, depending on various limited resources such as food or space. In our models, we assumed that growth is maximized at ½ N and that restricted space diminishes production at higher biomass levels as a result of self-shading (Burd and Dunton, 2001).We assumed equal amounts of carbon fixation to the amounts of O_2 evolved/fixed during photosynthesis-respiration (Fourqurean and Zieman, 1991; Adams et al., 2017), to convert between carbon exchange rates (in units of mg O_2 g^{-1} ABG DW h^{-1}) and growth rates (in units of h^{-1}). We firstly introduced a factor (1/1+[BAR]), in units of g ABG DW g^{-1} total DW) to account for the products of photosynthesis and respiration allocated to net growth of below-ground tissues. Secondly, we introduced a conversion factor K (g total DW mg^{-1} O_2) to account for the total biomass produced per net mass of oxygen evolved (for further information see Supplementary Text S1, Section S1.3). Combining all of the above considerations, the four investigated models all possess the form

$$\frac{dB}{dt} = K\frac{1}{1+[BAR]}\left(\frac{1}{2}P - (R + [RRR][BAR]\right)B\left(1-\frac{B}{N}\right) - \delta(B) \qquad (1)$$

where the factor of 1/2 in front of the gross photosynthesis rate term P accounts for the average difference in time over which photosynthesis and respiration (R) processes are occurring (12 hours per day vs 24 hours per day, respectively). The gross photosynthesis rate P (mg O_2 g^{-1} ABG DW h^{-1}) is implemented using the standard Michaelis-Menten formulation (Pérez and Romero, 1992; Marín-Guirao et al., 2022; Mayol et al., 2022),

$$P = \frac{P_{max}I}{I + I_k} \qquad (2)$$

where I is the instantaneous light (photosynthetically active radiation, in units µmol quanta m^{-2} s^{-1}).

2.3 Modelling physiological photoacclimation to light limitation

In the two models where photoacclimation is absent, the parameters for photosynthesis and respiration ($P_{\max}$, $I_{\rm k}$ and R) are set to constant values (corresponding to observed values of these parameters in seagrasses acclimated to high light conditions). Conversely, in the two models where photoacclimation is present, these three parameters are assumed to possess a nonlinear dependence on the benthic irradiance I. Here we provide justification for the mathematical formulations $P_{\max}(I)$, $I_{\rm k}(I)$ and $R(I)$ that are assumed in the two photoacclimation models.

Based on the data shown in Figure 2 (adapted from Marín-Guirao et al., 2022; see also Supplementary Table S1), all three parameter functions $P_{\max}(I)$, $I_{\rm k}(I)$ and $R(I)$ can be feasibly represented by sigmoidal functions (curves in Figure 2; Supplementary Table S2). Thus, for the photoacclimation models we assumed that:

$$P_{max}(I) = P_{gmax} + \frac{P_{gmin} - P_{gmax}}{1 + e^{\lambda_P(I - y_{cP})}} \qquad (3)$$

$$I_k(I) = I_{kmax} + \frac{I_{kmin} - I_{kmax}}{1 + e^{\lambda_K(I - y_{cK})}} \qquad (4)$$

$$R(I) = R_{max} + \frac{R_{min} - R_{max}}{1 + e^{\lambda_R(I - y_{cR})}} \qquad (5)$$

In equations (3) and (4) that are related to photosynthesis, P_{gmax} and I_{kmax} represent the maximum gross photosynthetic rate for seagrass acclimated to high light conditions (mg O_2 g^{-1} ABG DW h^{-1}) and the saturation irradiance for seagrass acclimated to high light conditions (µmol quanta m^{-2} s^{-1}), respectively. As irradiance I declines, the values of these two parameters decline towards minimum values: P_{gmin} which represents the maximum gross photosynthetic rate for seagrass acclimated to low light conditions, and I_{kmin} which represents the saturation irradiance for seagrass acclimated to low light conditions. The slopes (λ_P, λ_K) and the inflection points (y_{cP}, y_{cK}) of the curves in equations (3) and (4) determine the strength of the declines for $P_{\max}$ and I_k, respectively (Table 2). Similarly, in the above-ground respiration equation (5), R_{max} and R_{min} represent the leaf respiration rates (mg O_2 g^{-1} ABG DW h^{-1}) for seagrass acclimated to high and low light conditions respectively, and the slope λ_R and the inflection point y_{cR} have analogous definitions to λ_P, λ_K and y_{cP}, y_{cK} (Table 2).

These curves were fitted to the data obtained in field experiments (Marín-Guirao et al., 2022) by employing a robust and efficient implementation of the Levenberg-Marquardt algorithm for solving nonlinear least squares problems (via the *minpack.lm* R package; Elzhov et al., 2022). The nonlinear least-squares estimates of the parameters obtained from this model-data fitting, along with other parameters sourced from the literature for use in our models, are listed in Table 2 and justified in Supplementary Text S1.

2.4 Modelling seagrass mortality

To test the influence of seagrass mortality in the carbon balance models we considered two different mortality functions. In the first function, we assume the absence of self-facilitation (Figure 1; scenario 1 and 2), so seagrass mortality (δ) responds constantly (d_0) to the current seagrass biomass (B) and presents the form:

$$\delta(B) = d_0 B \qquad (6)$$

In the second function, self-facilitation (Figure 1; scenario 3 and 4) is assumed to yield a nonlinear relationship between the mortality rate (δ) and seagrass biomass (B) according to (Mayol et al., 2022),

$$\delta(B) = \left(\frac{1 + e^{-\lambda_B B_0}}{1 + e^{\lambda_B(B - B_0)}}\right) d_0 B \qquad (7)$$

where parameters λ_B (units of inverse biomass) and B_0 (units of biomass) control the shape of the nonlinear relationship between mortality rate and seagrass biomass.

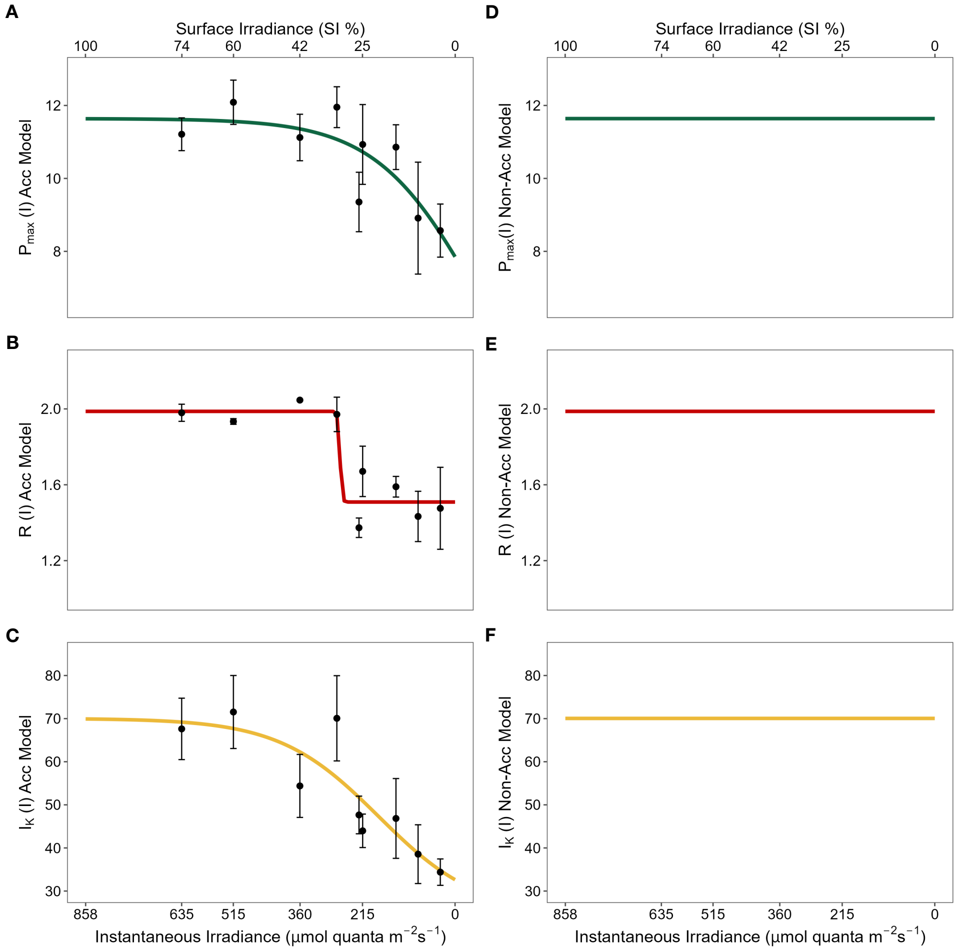

FIGURE 2
Physiological photoacclimation models compared (left vs right panels) under the light stress gradient. Y-axes represent values for each physiological mechanism along the gradient: maximum gross photosynthesis [P_{max}, **(A)** vs **(D)**]; above-ground respiration [R, **(B)** vs **(E)**]; and saturation irradiance [I_k, **(C)** vs **(F)**]. P_{max} and R are shown in units of mg O_2 g^{-1} ABG DW h^{-1} and I_k in µmol quanta m^{-2} s^{-1}. X-axes represent light values of total instantaneous irradiance (µmol quanta m^{-2} s^{-1}) (bottom) and percentage of surface irradiance (SI) (top). X-axes values ranged from 858.04 µmol quanta m^{-2} s^{-1} of instantaneous irradiance that equaled 100% SI after conversions derived from field shading experiments. While lines in left panels represent the best fit curve to the nine levels of light stress (black dots corresponding to 74, 60, 42, 32, 26, 25, 16, 10 and 4% SI) for each physiological mechanism in field shading experiments; lines in right panels are set to constant values corresponding to their maximum values observed at high light conditions.

2.5 Solving the models: determining minimum light requirements

To quantify how the four presented models of seagrass carbon balance are affected by the reduction of benthic irradiance I, we performed numerous mathematical evaluations of the model expression for dB/dt shown in Eqn. 1. To do so, we assumed that daily averaged light I_{daily} (i.e., light dose over one day) was approximately equal to half of a constant instantaneous light value I received during daylight hours, i.e., I_{daily} (mol quanta m^{-2} d^{-1}) in Marín-Guirao et al. (2022) ≈ ½ I (instantaneous irradiance in µmol quanta m^{-2} s^{-1}). We then calculated the equivalent percentage of surface irradiance (SI = 100%-0%), and solved all models up to their carrying capacity (N = 100 g total DW m^{-2}). After solving the four models of seagrass response to limiting light conditions, we determined the MLR of each model as the minimum quantity of benthic irradiance (both as instantaneous light received during daylight hours in µmol quanta m^{-2} s^{-1} and as daily averaged light in % SI) that allows a positive rate of change for seagrass biomass, dB/dt (g total DW m^{-2} h^{-1}).

To evaluate the influence of physiological photoacclimation and self-facilitation (clonal integration) on the stability of seagrass ecosystems, we calculated the equilibrium points resulting from each of the models. These equilibrium points can be stable (Figure 1 *black points*) or unstable (Figure 1 *gray points*), depending on whether the system tends towards an equilibrium point or moves away from them, respectively. When self-facilitation is present, the system can potentially express two stable equilibria separated by an unstable equilibrium point (a situation known as bistability). However, when self-facilitation does not occur, unstable equilibrium points are not expected to emerge and bistability would not take place. Thus, we used the R *rootSolve* package (Soetaert, 2009), which identifies all the equilibrium points within the pre-specified range, as well as whether they represent stable or unstable equilibria.

TABLE 2 Values of models parameters.

Parameter	Value	Description	Units	Reference
Non-acclimation Model				
P_{gmax}	11.64	Maximum Photosynthesis	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
I_{kmax}	70.04809	Saturation Irradiance	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	Marín-Guirao et al., 2022
R_{max}	1.987	Above-ground Respiration	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
Acclimation Model				
P_{gmax}	11.64	P_{max} (high light)	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
P_{gmin}	2.096	P_{max} (low light)	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
λ_P	0.008524	P_{max} Slope	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
y_{cP}	-49.1	P_{max} Threshold	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
I_{kmax}	70.04809	I_k (high light)	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	Marín-Guirao et al., 2022
I_{kmin}	24.54396	I_k (low light)	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	Marín-Guirao et al., 2022
λ_K	0.00863	I_k Slope	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
y_{cK}	177.45783	I_k Threshold	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
R_{max}	1.987	Above-ground Respiration (high light)	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
R_{min}	1.509	ABG Respiration (low light)	$mg\ O_2/(g\ ABG\ DW \cdot h)$	Marín-Guirao et al., 2022
λ_R	0.4567	ABG Respiration Slope	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
y_{cR}	267.1	ABG Respiration Threshold	$\mu mol\ quanta\ m^{-2}\ s^{-1}$	
Below-ground Parameters				
$[BAR]$	1	Below-Above Ratio	–	Pérez et al., 1994; Collier et al., 2017
$[RRR]$	0.1987	Roots/Rhizomes Respiration	$mg\ O_2/(g\ BG\ DW \cdot h)$	Staehr and Borum, 2011
Biomass and Growth/Mortality Parameters				
K	0.001075	Conversion Efficiency	$g\ total\ DW/mg\ O_2$	Nielsen and Pedersen, 2000; Zharova et al., 2008
N	100	Carrying Capacity	$g\ ABG\ DW\ m^{-2}$	
d_0	0.000116	Mortality Rate	h^{-1}	Mascaró et al., 2014
λ_B	0.05	Facilitation Slope	$(g\ ABG\ DW\ m^{-2})^{-1}$	Mayol et al., 2022
B_0	10	Threshold Facilitation	$g\ ABG\ DW\ m^{-2}$	Mayol et al., 2022

Full justification of these parameter values is provided in Supplementary Text S1.

2.6 Quantifying the ecological resilience to light limitation

Ecological resilience was quantified following the definition in Adams et al. (2018) for those models that expressed bistability:

$$Resilience = \frac{B_{stable} - B_{unstable}}{B_{stable}} \times 100\,\% \tag{8}$$

In this equation, B_{stable} and B_{unstable} are the strictly positive values of seagrass biomass (g DW m^{-2}) representing stable and unstable equilibrium points, respectively. In bistable ecosystems, the ecological resilience calculated from Eqn. (8) will always fall between 0% and 100%, with the system being more resistant to disturbance as the calculated resilience approaches 100%.

3 Results

Our models predicted that photoacclimation decreases the MLR of *Cymodocea nodosa* from 5.8% SI to 3.4% SI (Figure 3A), when other nonlinear mechanisms (i.e., reduction in mortality rate from clonal integration) are absent. Photoacclimation does not result in bistable behaviors of seagrass ecosystems (one stable equilibrium for each model in Figure 3A), despite it being a nonlinear process itself.

The inclusion in our models of the clonal integration mechanism (i.e., self-facilitation), also reduced the MLR, but not as substantially as the photoacclimation mechanism. Models predicted MLR of *C. nodosa* to be 5.1% SI and 2.9% SI in the absence and presence of photoacclimation, respectively (Figure 3B), when self-facilitation was introduced.

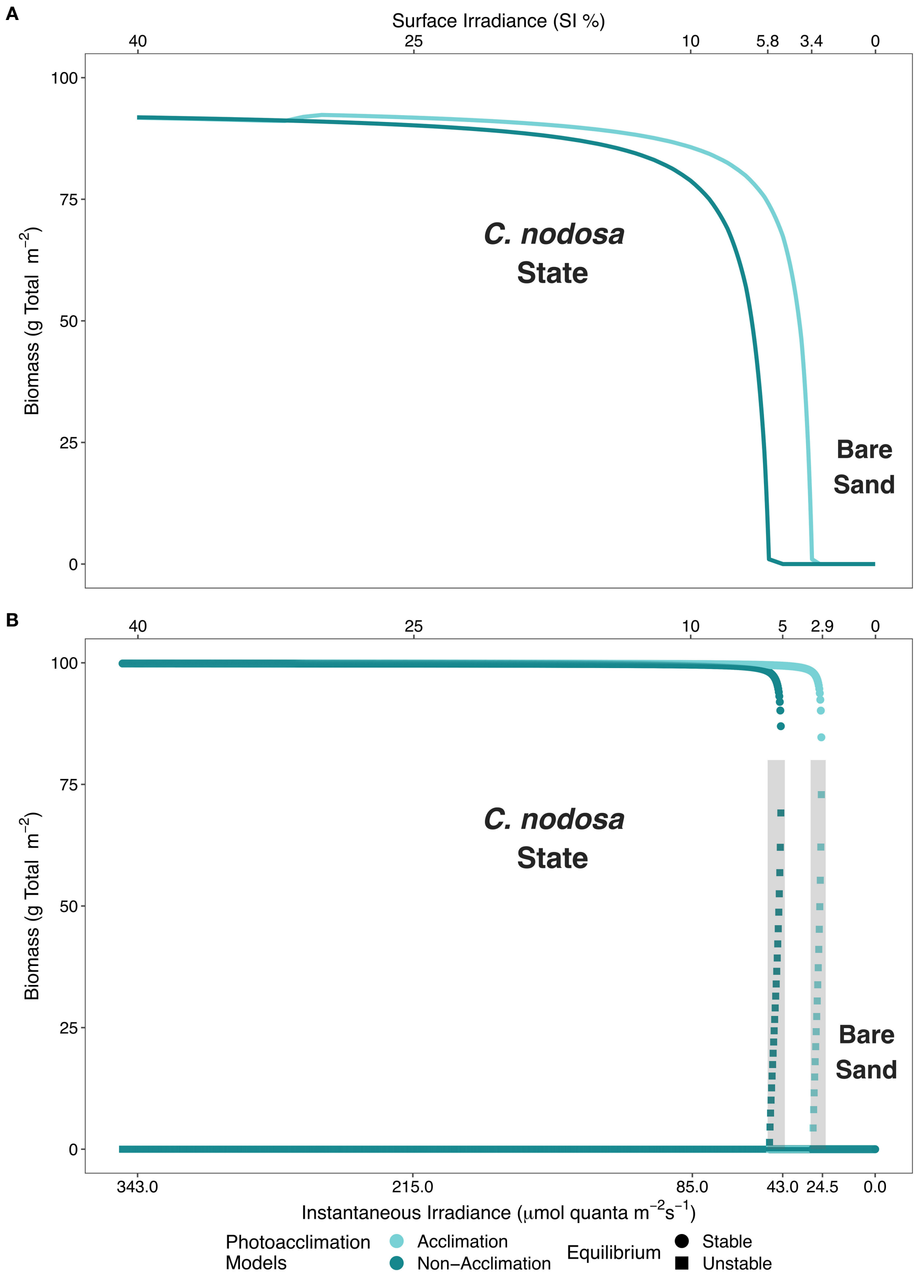

FIGURE 3

Minimum light requirements (MLR) are depicted for the four presented models: **(A)** physiological photoacclimation and non-acclimation models in absence of self-facilitation (clonal integration) and, **(B)** photoacclimation models in presence of self-facilitation. Physiological photoacclimation models are shown in light blue (acclimation) and dark blue (non-acclimation). In the presence of self-facilitation, bistability arises and circles (stable) and squares (unstable) represent equilibrium types. The shaded area in **(B)** represents the bistable region predicted by the models.

The self-facilitation (i.e., mortality reduction as plant biomass increases) also yielded bistability within specific ranges of benthic irradiance values, regardless of whether photoacclimation was present or not (shaded areas in Figure 3B). Hence, when photoacclimation was absent, the seagrass ecosystem formed by *C. nodosa* was bistable when the average daily irradiance was between 5.1% SI and 5.8% SI; and when photoacclimation was present, this ecosystem was bistable when the average daily irradiance was between 2.9% SI and 3.4% SI. The photoacclimation mechanism also permitted a greater range of irradiance values over which the seagrass has maximal resistance to disturbance (Figure 4).

We also explored the effect of changing the below-ground to above-ground biomass ratio on the MLR predicted by our four models. Crucially, we found that as the ratio of below-ground biomass to above-ground biomass ([*BAR*]) increases, there is a substantial increase in the MLR for plants both with and without photoacclimation capacities (Figure 5). However, plants that photoacclimate cope better with a relative increase of the biomass

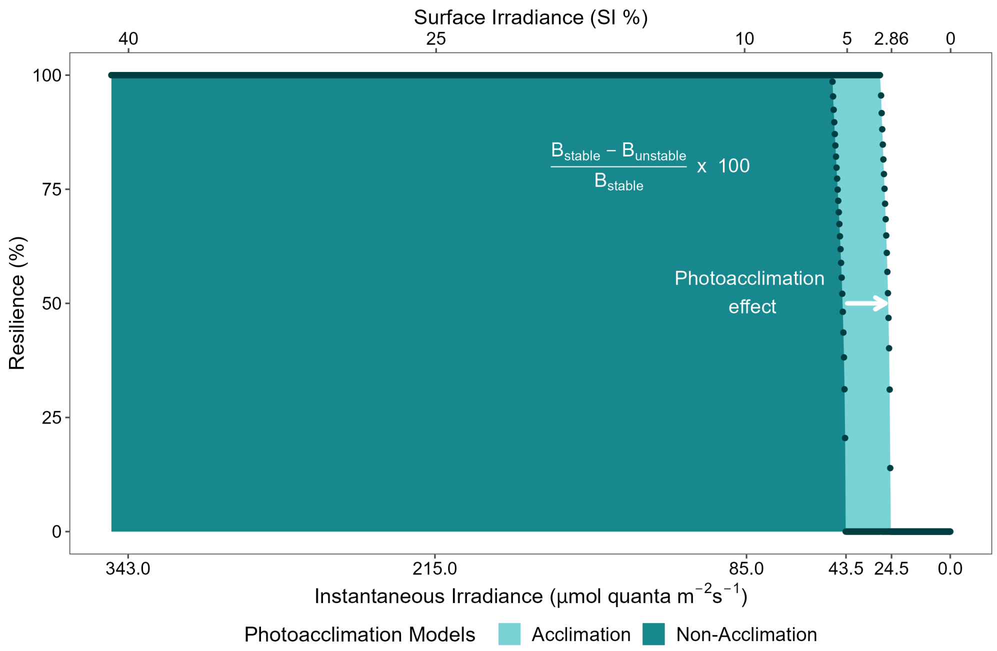

FIGURE 4
Ecological resilience for physiological photoacclimation (light blue) and non-acclimation (dark blue) models to light limitation, as a function of benthic irradiance (in instantaneous irradiance and % SI). Resilience is calculated following the mathematical definition provided in Adams et al. (2018) which has its basis in the conceptual definition provided in Gunderson (2000). Dots represent the calculated values of resilience (%) as a function of the values of instantaneous irradiance (μmol quanta m^{-2} s^{-1}) or surface irradiance (%SI), for each model.

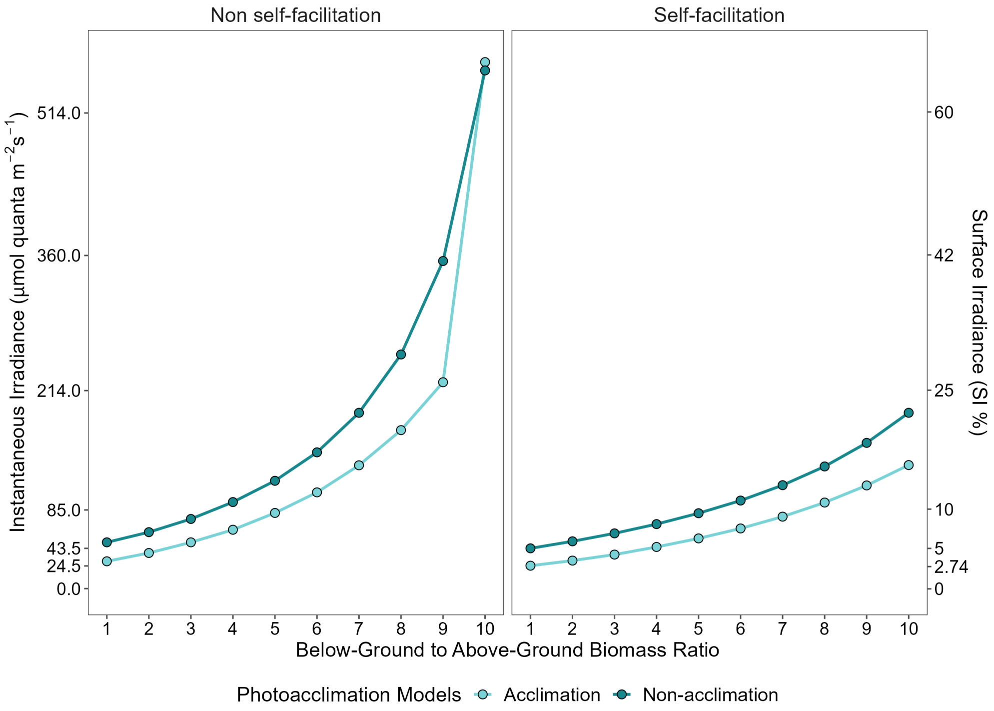

FIGURE 5
Predicted minimum light requirements as a function of below-ground to above-ground biomass ratio (model parameter [*BAR*]), for plants that express physiological photoacclimation (light blue) or not (dark blue). Left and right panels represent the absence and presence of self-facilitation, respectively.

ratio between below- and above-ground tissues, except when self-facilitation is absent and a threshold is exceeded (MLR at $[BAR]$ equal to 9, ~26.2% SI compared to ~41.5% SI) (Figure 5 left panel). After this threshold ($[BAR] = 9$) the MLR of *C. nodosa* that do not possess self-facilitation mechanism increases abruptly. On the contrary, in a system where self-facilitation is acting, and $[BAR]$ is equal to 10, the MLR of *C. nodosa* increases gradually – together with photoacclimation the MLR only reaches ~15.6% SI (Figure 5 right panel).

4 Discussion

In this modelling study, we used data from intensive field experimentation to test the effect of physiological photoacclimation on the minimum light requirements (MLR) and, then resilience, of seagrasses performing contrasting physiological strategies to cope with light stress gradients. Specifically, our models predict that the ability of *C. nodosa* to photoacclimate to low light approximately halves its threshold of collapse (MLR). In addition, the presence of self-facilitation mechanisms such as clonal integration, alleviating mortality rates with increasing biomass, can result in bistability and decrease MLR even further. On the other hand, photoacclimation increases the resilience of bistable meadows to light reduction by increasing plant resistance and their ability to recover (O'Brien et al., 2018), but it cannot yield bistability in seagrass beds. Therefore, the results from our models point to the critical role of physiological photoacclimation in conferring resilience to seagrasses against light deprivation, and also illustrate that other non-linear mechanisms (if present) can cumulatively contribute to this resilience and shape the recovery of seagrass ecosystems exposed to light reduction.

Using our modelling approach, we provide a coarse quantification of the MLR of *C. nodosa*, which can reorganize its photosynthetic apparatus to resist light limitation, and compare this to the equivalent MLR predicted if such plants are unable to photoacclimate. Our study uses data from field shading experiments that identified patterns of physiological acclimation mechanisms of *C. nodosa* to light-limiting conditions (see Marín-Guirao et al., 2022). MLR predicted through our mathematical modelling approach (2.9% – 3.4% SI for plants with and without self-facilitation respectively) are comparable to those found by previous experimental studies (e.g., 4.4% SI (Olesen et al., 2002) and 7.3% – 10.2% SI (Dennison et al., 1993)). Of particular note, a halving of MLR can yield a contraction of ≈1 m to ≈10 m at the deep limit, depending on the values of the light attenuation coefficient ($k = 0.07$ to $k = 0.57$ respectively, see Dennison et al., 1993; as calculated using the standard light extinction equation provided in Dennison, 1987).

The photoacclimation-mediated reduction in MLR is mainly related to *C. nodosa*'s capacity to decrease both its leaf respiration demand and saturation irradiance I_k as benthic irradiance decreases. Reducing leaf respiratory losses is critical for seagrasses to survive periods of light stress, as leaf respiration typically accounts for the majority of respiratory requirements in seagrasses (Fourqurean and Zieman, 1991; Masini et al., 1995). The decline in above-ground respiration observed at low light environments is a common photoacclimation mechanism in *C. nodosa* (Olivé et al., 2013; Marín-Guirao et al., 2022), but also among other seagrass species, making the outcomes found in this study potentially applicable to other seagrasses (Ruiz and Romero, 2001; Ruiz and Romero, 2003; Collier et al., 2009; Collier et al., 2012). In fact, several species of different genera have been found to reduce their above-ground tissues to balance the energetic demand under impoverished light environments (Mackey et al., 2007; Collier et al., 2012). Similarly, some seagrass species have been shown to reduce their total leaf area (i.e., self-thinning) as a strategy to cope with light reduction at depth, increasing their overall production (Enríquez et al., 2019). Our finding that reduced I_k at low light levels boosts the carbon balance of *C. nodosa* agrees with previous findings for this species (Olivé et al., 2013) and other seagrasses (Ruiz and Romero, 2001; Campbell et al., 2007). Interestingly, we also found that even though P_{max} decreases as benthic irradiance declines, this did not cause a detrimental effect on carbon production compared to plants unable to photoacclimate (constant P_{max}). This occurred because the reductions in both respiration demand and I_k of plants able to acclimate, counteract the simultaneous reduction of P_{max}, as light decreases. Therefore, in the present work we have been able to demonstrate how the cumulative changes in multiple physiological parameters at low light, allow seagrasses to more efficiently harvest light, compared to those plants with less variability in their physiological response. These results are in agreement with field experiments that found the plastic *C. nodosa* to be more resilient under adverse light conditions compared to other less plastic seagrasses like *Zostera marina* (Silva et al., 2013) or *Posidonia oceanica* (Olesen et al., 2002).

The results of our work show that presence of self-facilitation mechanisms, such as clonal integration leading to reduced mortality rates with increasing biomass, further reduces the MLR of *C. nodosa*, but also makes the ecosystem prone to bistability. Clonal integration might be the main reinforcing feedback in clonal seagrass plants (Nielsen and Pedersen, 2000), although a wide range of reinforcing feedbacks (e.g., enhancing sediment trapping, providing physical protection, etc.) could act similarly in reducing seagrass mortality with increasing biomass (Burkholder et al., 2007; Maxwell et al., 2017). Unlike self-facilitation mechanisms, photoacclimation alone did not cause bistability in the ecosystem formed by *C. nodosa*. Thus, we show that nonlinear trajectories in acclimation mechanisms (i.e., photoacclimation) do not always lead to the emergence of bistability and may not always be the cause of alternative stable states (McGlathery et al., 2013), but are still drivers of threshold behaviors that challenge the management of these ecosystems (van Katwijk et al., 2016). The presence of multiple alternative states (i.e., seagrass and bare sand states) for a given level of irradiance (i.e., bistability) is an indicator of hysteresis, which carries significant additional impediments for the recovery of the ecosystem as multiple feedbacks acting in the alternative state can reinforce its persistence (Moksnes et al., 2018). Given the prevalence of self-facilitation mechanisms alleviating mortality, the presence of bistability is a plausible scenario (van der Heide et al., 2007; Carr et al., 2010) in the ecosystems sustained by seagrasses independently of their photoacclimation capacities.

As is the case for many coastal ecosystems, seagrasses are exposed to multiple coexisting stressors (hurricanes or storms, overgrazing, etc.) eroding their resilience (Ruiz et al., 2009; Carlson et al., 2010; Infantes et al., 2011). These disturbances often cause uneven distributions of below- and above-ground plant tissues (i.e., leaves and rhizomes), eventually altering the below-ground to above-ground biomass ratio ([*BAR*]). We found that this ratio is essential for understanding seagrasses resilience to light-limiting conditions. As [*BAR*] increases, MLR increase too, making *C. nodosa* more vulnerable to light limitation. High below-ground to above-ground biomass ratios (e.g., $[BAR] \geq 10$) can be particularly challenging for maintaining positive carbon balance after heavier losses of photosynthetic tissues due to herbivory (Ruiz et al., 2009). In these situations, the effect of the physiological photoacclimation on increasing seagrass resilience to light deprivation may not be sufficient to counteract the effects of external stressors unless other compensatory mechanisms are also present (e.g., reduced respiration in the below-ground tissues, not investigated in this study). Reallocation of plant material between below-ground and above-ground tissues could also potentially be a strategy to boost carbon availability in periods when photosynthesis is suboptimal (Zimmerman et al., 1995; Alcoverro et al., 1999). However, large below-ground structures can also paradoxically be considered a heavy burden in periods of reduced light due to their respiratory requirements (Fourqurean and Zieman, 1991; Hemminga, 1998; Alcoverro et al., 2001). For this reason, further investigation is required to understand the actual role of below-ground tissues, which may increase the predictive power of seagrass production models and, therefore, their utility for making effective management decisions (Burd and Dunton, 2001). In the current era of global change, understanding the limits of acclimation capacity under the cumulative effects of human impacts on seagrasses influencing their resilience becomes imperative (Adams et al., 2020).

Overall, the goal of these models was to assess the effect of *C. nodosa*'s photoacclimation capacity on reducing their MLR (increased resistance) and enhancing its resilience to light deprivation. To accomplish this, our models included few essential mechanisms, making easier to understand the gaps in our knowledge and did not include all relevant processes influencing seagrass carbon balance (Burd and Dunton, 2001). Given this, we found that in all the scenarios explored, transitions followed non-linear dynamics. However, unlike self-facilitation, photoacclimation did not lead to bistability of *C. nodosa*'s seagrass beds. Nonlinearities carry critical implications for the predictability of abrupt shifts in the ecosystems formed by seagrasses, particularly for those exhibiting bistable behaviors (due to potential hysteresis). Our results foresee that under increasing light disturbances related to global change (Unsworth et al., 2019b), seagrass species that have evolved greater photosynthetic plasticity might be less vulnerable to anthropogenic reductions in light availability. Equally important, our models demonstrate that seagrass ecosystems that possess self-reinforcing mechanisms to reduce their mortality rates when biomass is high can be bistable.

Since not all species are equally able to acclimate to light reduction (Minguito-Frutos et al., 2023) nor do the meadows they form possess the same ecosystem components, there is an imminent need to identify differences in species acclimation capacity and prevalence of feedback mechanisms (Maxwell et al., 2017). This will help create management plans that account for species-specific vulnerability to stressors as light deprivation. Considering that light limitation is the main factor affecting seagrasses at different organizational scales: physiological, morphological and population (Ralph et al., 2007), our study therefore contributes to an improved understanding of seagrass ecosystem functioning which is valuable for conservation efforts. Specifically, we show how plastic seagrasses such as *C. nodosa* with potentially multiple reinforcing feedbacks give a wider operational space for managerial action to conserve the ecosystems formed by these species. Continued strategies to manage and conserve seagrass ecosystems can help to avoid sudden collapses in seagrass beds, which in some cases could be potentially irreversible (Lee et al., 2007; van der Heide et al., 2007).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

Author contributions

All authors contributed to the study design. MM-F, MA, DA, EM, TA, and JB led the modelling and statistical analyses. LM-G, JB-E and JR carried out the *Cymodocea nodosa* field experiment that served as the basis of this modeling study. MM-F, MA, MV, TA, and JB led the writing of the manuscript with contributions of all the authors. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2023.1186538/full#supplementary-material

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RESEARCH ARTICLE

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Species-specific acclimatization capacity of key traits explains global vertical distribution of seagrass species

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Abstract

Aim: The global vertical depth distribution of seagrass species remains poorly understood. Locally, the abundance and distribution of seagrasses is determined by light penetration, but at global levels each seagrass species has very distinct maximum distributional depth ranges, indicating that plant-associated traits must also influence their specific depth ranges. Seagrass-specific attributes, such as plant size or architecture, growth or reproductive strategy and their physiological and/or morphological acclimatization potential, have been suggested to be responsible for this variety of vertical distributions. We investigate here whether these species-specific traits drive differences in the global maximum vertical distribution of seagrasses.

Location: Global.

Time period: Publications between 1982 and 2020.

Major taxa studied: Seagrasses (order Alismatales).

Methods: We tested whether the species-specific maximum vertical distribution of seagrasses can be predicted by (1) their rhizome diameter (a proxy for plant size); (2) their functional resilience (growth/reproductive strategy); or (3) their acclimatization capacity. For the last aspect, we used a systematic review followed by meta-analytical approaches to select key seagrass traits that could potentially acclimatize to extreme light ranges across different seagrasses.

Results: We found that vertical distribution is best explained by the species-specific acclimatization capacity of various seagrass traits, including saturation irradiance (physiological trait), leaves per shoot (morphological trait) and above-ground biomass (structural trait). In contrast, our results indicate no predictive power of seagrass size or growth/reproductive strategy on the vertical distribution of seagrasses.

Main conclusions: Across the globe, the ability of seagrass species to thrive at a wide range of depths is strongly linked to the species-specific acclimatization capacity of key traits at different organizational levels.

KEYWORDS

acclimatization, depth, light, seagrasses, species traits, vertical distribution

1 | INTRODUCTION

Like every other photosynthetic marine species, the abundance and distribution of seagrasses along the vertical gradient are strongly determined by light (Duarte, 1991a; Duarte et al., 2007). Light attenuates sharply with depth in the ocean, placing increasing demands on the photosynthetic machinery of the plant, and beyond a point, few species can cope (Dennison et al., 1993). Underwater irradiance is determined by the light attenuation coefficient (k), which, in turn, is mediated by a range of abiotic and biotic factors (e.g., eutrophication leading to phytoplankton blooms, natural or anthropogenic turbidity and sedimentation, latitude, topography; Lee et al., 2007). The parameter k has, on its own, been proposed as a powerful predictor of seagrass depth limits (Duarte, 1991a; Duarte et al., 2007). However, in similar environmental conditions, distinct seagrass species have very different abilities to colonize depth ranges (Lee et al., 2007). For example, in the Mediterranean Sea, *Posidonia oceanica* can colonize waters between 0 and 45 m in very clear conditions, whereas *Zostera noltii*, in the same conditions, has a highly restricted distributional range (between 0 and 10 m) (Short et al., 2011). Variations in seagrass strategies might drive differences in species-specific vertical distributions (i.e., the maximum depth ranges that each seagrass can colonize) (Short et al., 2011), raising the question of what traits and at which organizational level (from physiological to meadow scale) allow some species to occupy vast depth ranges, whereas others remain always limited to shallow waters across their global distribution.

Seagrasses are not a species-rich group but differ considerably in their vertical colonization abilities. Although most seagrass species are able to colonize the very shallowest waters (with some exceptions; Short et al., 2011), the vertical distribution in most seagrasses seems to be determined largely by their depth limit. At a global level, species such as *Posidonia sinuosa* can be found from shallow waters to a maximum of 15 m. In stark contrast, species such as *Halophila stipulacea* can have very large vertical colonization ranges and have been recorded from 0 to 70 m (Short et al., 2011). Thus, different seagrass species have characteristic maximum vertical distributional ranges independent of their environmental conditions. Several species-specific traits of seagrasses, such as plant size/architecture and growth/reproductive strategy (Duarte, 1991a), or physiological and morphological adaptations (Dennison et al., 1993) have been proposed to account for this variance in species-specific seagrass depth limits. It is possible that large species colonize a wider range of depths given their capacity to store carbohydrates in rhizomes and their larger photosynthetic tissue, which are crucial to compensate for plant carbon gains at light-poor depths for extended periods (Alcoverro et al., 1999). In contrast, larger sizes can also be a burden for respiration in the same light-limiting conditions (Alcoverro et al., 2001). Differences in photophysiology might also allow some species to photosynthesize more efficiently in reduced light conditions (Bité et al., 2007; Silva et al., 2013). Vertical distribution can also vary between seagrass functional resilience linked to their life history, including growth or reproductive strategies in response to disturbances (Kilminster et al., 2015). Species with a high capacity for spatial recolonization and competition (fast-growing or pioneer species) (Fourqurean et al., 1995) might be advantaged by quickly colonizing deeper locations. However, seagrasses of very different sizes, rhizome diameters and growth strategies have been recorded with similar depth ranges. For instance, *P. oceanica* (large and "persistent" *sensu* Kilminster et al., 2015) and *H. stipulacea* (small and "colonizing" *sensu* Kilminster et al., 2015) both have extremely wide vertical ranges, from 0 to 45 and 70 m, respectively. The ability to colonize wide vertical ranges and adjust to changing light conditions is therefore dependent not merely on species-specific traits, but on the acclimatization potential of those traits (Schubert et al., 2018).

Studies describing specific acclimatization abilities of different seagrasses to light limitation are common, focusing on different levels of organization (i.e., physiological, morphological, structural or growth). These studies typically use field shading experiments or naturally occurring depth gradients (Collier et al., 2009; Enríquez et al., 2019; Marín-Guirao et al., 2022; Ruiz & Romero, 2001). The few studies that include more than one species observe that some species are characterized by more plastic phenotypes and traits that allow them to cope better with low-light environments than others (Bité et al., 2007; Olesen et al., 2002; Silva et al., 2013). In a similar vein, recent studies with several Mediterranean macroalgae show that their depth distributional range is closely related to species-specific photo-acclimatization capacities and light-harvesting strategies (Sant & Ballesteros, 2021). However, most studies of light acclimatization in seagrasses focus on a single species and often do not study plant responses across organizational levels (Schubert et al., 2018). A more holistic approach is required to understand how the ability of species to acclimatize by modulating particular seagrass traits can mediate differences in their vertical distribution.

In this study, we assessed whether the global maximum vertical distribution of seagrass species (obtained from Short et al., 2011) could be predicted by a series of species-specific plant attributes/traits (including size or growth/reproductive strategies) or the inherent acclimatization potential of traits (physiological, morphological, structural or growth traits). The average species-specific traits associated with size (Duarte, 1991b; Marbà & Duarte, 1998; Roca et al., 2016) and growth/reproductive strategies (Kilminster et al., 2015) were obtained from the literature, and the acclimatization capacity of the physiological, morphological, structural or growth traits was obtained with a systematic review and a meta-analytical approach.

2 | MATERIALS AND METHODS

2.1 | Relationship between the maximum vertical distribution of seagrass species and their size and growth/reproductive strategy

We tested the relationship between the maximum recorded vertical distribution (i.e., maximum depth range of colonization ever recorded) of seagrasses around the world (data from Short et al., 2011) and two potential predictors: (1) rhizome diameter (data from

Duarte, 1991b; Marbà & Duarte, 1998 and Roca et al., 2016); and (2) growth/reproductive strategy (data from Kilminster et al., 2015), with two separate linear models. For the first model, we used data from 37 species and 11 different seagrass genera, and for the second we used data of 62 species grouped into five different categorical predictors (colonizing, colonizing–opportunistic, opportunistic, opportunistic–persistent and persistent; *sensu* Kilminster et al., 2015). Model assumptions were checked visually and statistically using the functions of the "DHARMa" R package (Hartig, 2022). Assumptions were met adequately after logarithmic and square root transformation of the response variable "vertical distribution" for the first and second models, respectively (Zuur et al., 2009).

2.2 | Relationship between maximum vertical distribution and seagrass trait acclimatization potential

We tested the relationship between the globally maximum recorded vertical distribution of different seagrass species (data from Short et al., 2011) and selected key seagrass traits that could potentially acclimatize to extreme low-light conditions. To identify traits with potential acclimatization capacity, we first conducted a systematic review followed by a meta-analytical approach. Our review examined studies that included seagrass traits data in field shading experiments (with extreme low values vs. control) and depth-based studies comparing shallow versus depth limit (or close to) values. To be included in our study, the publication had to provide information on seagrass trait responses to light reduction at different organizational levels: (1) physiological [saturation irradiance (grouping data from I_k and E_k), maximum photosynthetic rate (grouping data from $P_{\max}$ and $\mathrm{ETR}_{\max}$) or photosynthetic efficiency (α)]; (2) morphological (leaf length, leaf width or leaves per shoot); (3) structural (shoot density or above-ground biomass); or (4) growth (shoot growth). We selected works published between 1982 and 2020. The search was conducted in Web of Science (WOS), with the following string for title, abstract and keywords: (seagras* OR eelgras* OR turtlegras*) AND ("shad*" OR "depth" OR "bathymetric distribution*" OR "light*") AND ("photosynthe*" OR "photo-physio*" OR "photo-acclima*" OR "acclima*" OR "morpho*"); and in Scopus with the following search string: TITLE-ABS-KEY((seagras* OR eelgras* OR turtlegras*) AND ("shad*" OR "depth" OR "bathymetric distribution*" OR "light*") AND ("photosynthe*" OR "photo-physio*" OR "photo-acclima*" OR "acclima*" OR "morpho*")) AND (LIMIT-TO (SUBJAREA, "AGRI") OR LIMIT-TO (SUBJAREA, "ENVI") OR LIMIT-TO (SUBJAREA, "EART")). These two searches yielded 617 and 695 scientific papers, in WOS and Scopus, respectively. Our final list did not include 11 relevant publications that we included manually in the list of selected studies, in addition to one publication conducted with collaborators, for which we had data prior to publication. For more details on the systematic review and meta-analyses (literature review, inclusion criteria, data extraction, calculation of the effect size and data analyses), see the Supporting Information (Appendix S1). After scrutinizing all these publications, we ended up with a total of 78 scientific studies (see Figure 1; Supporting Information Table S1 in Appendix S1). The final list summarizing the number of publications, studies and species, grouped by trait, that we finally selected, is shown in Table 1. The Supporting Information (Figure S1 in Appendix S1) shows the species for which data meeting the criteria were available and the traits that were evaluated for each of them. We therefore obtained data on species-specific acclimatization potential to light reduction that were pooled by trait (effect sizes of each physiological, morphological, structural or growth trait) to be used as predictors of seagrass vertical distribution in the linear models.

Once effect sizes were obtained for each chosen trait, we fitted linear mixed-effects models (LMMs) with a logarithmic transformation of the response variable, maximum recorded vertical distribution ("vertical distribution"). In the model, we also included "article" as a random factor and incorporated the weights obtained from the separate meta-analytical models to provide robustness to linear models. We tested the effect of the random factor based on the Akaike information criterion (AIC) and likelihood ratio tests (Zuur et al., 2009). Thus, we used LMMs or linear models (LMs) when the random effect did not provide useful information to the model. Whenever possible (sample size permitting), linear models also included the effect of the type of study (experimental shading or depth-based study) and their interaction ("effect size" and "type of study"). Model assumptions were checked visually and statistically using functions from the R package "DHARMa" (Hartig, 2022). When residuals did not meet the assumption of homogeneity of variances (i.e., leaves per shoot), we estimated the model coefficients and quasi-*t* Wald test, using the "HC4m" proposed by Cribari-Neto and da Silva (2011), as the corrected estimates of the covariance matrix for inconstant variances (heteroscedasticity).

3 | RESULTS

3.1 | Relationship between the maximum vertical distribution of seagrass species and their size and growth/reproductive strategy

We found no evidence of a relationship between the vertical distribution of seagrass species and rhizome diameter (our proxy for seagrass size, $p = .823$; Figure 2a; Supporting Information Table S2 in Appendix S1). In addition, there was no evidence of systematic differences in the vertical distribution of seagrasses according to their growth/reproductive strategies (using the classification of Kilminster et al., 2015; $p = .178$; Figure 2b; Supporting Information Table S3 in Appendix S1).

3.2 | Relationship between maximum vertical distribution and seagrass trait acclimatization potential

3.2.1 | Selecting seagrass traits with acclimatization potential: Separate meta-analyses

According to the results of our meta-analyses, there was evidence of an overall effect for seven of the nine traits studied in response to reduced incoming light: saturation irradiance (I_k), maximum photosynthesis

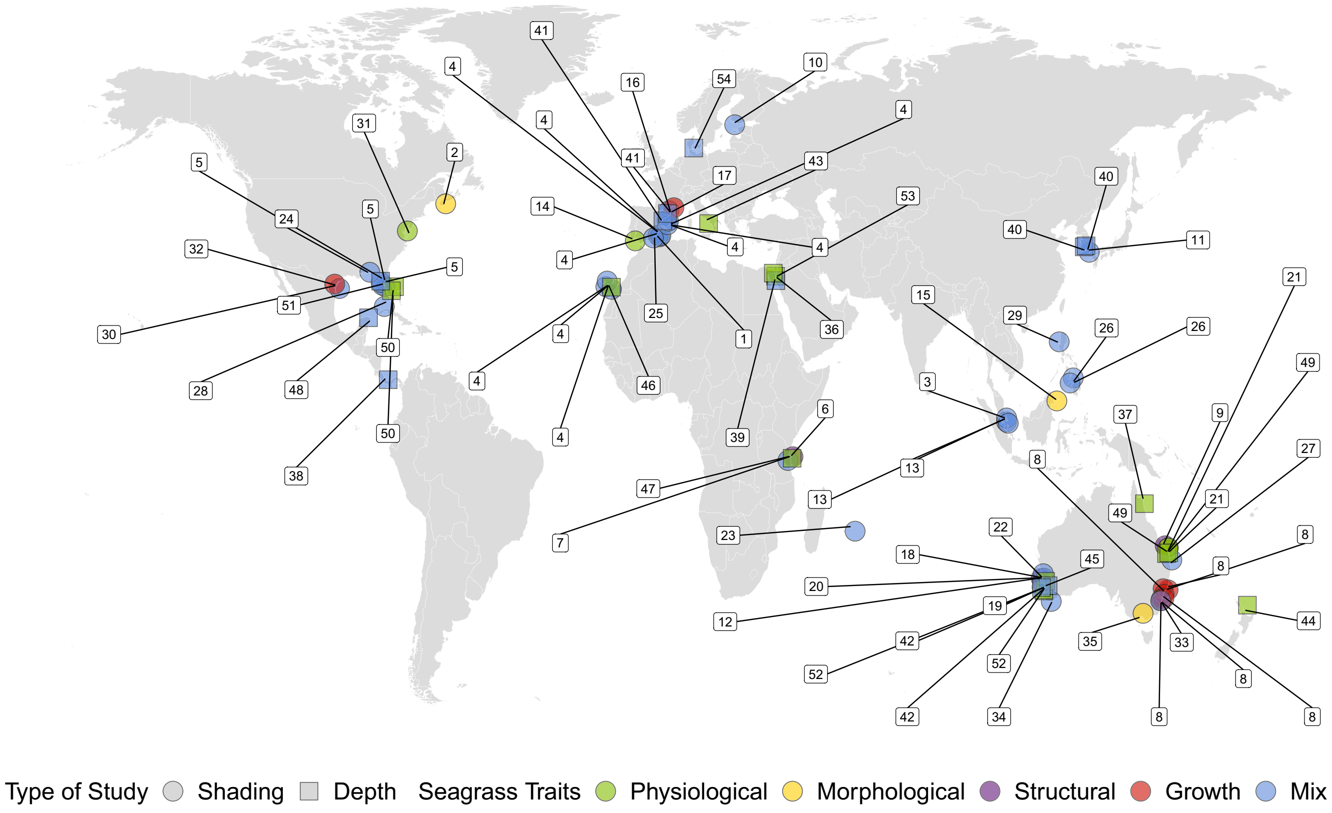

FIGURE 1 Results of the literature review. Shape shows the type of study (manipulative shading and depth-based studies) and colour the type of trait (physiological, morphological, structural and growth) studied in each publication (54 publications and 78 studies). The numbers related to each point represent the ID number corresponding to each publication in the Supporting Information (Table S1 in Appendix S1).

TABLE 1 Search results ordered by type of trait, with number of articles, studies and species for shading and depth-based investigations meeting our criteria.

Type of trait	Trait	Publications	Studies	Species
Physiological	Saturation irradiance (I_k and E_k)	17	35	13
	Maximum photosynthesis (P_{max} and ETR_{max})	25	45	14
	Photosynthetic efficiency (α)	22	40	14
Morphological	Leaf length	19	26	13
	Leaf width	16	24	9
	Leaves per shoot	11	16	7
Structural	Shoot density	25	49	15
	Above-ground biomass	19	27	12
Growth	Shoot growth	20	42	13

(P_{max}), photosynthetic efficiency (α), leaves per shoot (LXS), shoot density (Sh.Dens), above-ground biomass (Ab.b) and shoot growth (Sh.G) (Figure 3; see Supporting Information Table S4 in Appendix S1). In contrast, leaf length (L.Length) and leaf width (L.Width) did not show an overall effect in response to contrasting light environments. We found very strong evidence for saturation irradiance ($p < .0001$) and strong evidence for maximum photosynthesis ($p = .0012$) decreasing as a result of light reduction, and data revealed strong evidence for an influence of light reduction in increasing photosynthetic efficiency ($p = .0015$). In the case of morphological traits, there was moderate evidence for a decrease in the number of leaves per shoot ($p = .0165$) with light reduction, but there was no evidence for an influence of light reduction on leaf length ($p = .2490$) or width ($p = .8739$). There was also very strong evidence for structural traits, such as shoot density ($p < .0001$) and above-ground biomass ($p < .0001$), decreasing in lower light treatments. Finally, we found very strong evidence for shoot growth declining with light reduction ($p = .0002$).

3.2.2 | Influence of the selected traits on seagrass maximum vertical distribution

The acclimatization potential of the seagrass traits saturation irradiance, number of leaves per shoot and above-ground biomass

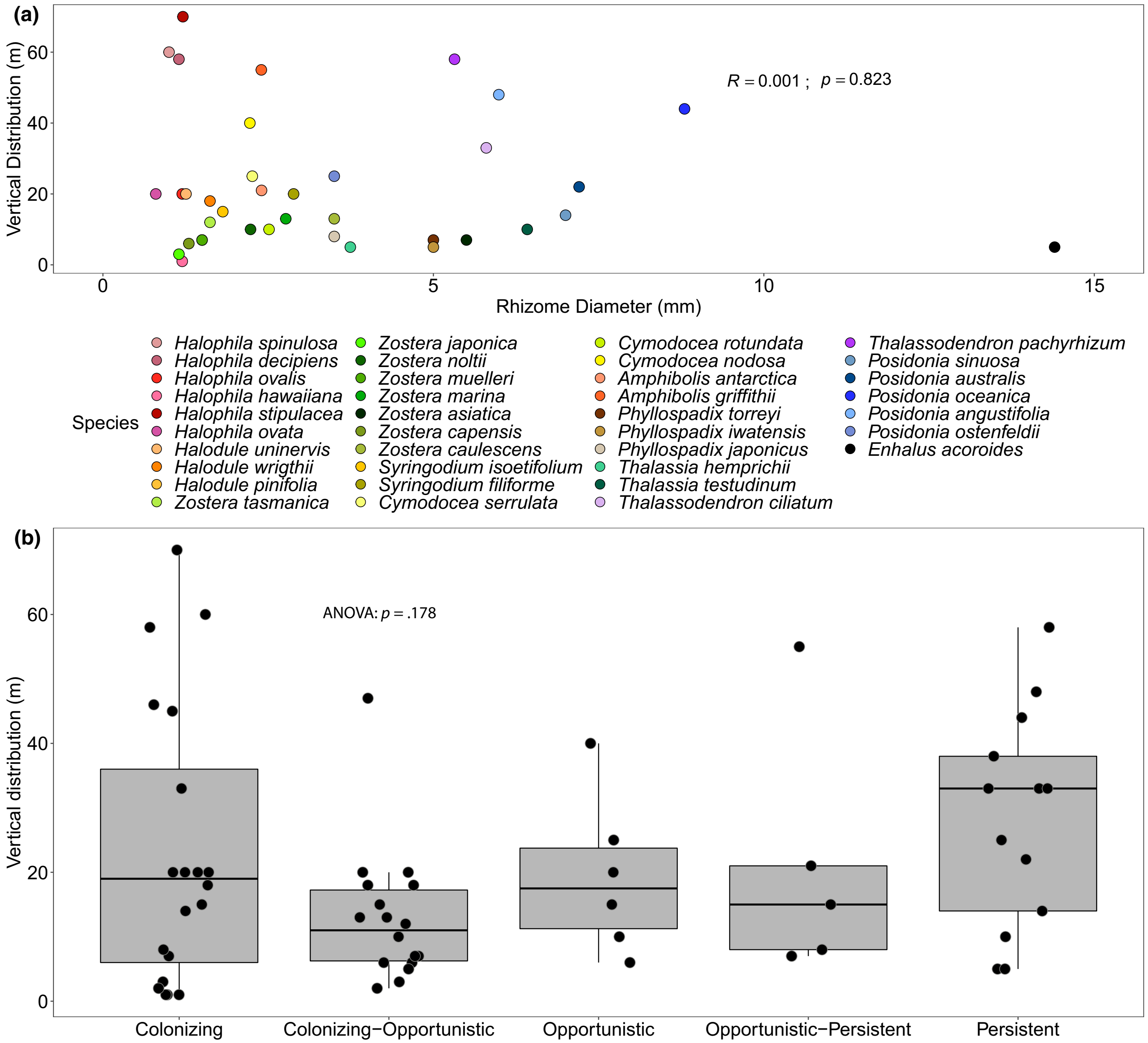

FIGURE 2 (a) Relationship between rhizome diameter and the maximum vertical distribution (i.e., maximum depth range of colonization) of 37 seagrass species. (b) Relationship between the maximum vertical distribution of 62 seagrass species and their classification according to seagrass growth/reproductive strategies. Points in panel (b) have been jittered horizontally to avoid overlapping.

(Figures 4 and 5) clearly explained the maximum vertical distribution of the analysed seagrass species. We found strong evidence for acclimatization potential (i.e., weighted effect sizes) of saturation irradiance (physiological trait) explaining the vertical distribution of seagrasses ($p = .004$; Supporting Information Table S5 in Appendix S1), in addition to very strong evidence for the acclimatization potential of leaves per shoot (morphological trait; $p < .001$; Supporting Information Table S6 in Appendix S1) and moderate evidence for above-ground biomass (structural trait; $p = .0288$; Supporting Information Table S6 in Appendix S1). In contrast, there was no evidence for the acclimatization potential of any other traits providing an adequate explanation of the vertical distribution of seagrasses (see Supporting Information Table S5 in Appendix S1)

4 | DISCUSSION

The reducing transparency of coastal seas is one of the surest imprints of human pressures on nearshore waters. Photosynthetic dependence places firm limits on how much reduction in water quality marine plants can take (Dennison et al., 1993; Duarte, 1991a), and the upward march of once-extensive seagrass meadows over the last few decades is a clear sign of accelerating environmental stress (Waycott et al., 2009). What is additionally worrying about the light requirements of seagrass meadows is that these systems are often strongly nonlinear in their behaviour (Marín-Guirao et al., 2022), implying that restoration of water clarity might not guarantee meadow recovery (Katwijk et al., 2016). Understanding what allows some species to

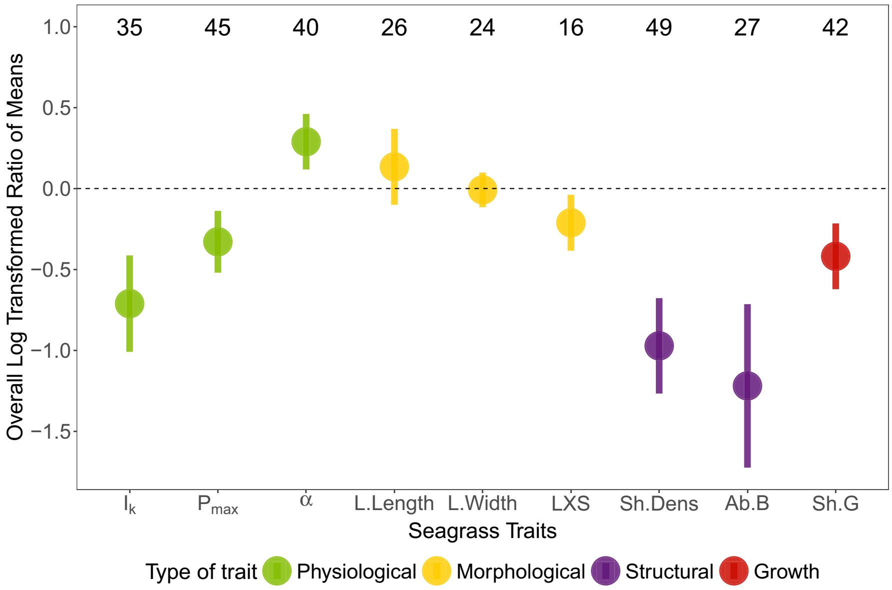

FIGURE 3 Overall effect sizes against light reduction calculated for each seagrass trait. Colours define the type of trait: physiological (green), morphological (yellow), structural (purple) and growth (red). Numbers above each trait represent the number of scientific studies for each seagrass trait analysed (for further explanation of these numbers, see Table 1). Seagrass traits shown from left to right, I_k, saturation irradiance; P_{max}, maximum photosynthesis; α, photosynthetic efficiency; L.Length, leaf length; L.Width, leaf width; LXS, leaves per shoot; Sh.Dens, shoot density; Ab.B, above-ground biomass; Sh.G, shoot growth.

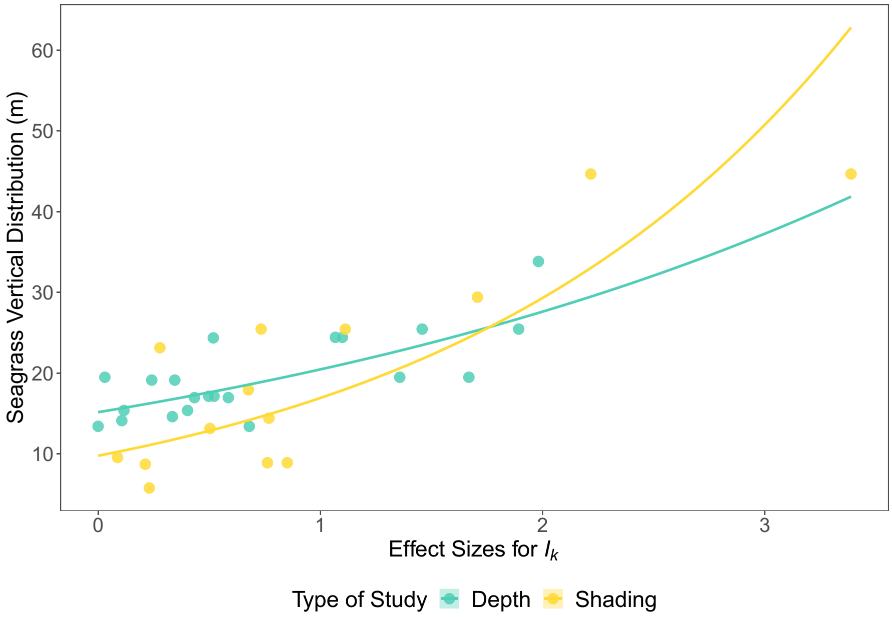

FIGURE 4 Relationships between seagrass maximum vertical distribution (in metres) and predictor variables, effect sizes (acclimatization potential for saturation irradiance, I_k) and type of study (depth-based and field shading). Data points represent distribution of standardized partial residuals of the fitted linear mixed model, where continuous lines represent the model fit through the data.

occupy wide depth distributions whereas others remain limited to much shallower ranges is therefore crucial to determine the differential susceptibility of seagrass assemblages to reduced water quality. Our survey of a large proportion of seagrass species world-wide indicates that their vertical distribution scales with acclimatization potential in key physiological, morphological and structural traits associated with low light. This ability transcends species size or functional groups, with trait acclimatization capacity found across species with large differences in rhizome width (our proxy for species size) or plant strategies. In addition, we found that these traits were not limited to a single organizational level but were a mix of physiological, morphological and structural traits. Of the traits we explored, the vertical distribution of seagrass species was best explained by the degree of species-specific capacity to reduce saturation irradiance (physiological trait), along with the capacity to reduce leaves per shoot and above-ground biomass (morphological and structural traits, respectively) as light conditions worsened.

4.1 | Seagrass maximum vertical distribution and species size

Despite the strong negative relationship between the light attenuation coefficient (k) and the depth limit of seagrass meadows (Duarte et al., 2007), light availability alone cannot accurately predict species-specific vertical distributions of seagrasses (Koch, 2001). Earlier studies have already highlighted the striking interspecific differences in seagrass depth ranges, which were attributed to seagrass

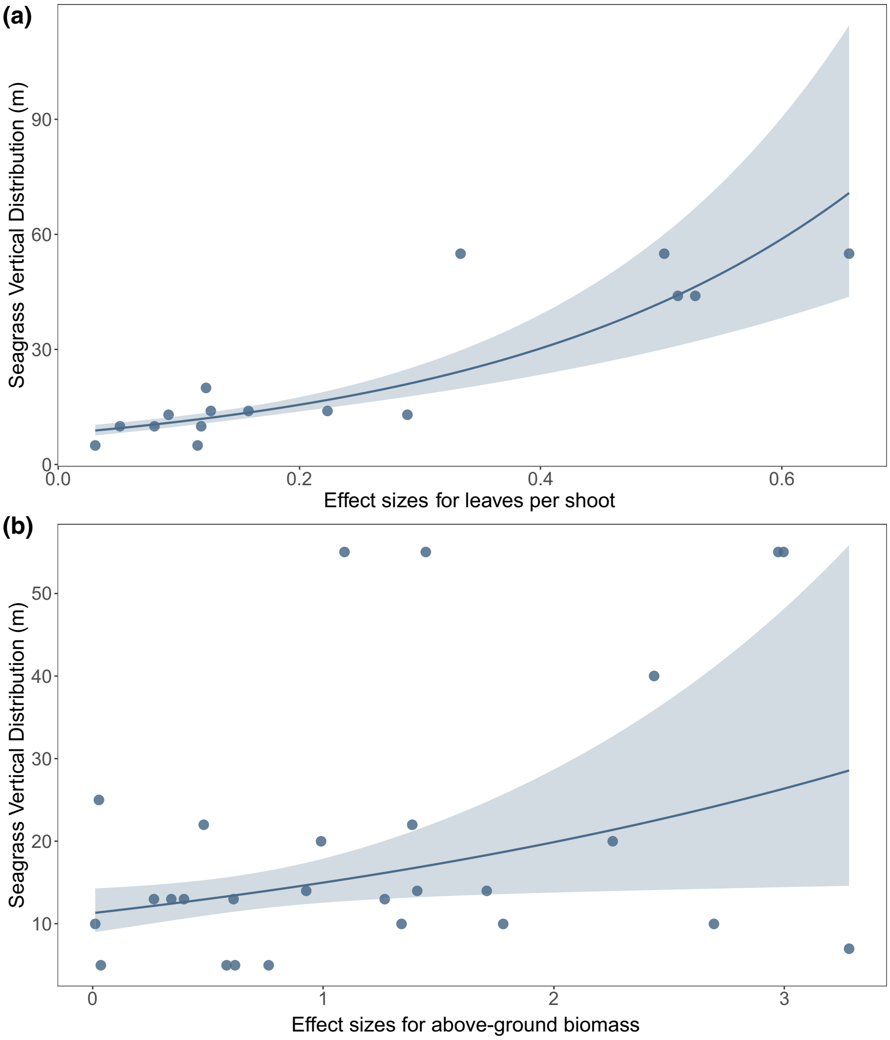

FIGURE 5 Relationships between seagrass maximum vertical distribution (in metres) and predictor variables, effect sizes: acclimatization potential for (a) leaves per shoot and (b) above-ground biomass. Data points represent distribution of standardized partial residuals of the fitted linear model, where continuous lines represent model fit through the data and the shades show 95% confidence intervals.

growth strategies or architecture (Duarte, 1991a). For instance, it has been proposed that larger rhizomes are linked to better carbon allocation abilities, which could help to boost the carbon balance of plants against declines in benthic light and promote seagrass growth through increased carbohydrate reserves (Alcoverro et al., 1999). Our results, however, conclusively rule out plant size or architecture, which is strongly related to rhizome diameter (Duarte, 1991b), as the primary predictor of seagrasses colonizing deeper depths. In fact, large rhizomes might place a heavy respiratory burden on plant physiology at depth or during periods of severe light reduction (Alcoverro et al., 2001; Duarte, 1991a; Fourqurean & Zieman, 1991; Hemminga, 1998). This respiratory demand might well offset the reserve advantages of larger rhizomes. Having large rhizomes to allocate resources has clear advantages and might provide seagrasses with considerable resilience to seasonal light trends or in the face of disturbances such as herbivory, sedimentation or occasional light reduction (Roca et al., 2014; Ruiz & Romero, 2003; Vergés et al., 2008). However, the maintenance costs of this architecture make it untenable in low-light conditions (Hemminga, 1998), and some species might have to trade off resistance to short-term light deprivation against a larger vertical distribution.

4.2 | Seagrass maximum vertical distribution and growth/reproductive strategy

Our results show no evidence that growth/reproductive strategies reflect differences in the vertical distribution of seagrass species. Colonizing, opportunistic, persistent and their intermediate life-history strategies are a useful way to classify seagrasses of the world in relationship to their functional resilience. As conceived by Kilminster et al. (2015), they combine a range of species-specific attributes, including shoot turnover, sexual maturity and investment in dormant seeds, to characterize how species are likely to respond to disturbances. Colonizing plants are characterized by faster growth rates, shorter time to sexual maturity and a higher investment in dormant seeds. Persistent species, in contrast, adopt a contrasting strategy, taking longer to reach maturity, growing more slowly and investing more in vegetative growth. Opportunistic species adopt a mixed strategy (Kilminster et al., 2015). It has been suggested that some of these traits, such as a reduced leaf/shoot turnover in persistent species, might be a long-term tolerance mechanism against reduced light conditions. For a relatively minor loss of acquired resources, plants could maintain large amounts of biomass, to cope with light reduction better

(Olesen et al., 2002). However, what emerges from our analysis is that resilience strategies do not clearly map to vertical distribution.

4.3 | Seagrass maximum vertical distribution and trait acclimatization potential

The ability to deal with reducing light conditions represents a slightly different set of physiological challenges from other environmental or biotic stressors and requires a unique set of plant strategies. Thus, what separates species with the largest vertical distributions, such as *P. oceanica*, *Cymodocea nodosa*, *H. stipulacea* or *Amphibolis griffithii*, is not so much their morphologies (they have diverse above- and below-ground structures) or their resilience strategies (which differ considerably among them), but the remarkable acclimatization potential in their physiological and morphological responses with changing light (Mackey et al., 2007; Ruiz & Romero, 2001; Silva et al., 2013; Tuya et al., 2019). In contrast, species with lower acclimatization capacity in their photosynthetic traits have never been observed at great depths. These photosynthetically limited species include *P. sinuosa* (Collier et al., 2008), *Syringodium filiforme* (Major & Dunton, 2000) and *Thalassia testudinum* (Enríquez et al., 2019). Interestingly, the photo-acclimatization responses identified in this analysis range from physiological acclimatization through to the ability to modify morphologies and above-ground structure. Studies of individual species identify this acclimatization potential as being essential in dealing with light reduction (Bité et al., 2007; Campbell et al., 2007; Collier et al., 2009; Ruiz & Romero, 2001; Silva et al., 2013); our approach allows us to generalize this across species, linking it clearly to depth distributions.

Perhaps unsurprisingly, higher physiological acclimatization capacity in the photosynthetic machinery of the plant is crucial to their ability to occupy a wide range of light regimes. As light conditions reduce with depth, only species with the ability to acclimatize by counterbalancing their carbon gains can persist (Ruiz & Romero, 2001; Ruiz & Romero, 2003). This response is typically the primary mechanism by which plants deal with light reduction (Collier et al., 2012; McMahon et al., 2013; Ralph et al., 2007). Of the three physiological parameters we examined, the reduction in the saturation irradiance (I_k) allows plants, albeit at the cost of also reducing their maximum photosynthesis, to obtain higher photosynthetic efficiencies in low-light conditions (Marín-Guirao et al., 2022). Past studies have highlighted that a photo-acclimatization response in this trait might explain more efficient use of light, in addition to differences in vertical distribution for a limited set of species (Bité et al., 2007; Campbell et al., 2007). For instance, a recent paper by Park et al. (2021) indicates that interspecific variation in physiological traits, among other traits, helps to explain differences in the vertical distribution of three *Zostera* spp. (*Zostera japonica*, *Zostera marina* and *Zostera caespitosa*). Likewise, Silva et al. (2013) showed that *C. nodosa*, with larger vertical distributions, is better photosynthetically adapted to low-light conditions than the less plastic *Z. marina*. Our study shows that the acclimatization potential of physiological traits, specifically the ability to modulate I_k, works across species and powerfully predicts the vertical distributions that might hold across the seagrass assemblage.

Acclimatization potential as a determinant of vertical distribution was also found at higher levels of plant organization. Across the assemblage, seagrasses showed considerable intraspecies variability in morphological, structural and growth traits, with a few notable exceptions. Crucially, the ability of the plant to reduce leaves per shoot and above-ground biomass explained species-specific vertical distributions. Many large seagrass species that form dense meadows (*P. oceanica*, *C. nodosa* and *A. griffithii* among them) adopt a leaf-reduction mechanism (defoliation) to minimize self-shading, an ideal strategy when colonizing deeper, darker locations (Mackey et al., 2007; Ruiz & Romero, 2001). For these species, defoliation might serve to mobilize carbohydrates (Silva et al., 2013). In addition, carbohydrate losses could be minimal if the leaf loss is restricted to older leaves, which make a minor contribution to carbon production (Alcoverro et al., 1999). This is also an ideal method for reducing the costs of above-ground respiration in impoverished light environments (Collier et al., 2009; Fourqurean & Zieman, 1991; Mackey et al., 2007). However, species showing limited ability to modify their leaves per shoot or above-ground biomass, compared with other species (for instance, *T. testudinum*, *Thalassia hemprichii* or *P. sinuosa*), are confined to shallower waters (Collier et al., 2009). Of the traits we measured, leaf dimensions (length and width) demonstrated a poor ability to change with light limitation across all species. This reduces the ability of seagrass species to expand their photosynthetic areas or (by growing taller) access shallower, more light-rich waters. For instance, leaf length and width have been found to decrease with light reduction in species such as *P. sinuosa* (Collier et al., 2009). In general, leaf morphology might be an unreliable predictor of seagrass responses to low-light environments (Tuya et al., 2019). Instead, at the deeper ends of their vertical distributions, seagrass species adopt strategies to minimize energy expenditure with structural modifications.

Across the assemblage, shoot density and shoot growth reduced, in general, with light reduction for most species in our dataset. Although the pattern of decline with reducing light was similar within species and within studies (see Supporting Information Appendix S1), the acclimatization potential of these traits did not adequately explain the specific vertical distributions of seagrasses. Declines in shoot density are strongly linked to the ability to store carbohydrate reserves, particularly in larger species possessing larger rhizomes (Alcoverro et al., 2001). Nevertheless, for structural traits, the relatively short timing and duration of shading studies might have influenced our results (Collier et al., 2009). In fact, for experimental studies, long-term responses are expected to see the effect of light not only in the survival, but also in the full development of true meadows at their edges.

A potential limitation of our study is that we did not control for other abiotic factors that vary with depth that could also play a role in determining vertical depth distributions (Beer & Waisel, 1982; Carr et al., 2010). We limited our investigation to depth-based studies and shading manipulative experiments, where the only modified condition was light reduction. Our purpose was to obtain metrics related to plant identity that could explain depth distribution, but we cannot disentangle whether other factors, such as turbulence or sediment grain size, or overall differences between temperate and tropical waters additionally influenced these patterns. Our results are based on only a subset of species, because we do not yet have a comprehensive understanding of the responses of many seagrass species to reduced light. Shading experiments or comparative depth-based studies do not exist for all seagrass species, but represent *c*. 30% of the entire seagrass pool. As previous studies have already highlighted, our ability to generalize is necessarily circumscribed by gaps in research effort (McMahon et al., 2013). Moreover, this lack of species representation combines with an unequal distribution of our data across the entire range of depths suitable for seagrasses, which could have shaped the results found in this study.

5 | CONCLUSIONS

What seems clear is that seagrass species use different strategies, at different levels of organization, to colonize deeper locations. Physiological acclimatization is geared towards maximizing their light-harvesting strategy in the deep, whereas higher-level strategies are directed at minimizing costs and reducing plant architecture. These strategies work in tandem. The seagrass species with the greatest vertical distribution were able to acclimatize physiological, morphological and structural traits (I_k, leaves per shoot and above-ground biomass) simultaneously. A combined acclimatization ability at physiological and higher levels is what makes these species particularly successful across the entire depth gradient.

Although the decline in areal extent of seagrass meadows is easy to see as coasts succumb to a host of local and global stressors, the vertical contraction of meadows is often less visible. Yet it is one of the surest signs of an ecosystem in decline and serves as a warning of worsening ecological conditions. Identification of the mechanisms by which different seagrass species thrive within their natural depth ranges is crucial to establish species-specific baselines against which to measure this retreat and calibrate recovery programmes. Seagrass species have different vulnerabilities to declining light conditions, with some being particularly sensitive to even small changes in light regimes. What our work shows is that the ability to deal with reduced light is not linked to a few specialized traits, but with the acclimatization potential to modify trait parameters at physiological, morphological and structural levels. There are, however, limits to trait acclimatization, and many meadows are increasingly depth restricted as stressors increase. Reversing this retreat will require concerted and coordinated efforts to improve water quality but are essential to conserve the diversity and function of seagrass meadows across their depth range.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and R code that support the findings of our study are available in the Supporting Information of this article at: https://zenodo.org/record/7659364#.Y_Q7sXZBy3A

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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