Caractérisation structurelle et fonctionnelle des communautés d'élasmobranches d'Atlantique Nord-Est dans le contexte du changement climatique

Noémie Coulon

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THESE

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Caractérisation structurelle et fonctionnelle des assemblages d’élasmobranches d’Atlantique Nord-Est dans le contexte du changement climatique

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<< Chouette ! Où est-ce qu'on va ? >>

Peregrin Touque

-La communauté de l'anneau, 1954, J.R.R. Tolkien-

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Résumé

Les prises accessoires et la dégradation de l'habitat conduisent à l'extinction de près de la moitié des élasmobranches dans l'Atlantique Nord-Est. Parallèlement, la pression du changement climatique sur les organismes marins s'est intensifiée, entraînant des transformations écologiques irréversibles. Étonnamment, on pensait que les raies et les requins, ayant évolué à des périodes où le taux de CO_2 atmosphérique était plus élevé, pourraient tolérer ces conditions futures. En conséquence, les effets potentiels de l'acidification et du réchauffement des océans ont été largement sous-estimés. Il était donc impératif de mener des recherches pour évaluer la vulnérabilité des élasmobranches face à ces nouvelles pressions. Dans un premier temps, j'ai quantifié l'impact des changements environnementaux observés entre 1997 et 2020 sur l'aire de distribution de neuf espèces et la structure fonctionnelle de leur assemblage, en utilisant des données de campagnes scientifiques de chalutage de fond. Les résultats ont révélé des déplacements d'espèces vers des eaux plus profondes et des modifications de la structure trophique des assemblages d'élasmobranches. Je me suis ensuite concentrée sur les effets de l'élévation de la température et de l'acidification sur les jeunes stades de la petite roussette (*Scyliorhinus canicula*), espèce modèle pour les élasmobranches ovipares. Cette étude expérimentale a évalué les réponses des embryons et des juvéniles à deux scénarios climatiques, avec ou sans mesures d'atténuation. Les températures et pH correspondaient aux projections pour 2100 selon les scénarios CMIP6 du GIEC : SSP2, « Middle of the Road », et SSP5, « Fossil-fueled Development » (+2 et +4 °C, ΔpH = -0,2 et -0,4). Les résultats ont été comparés à une condition témoin basée sur les données historiques de 1995 à 2014. Une mortalité élevée a été observée durant la période estivale, variant de 18 % dans les scénarios historiques et SSP2 à 89 % pour le traitement SSP5. L'impact dramatique de cette mortalité dans le scénario SSP5 pourrait fortement perturber la dynamique des populations. La troisième partie de ma thèse a donc consisté à prédire la taille et la structure des populations de *S. canicula* d'ici 2100, en utilisant une approche individu-centrée permettant de moduler les traits d'histoire de vie en fonction de la température. Les réponses de *S. canicula* ont été comparées à celles d'une espèce phylogénétiquement proche, la grande roussette (*S. stellaris*), qui présente une distribution spatiale et des traits d'histoire de vie différents. Nos résultats ont montré que même le réchauffement modéré du scénario SSP2 a eu des effets notables sur la maturation des individus des deux espèces. En revanche, le réchauffement plus intense du scénario SSP5 a provoqué des impacts négatifs marqués, particulièrement pour *S. stellaris*, dont les populations pourraient s'effondrer localement. Les modèles individu-centrés développés ont fourni un cadre solide pour traduire des données

physiologiques limitées sur la croissance en dynamiques de population chez les requins ovipares. Toutefois, leur élaboration a mis en évidence des lacunes concernant l'impact de la température sur la fertilité des élasmobranches. J’ai donc approfondi cette question dans la dernière partie de la thèse, en examinant les effets de la température, de la gamétogenèse à la production d'œufs ou de nouveau-nés, à partir des articles scientifiques disponibles. Cette thèse a ainsi permis d’explorer l'impact du changement climatique tant sur les individus que sur la dynamique à long terme des populations. Ces connaissances sont cruciales pour orienter les stratégies de conservation et de gestion des élasmobranches face aux changements environnementaux, nécessitant des décisions éclairées pour atténuer les impacts sur ces espèces vulnérables.

Abstract

Bycatch and habitat degradation are leading to the extinction of nearly half of the elasmobranchs in the Northeast Atlantic. Meanwhile, the pressure of global change on marine organisms has intensified, causing irreversible ecological transformations. Surprisingly, it was thought that rays and sharks, which evolved during periods of higher atmospheric CO2 levels, could tolerate these future conditions. As a result, the potential effects of ocean acidification and warming have been largely underestimated. It is therefore imperative to conduct research to assess the vulnerability of elasmobranchs to these emerging pressures. Initially, I quantified the impact of environmental changes observed between 1997 and 2020 on the distribution range of nine species and the functional structure of communities, using data from scientific bottom trawl surveys. The results revealed species shifts to deeper waters and changes in the trophic structure of elasmobranch communities. Then, I focused on the effects of temperature increase and acidification on the early life stages of the small-spotted catshark (*Scyliorhinus canicula*), a model species for oviparous elasmobranchs. This experimental study assessed the responses of embryos and juveniles to two climatic scenarios, with or without mitigation measures. The temperatures and pH levels corresponded to the projections for 2100 according to the IPCC CMIP6 scenarios: SSP2, “Middle of the Road,” and SSP5, “Fossil-fueled Development” (+2 and +4 °C, ΔpH = -0.2 and -0.4). The results were compared to a control condition based on historical data from 1995 to 2014. High mortality rates were observed during the summer period, ranging from 18% in the historical and SSP2 scenarios to 89% for the SSP5 treatment. The dramatic impact of this mortality in the SSP5 scenario could severely disrupt population dynamics. Therefore, the third part of my PhD thesis aimed to predict the size and structure of *S. canicula* populations by 2100, using an individual-based approach that allows modulation of life history traits based on temperature. The responses of *S. canicula* were compared to those of a phylogenetically related species, the nursehound (*S. stellaris*), which has different spatial distribution and life history traits. Our results showed that even the moderate warming of the SSP2 scenario had notable effects on the maturation of individuals of both species. In contrast, the more intense warming of the SSP5 scenario caused significant negative impacts, particularly for *S. stellaris*, whose populations could collapse.The individual-based models developed provided a solid framework for translating limited physiological data on growth into population dynamics for oviparous sharks. However, their development highlighted gaps regarding the impact of temperature on elasmobranch fertility. Therefore, I delved deeper into this question in the final part of this PhD thesis, examining the effects of temperature from gametogenesis to the production of offspring, based on available scientific

literature. Finally, this PhD thesis has explored the impact of global change on both individuals and the long-term dynamics of populations and communities. This knowledge is crucial for guiding conservation and management strategies for elasmobranchs in the face of environmental changes, necessitating informed decisions to mitigate impacts on these vulnerable species.

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LISTE DES ILLUSTRATIONS

LISTE DES TABLEAUX

LISTE DES ABREVIATIONS

ATP	Adénosine triphosphate
DAG	Directed Acyclic Graph
DEB	Dynamic Energy Budget
HIF	Hypoxia Inducible Factor
HSP	Heat Shock Protein
GES	Gaz à Effet de Serre
GIEC	Groupe d'experts intergouvernemental sur l'évolution du climat
HMSC	Hierarchical Modelling of Species Communities
IBM	Individual-Based Models
JSDM	Joint Species Distribution Models
MCMC	Markov Chain Monte Carlo
pCO_2	Pression partielle de dioxyde de carbone
PEB	Physiological Energy Budget
pO_2	Pression partielle d'oxygène
PSU	Practical Salinity Units
ROS	Reactive Oxygen Species
SDM	Species Distribution Models
SGF	Scope For Growth
SMR	Standard Metabolic Rate
SSDM	Stacked Species Distribution Modelling
WEB	Wisconsin Energy Budget

INTRODUCTION

I- Facteurs de stress associés aux changements climatiques

1. Le réchauffement des océans

Le réchauffement global est principalement attribué à l'augmentation des concentrations de gaz à effet de serre (GES) dans l'atmosphère, tels que le dioxyde de carbone (CO_2), le méthane (CH_4) et le protoxyde d'azote (N_2O) (IPCC, 2021 ; NASA, 2021). Ces GES, issus principalement de la combustion de combustibles fossiles, des activités industrielles et agricoles, ainsi que de la déforestation (IPCC, 2014), piègent la chaleur émise par la surface terrestre en formant une couche isolante autour de la planète. Ce phénomène, connu sous le nom d'effet de serre, conduit à une accumulation progressive de chaleur dans l'atmosphère terrestre (IPCC, 2021). En conséquence, depuis 1993, environ 93 % de l'excès de chaleur généré a été absorbé par les océans, un phénomène appelé réchauffement des océans (Bindoff et al., 2019). Selon le Groupe d'experts intergouvernemental sur l'évolution du climat (GIEC), la température moyenne des eaux de la surface des océans a augmenté d'environ 0,13 °C par décennie depuis les années 1970 (Hartmann et al., 2013 ; Bindoff et al., 2019 ; Whitney et al., 2007). De plus, des records sont de plus en plus enregistrés, comme en 2023, où les températures ont atteint des niveaux sans précédent, avec des anomalies atteignant jusqu'à 1 °C au-dessus de la moyenne de la période 1971-2000 dans certaines régions (NOAA, 2023). Ce réchauffement affecte également les profondeurs océaniques. Entre 1960 et 2019, les températures dans les 2 000 premiers mètres de l'océan ont globalement augmenté de 0,07 °C par décennie (Bindoff et al., 2019).

2. L'acidification des océans

L'acidification des océans est un phénomène provoqué par l'augmentation des concentrations de CO_2 atmosphérique, essentiellement dû aux activités humaines telles que la combustion de combustibles fossiles. Lorsque le CO_2 est absorbé par les océans, il réagit avec l'eau pour former de l'acide carbonique (H_2CO_3), qui se dissocie en ions hydrogène (H^+) et bicarbonate (HCO_3^-). Une partie des ions bicarbonate se dissocie également en ions carbonate (CO_3^{2-}) et H^+. L'augmentation des ions H^+ entraîne une diminution du pH, rendant l'eau plus acide.

Équations de l'équilibre du système carbonique en solution aqueuse :

$$CO_2 + H_2O \Leftrightarrow H_2CO_3$$

$$H_2CO_3 \Leftrightarrow H^+ + HCO_3^-$$

$$HCO_3^- \Leftrightarrow H^+ + CO_3^{2-}$$

$$pH = -\log\left[H^+\right]$$

Depuis le début de l'ère industrielle, le pH moyen des océans en surface a diminué d'environ 0,1 unité, passant de 8,2 à 8,1 (IPCC, 2013). Bien que cette réduction puisse sembler minime, elle correspond à une augmentation de 26 % de la concentration en H^+. Actuellement, le taux de diminution du pH varie entre 0,017 et 0,026 unité pH par décennie, en fonction des régions océaniques et des conditions locales (Dore et al., 2009 ; Bindoff et al., 2019 ; Olsen et al., 2016). Selon les projections basées sur les scénarios d'émissions de gaz à effet de serre, le pH des océans pourrait encore baisser de 0,3 à 0,4 unité d'ici la fin du 21e siècle, entraînant une augmentation de 100 à 150 % de l'acidité des océans par rapport aux niveaux préindustriels (Caldeira et Wickettt, 2005 ; Bindoff et al., 2019). Cette acidification affecte non seulement la surface, mais également les eaux côtières profondes (Cai et al., 2011) et les profondeurs océaniques (Sabine et al., 2004). Par exemple, le taux d'acidification près du fond de la mer du Japon est 27% plus élevé que le taux à la surface (Chen et al., 2017).

3. La désoxygénation des océans

La désoxygénation des océans est un phénomène complexe qui évolue à des échelles spatiales et temporelles distinctes de celles du réchauffement et de l'acidification. Depuis 1960, la concentration en oxygène des océans a diminué de plus de 2 %, soit une perte d'environ 4,8 ± 2,1 $\mu mol.L^{-1}$ (Bograd et al., 2008 ; Helm et al., 2011 ; Schmidtko et al., 2017 ; Stramma et al., 2008 ; Whitney et al., 2007). Cette diminution résulte de plusieurs facteurs interconnectés. Parmi eux, l'augmentation des températures océaniques réduit la solubilité de l'oxygène dans l'eau, limitant ainsi la quantité disponible pour les organismes marins. Parallèlement, la hausse des températures stimule la respiration microbienne et la décomposition des matières organiques, augmentant la consommation biologique d'oxygène (Pörtner et al., 2014 ; Robinson, 2019). De plus, le réchauffement induit une stratification accrue des couches d'eau, créant une séparation plus marquée entre les couches superficielles chaudes et les couches profondes plus froides, ce qui réduit le mélange vertical et limite le renouvellement de l'oxygène dans les profondeurs (Breitburg et al., 2018 ; Schmidtko et al., 2017). Cette dynamique de désoxygénation est susceptible de s'intensifier au cours du 21e siècle, exacerbée par l'augmentation continue des températures océaniques. Les projections suggèrent que cette tendance pourrait entraîner une diminution de la concentration en oxygène dans les couches océaniques situées entre 100 et 600 mètres, avec une baisse potentielle variant de 18,55 $\mu mol.L^{-1}$ à 3,44 $\mu mol.L^{-1}$ par rapport à la période 1870-1899, en fonction du scénario climatique envisagé (Kwiatkowski et al., 2020).

4. La diminution de la salinité des océans

Le réchauffement global impacte profondément les régimes hydrologiques à l'échelle planétaire, entraînant une augmentation significative des apports d'eau douce dans les milieux marins. Deux processus majeurs expliquent cette dynamique : la fonte accélérée des glaciers et des calottes glaciaires, et l'augmentation des précipitations continentales et du ruissellement. La fonte des glaciers et des calottes glaciaires libère des quantités considérables d'eau douce dans les océans, ce qui contribue non seulement à l'élévation du niveau de la mer mais modifie également la salinité des eaux côtières et des régions polaires. Les calottes glaciaires du Groenland et de l'Antarctique perdent environ 5000 milliards de tonnes d'eau douce par an (Rignot et al., 2019), tandis que les glaciers de montagne ont perdu environ 2670 milliards de tonnes entre 1961 et 2016 (Zemp et al., 2019). Cette fonte contribue à une élévation moyenne du niveau des mers d'environ 5.7 cm entre 1865 et 1990, avec une accélération notable au cours des dernières décennies (Zuo et Oerlemans, 1997 ; IPCC 2021). En parallèle, l'intensification des précipitations et des événements météorologiques extrêmes, tels que les tempêtes et les inondations, accroît le volume d'eau douce se déversant dans les océans via les rivières et les estuaires (Eilander et al., 2020).

L'entrée d'eau douce, moins dense que l'eau salée, accentue la stratification entre les eaux superficielles et les couches plus profondes, plus salées. Ce phénomène de stratification peut perturber les courants océaniques qui dépendent de la différence de densité entre les couches d'eau pour générer et maintenir leur circulation. Ces changements peuvent avoir des répercussions sur les régimes climatiques régionaux et globaux, affectant les conditions météorologiques et climatiques à long terme (Schott et al., 2009). La stratification accrue peut également limiter le mélange vertical des couches d'eau, un processus crucial pour le transfert de nutriments et la distribution de chaleur dans les océans. Dans les régions où la stratification est renforcée, le mélange vertical est réduit, ce qui peut entraîner une accumulation de nutriments dans les couches profondes et une diminution de la productivité biologique en surface.

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II- Aperçu des impacts des changements climatiques sur les systèmes biologiques des poissons osseux et cartilagineux

Dans cette thèse, nous avons sélectionné le pH et la température comme principaux facteurs de pression sur les organismes, car ces paramètres étaient disponibles pour le Nord-Est Atlantique à des échelles spatio-temporelles précises, permettant une continuité dans l'analyse des pressions passées et futures. Cependant, la baisse de la concentration en oxygène, en synergie avec l'augmentation de la température, ainsi que la diminution de la salinité dans les zones côtières, peuvent également induire des réponses biologiques à travers l'ensemble des systèmes des poissons osseux et cartilagineux. De plus, bien qu'il s'agisse ici d'une thèse en écologie marine centrée sur les impacts à l'échelle des individus, des populations et des communautés, il est essentiel de replacer ces résultats dans le contexte des réponses aux changements climatiques à des échelles biologiques plus fines. Par conséquent, cette partie de l'introduction présente ainsi un état de l'art des impacts du changement climatique sur les systèmes biologiques des poissons osseux et cartilagineux.

1. Des réponses moléculaires aux réponses (sub)cellulaires

Les fluctuations environnementales, telles que les variations de température, les changements de pH, la diminution des niveaux d'oxygène et la diminution de la salinité, induisent des réponses adaptatives complexes au niveau moléculaire chez les poissons (Heuer et Grosell, 2014 ; Petitjean et al., 2019). La méthylation de l'ADN est le principal mécanisme épigénétique responsable des changements phénotypiques, en modulant l'activation et la désactivation de gènes spécifiques (Anastasiadi et al., 2017 ; 2021 ; Metzger et Schulte, 2017). Parmi ces gènes, ceux codant pour les protéines de choc thermique (HSP, Heat Shock Protein) sont essentiels pour protéger les cellules contre les dommages thermiques en facilitant le repliement correct des protéines et en réparant celles qui sont endommagées (Hochachka et Somero, 2002 ; Feder et Hofmann, 1999). En réponse à des températures élevées, l'expression des HSP peut augmenter dans les tissus musculaires des poissons, contribuant ainsi à maintenir la stabilité cellulaire et fonctionnelle malgré des conditions de chaleur extrême (Lindquist et al., 1988 ; Lund et al., 2002). Par exemple, lors d'un pic de chaleur de 15°C à 21°C, une augmentation significative des niveaux des HSP70 a été observée chez l'aiguillat commun (*Squalus acanthias*) (Bockus et al., 2020 ; Figure 1).

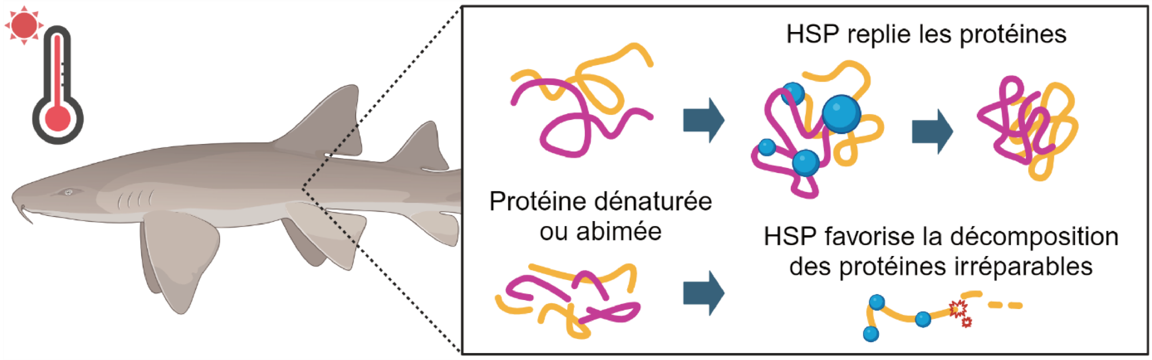

Figure 1 : Rôle des protéines de choc thermique (HSP, Heat Shock Proteins). Créée avec Biorender.com

En période de forte chaleur, les poissons doivent souvent également faire face à des évènements de désoxygénation. En réponse, ils montrent une augmentation notable de l'expression des gènes régulés par le facteur inductible par l'hypoxie (HIF, Hypoxia Inducible Factor), notamment ceux codant pour l'hémoglobine, une protéine essentielle au transport de l'oxygène. Cette production accrue optimise ainsi l'efficacité de l'utilisation de l'oxygène dans les tissus (Nikinmaa et Rees, 2005 ; Shahjahan et al ., 2022). De plus, les HIF-1 induisent partiellement l'expression des transporteurs de glucose, dont l'augmentation sous hypoxie semble liée à une demande énergétique accrue dans les branchies (Hall et al., 2005 ; Terova et al., 2009). Chez les élasmobranches, bien que de nombreuses espèces montrent une augmentation de leur hématocrite en réponse à une élévation de la température (Bouyoucos et al. 2020; Butler etTaylor 1975; Neale et al., 1977) ou à l'acidification (Rummer et al., 2020), les stratégies d'adaptation à l'anoxie varient, même chez des espèces de requins étroitement apparentées (Chapman et Renshaw, 2009). Par exemple, le requin-chabot ocellé (*Hemiscyllium ocellatum*) montre une augmentation importante de l'hématocrite et une diminution de la concentration en hémoglobine, ce qui indique que ses érythrocytes gonflent en réponse à l'anoxie. En revanche, le requin-chabot bambou (*Chiloscyllium punctatum*) présente une augmentation de l'hématocrite, du nombre d'érythrocytes et de la concentration en hémoglobine, suggérant que cette espèce libère plus d'érythrocytes dans la circulation et/ou augmentent la concentration de ses érythrocytes en réponse à l'anoxie. Pour autant, les concentrations plasmatiques de glucose restent stables pendant l'anoxie pour les deux espèces. Parallèlement, les variations du pH sanguin induites par l'acidification des océans modifient l'affinité de l'hémoglobine pour l'oxygène, impactant ainsi la capacité des poissons à le transporter et à le libérer efficacement (Shahjahan et al ., 2022). L'effet Bohr illustre ce phénomène : lorsque le pH diminue, l'affinité de l'hémoglobine pour l'oxygène baisse, permettant une libération accrue d'oxygène dans les tissus où la concentration en CO_2 est élevée et le pH plus bas (Jensen, 2004). De plus, l'effet Haldane décrit comment la désoxygénation de l'hémoglobine augmente sa capacité à transporter le CO_2 des tissus vers les branchies, où il est ensuite expulsé.

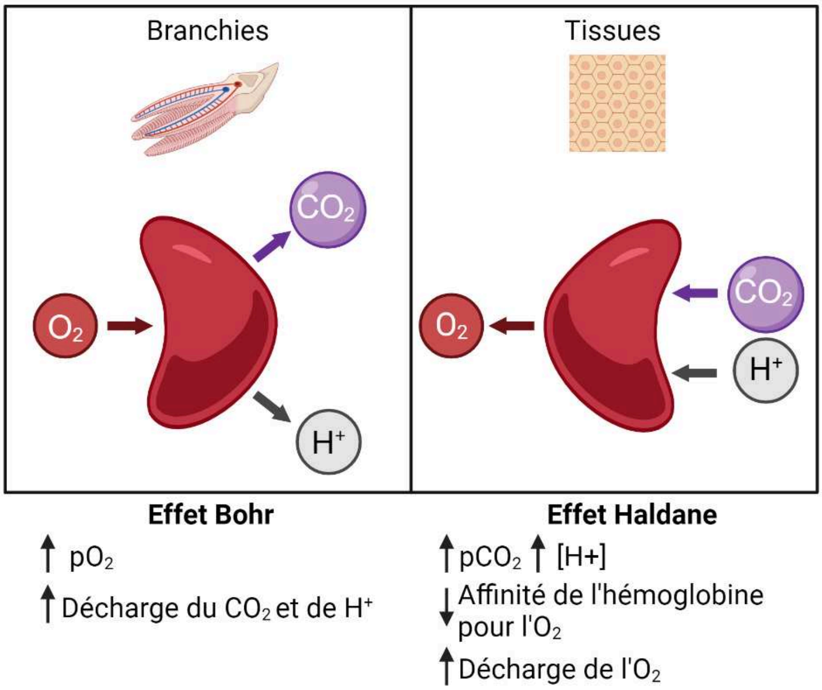

Figure 2 : Effet Bohr-Haldane. Ce phénomène décrit le transport du CO_2 et de l'O_2 par les érythrocytes. Un environnement plus acide favorise la capture du CO_2 et la libération de l'O_2. La partie rouge illustre le changement de conformation des molécules d'hémoglobine lorsqu'elles lient ou relâchent le CO_2 et l'O_2. La présence d'hémoglobine oxygénée déplace la courbe de dissociation du CO_2 vers la droite, tandis que la présence d'hémoglobine désoxygénée la déplace vers la gauche. Créée avec Biorender.com

Chez les élasmobranches, les hémoglobines ont une affinité plus élevée pour l'oxygène comparée à celle des poissons osseux. En général, les phosphates organiques (comme l'ATP) se lient à l'hémoglobine et réduisent son affinité pour l'oxygène, facilitant ainsi la libération d'oxygène là où il est nécessaire. Cependant, chez les élasmobranches, ce rapport est plus bas, contribuant à une meilleure capacité de l'hémoglobine à maintenir l'oxygène. De plus, l'urée, qui joue un rôle crucial dans l'osmorégulation des élasmobranches, exerce un effet stabilisateur en contrebalançant l'effet des phosphates organiques sur l'affinité de l'hémoglobine pour l'oxygène. Malgré la présence des effets Bohr et Haldane, les élasmobranches bénéficient d'une forte capacité de tamponnement. Cette capacité est renforcée par la présence de l'anhydrase carbonique dans le plasma, ce qui réduit l'impact des échanges d'O_2 et de CO_2 sur leur respiration, contrairement aux téléostéens où ces échanges sont plus directement liés (Giareta et al., 2023 ; Nikinmaa et al., 2019). Cependant la capacité des élasmobranches à gérer l'excrétion d'urée et d'ammoniac semble affectée par la température ce qui pourrait réduire ces différences (Giacomin et al., 2017). L'expression des gènes impliqués dans l'équilibre acido-basique comme les gènes régulant les pompes à protons et les transporteurs d'ions est également modifié pour compenser les changements de pH dans les fluides corporels (Heuer et Grosell, 2014 ; Shahjahan et al ., 2022). Par exemple, l'exposition de la morue (*Gadus morhua*) à des conditions d'acidification a entraîné une augmentation significative de l'expression des gènes codant pour les pompes à protons de type ATPase, avec une réponse dépendante de la température (Michael et al., 2016). Ces pompes, également sensible à la salinité (Kulac et al., 2012) jouent un rôle crucial dans la régulation du pH intracellulaire en expulsant les H^+ des cellules, permettant ainsi à l’organisme de compenser les variations de pH dans ses fluides corporels. De plus, les gènes codant pour les transporteurs d'ions tels que les cotransporteurs Na^+/H^+, Na^+/HCO_3^- et l’échangeur Cl^-/HCO_3^- montrent également une expression accrue pour faciliter l'échange d'ions et la régulation du pH sanguin, assurant une meilleure homéostasie interne malgré les conditions environnementales défavorables (Claiborne et al., 2002 ; Deigweiher et al., 2008 ; Michael et al., 2016). Enfin, la diminution de la salinité pourrait influencer l'expression des gènes impliqués dans les canaux ioniques et les transporteurs de sodium et de chlore (Evans et Kültz, 2020 ; Shahjahan et al., 2022). Par exemple, une augmentation de 43 % de l'expression des gènes codant pour le canal ionique Na^+/K^+-ATPase a été observée chez des saumons Atlantique (*Salmo salar*) exposés à une salinité réduite, indiquant l'importance de cette enzyme dans l'osmorégulation (Bystriansky et Schulte, 2011). Les changements de salinité activent également des voies de signalisation spécifiques au stress osmotique, affectant des protéines comme les MAP kinases qui jouent un rôle dans la réponse au stress cellulaire et sont également impliqués dans la régulation de l’activité des HIF (Burg et al., 2007 ; Bracken et al., 2003 ; Tian et al., 2019).

Les variations de température influencent également les processus biochimiques, notamment l'activité enzymatique et les interactions entre les enzymes et leurs substrats (Hochachka et Somero, 2002 ; Little et al., 2020). La température affecte la vitesse des réactions enzymatiques, suivant la loi d'Arrhenius. Selon cette loi, le taux de réaction (k) est une fonction exponentielle de la température (T) :

$$k = A \times exp^{-\frac{E_a}{RT}}$$

Où A est la fréquence des collisions, E_a est l'énergie d'activation de la réaction, R est la constante universelle des gaz parfaits (8,314 $J.mol^{-1}.K^{-1}$), T est la température absolue. Lorsque les températures augmentent, les enzymes qui catalysent ces réactions réduisent l'énergie d'activation nécessaire, rendant les processus métaboliques plus efficaces. Toutefois, une température trop élevée peut altérer leur structure tridimensionnelle (Hochochka et Somero, 2002). La dénaturation entraîne une baisse de l'activité enzymatique, illustrant un point critique où le taux de réaction ne suit plus la loi d'Arrhenius de manière simple, car les enzymes ne peuvent plus catalyser les réactions de manière optimale. En résumé, l'effet de la température sur les réactions biochimiques est double : elle accélère les réactions jusqu'à un point optimal, au-delà duquel l'efficacité enzymatique peut diminuer en raison de l'inactivation ou de la dénaturation des enzymes (Daniel et al., 2010). Un pH plus bas peut également modifier les charges des acides aminés sur le site actif de l'enzyme, affectant ainsi sa capacité à lier les substrats (Davies et al., 2005). Réciproquement, les changements de pH et de l'osmolarité du milieu aquatique peuvent affecter la protonation des substrats et modifier leur conformation, entraînant une diminution de leur affinité pour les enzymes (Tipton et al., 2009). En ce qui concerne les élasmobranches, aucune augmentation significative (Rosa et al. 2016b) et même une diminution (Tullis et Baillie 2005) de l'activité de la citrate synthase, une enzyme clé impliquée dans la production d'ATP, ont été observés chez deux espèces du genre *Chiloscyllium* en réponse au réchauffement. En conditions acides, la diminution de l'activité de la citrate synthase a été associée à une réduction des taux d'absorption d'oxygène chez les juvéniles de requin-chabot bambou qui ont été exposés à cette acidité tout au long de leur embryogenèse (Rosa et al., 2014 ; 2016b). De plus, une augmentation de l'activité de la lactate déshydrogénase, une enzyme qui catalyse la conversion du lactate en pyruvate (ou inversement) dans les vois métaboliques aérobie et anaérobie a été observées chez ces individus (Rosa et al. 2016a).

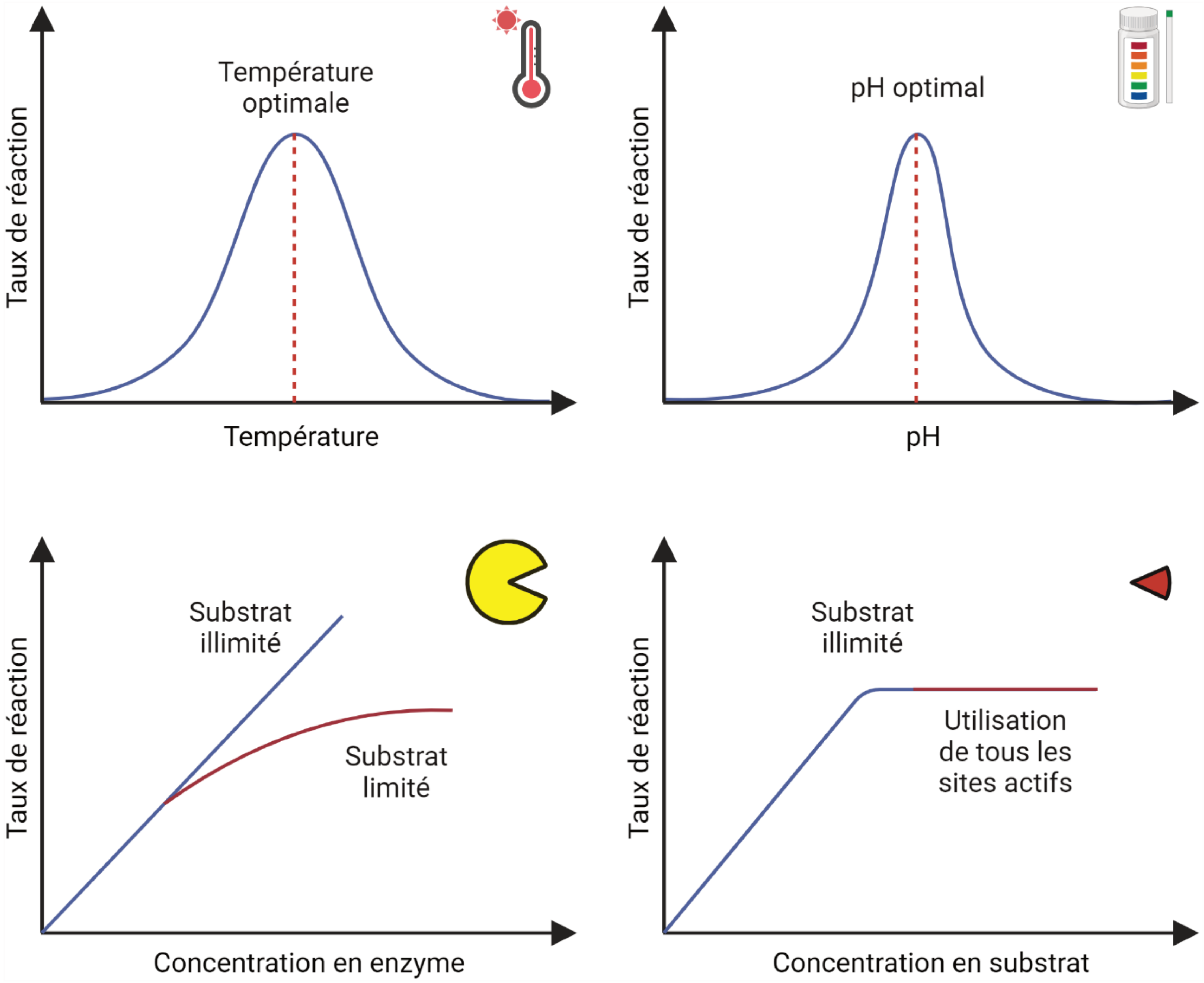

Figure 3 : Facteurs influençant l'activité enzymatique. Les enzymes fonctionnent de manière optimale dans des conditions spécifiques. L'activité enzymatique est modulée par divers facteurs, tels que la température, le pH, la concentration en enzyme et en substrat, la présence d'inhibiteurs, ou l'accumulation de produits finaux. Ces facteurs peuvent altérer la conformation et la structure de l'enzyme, impactant ainsi sa capacité à se lier au substrat et à catalyser efficacement la réaction**.** Crée avec Biorender.com

L'acidification peut également affecter les voies neuroendocriniennes en provoquant une hyperpolarisation des cellules nerveuses dans le système nerveux central et périphérique des poissons. Les neurotransmetteurs inhibiteurs, tels que l'acide γ-aminobutyrique, se lient à leurs récepteurs sur les neurones, entraînant une hyperpolarisation de la membrane cellulaire. Cette hyperpolarisation diminue la probabilité que les neurones génèrent un potentiel d'action en réponse à une stimulation, perturbant ainsi la transmission des signaux nerveux et pouvant entraîner des altérations comportementales. Ces impacts incluent des altérations des comportements liés à l'olfaction (Ou et al., 2015 ; Cripps et al., 2011), à la vision (Chung et al., 2014), à la latéralisation cérébrale (Hamilton et al., 2017 ; Lopes et al., 2016 ; Lai et al., 2015), ainsi qu'une augmentation de l'anxiété (Ou et al., 2015 ; Hamilton et al., 2013). Bien que des modifications du comportement des requins aient été observées dans des conditions simulées de réchauffement des océans (Pistevos et al., 2017 ; South et Dick, 2017 ; Vila Pouca et al., 2018 ; 2019) et d'acidification (Green et Jutfelt, 2014 ; Pegado et al., 2018 ; Pistevos et al., 2015), les mécanismes neuroendocriniens sous-jacents à ces changements restent toutefois largement méconnus.

Les variations thermiques, l'acidification et la diminution de la salinité exercent également des impacts significatifs sur la fluidité des membranes cellulaires, influençant leur perméabilité et, par conséquent, le transport des ions et des molécules à travers celles-ci (Hazel, 1995). L'exposition à des températures élevées entraîne une augmentation des acides gras insaturés tandis que des modifications de l'osmolarité peuvent perturber les fonctions des protéines membranaires essentielles à la signalisation cellulaire, à la communication intercellulaire, et à la régulation du volume cellulaire (Hochachka et Somero 2002). En particulier, l'augmentation de la fluidité des membranes mitochondriales peut entraîner une diminution de la production d'ATP et perturbant les processus énergétiques vitaux pour le métabolisme cellulaire (Caldwell et Vernberg, 1970 ; Little et al., 2020). En tant que dernier accepteur d'électrons dans la chaîne de transport des électrons, l'oxygène joue également un rôle crucial dans la respiration cellulaire aérobie. La réduction des niveaux d'oxygène dans les océans compromet l'efficacité de cette chaîne respiratoire et peut également conduire à une production accrue d'espèces réactives de l'oxygène (ROS, Reactive Oxygen Species) (Abele, 2002 ; Blier et al., 2012 ; Christen et al., 2018). Chez les élasmobranches, ce stress oxydatif est en grande partie régulé grâce à la présence de composés antioxydants enzymatiques comme la catalase (CAT) et le glutathion peroxydase (GPx) qui éliminent le H_2O_2, évitant ainsi son accumulation dans les cellules et les tissus (Halliwell et Gutteridge 2015 ; Ighodaro et Akinloye, 2018). Ces enzymes sont complétées par des piégeurs de ROS non enzymatiques, tels que l'urée (Lopes et al., 2018 ; Vélez-Alavez et al., 2015 ; Wang et al., 1999), dont les effets hautement toxiques sont eux-mêmes neutralisés par la triméthylamine N-oxyde (TMAO) en stabilisant les protéines et prévenant leur dégradation (Bockus et Seibel, 2018 ; Samerotte et al., 2007 ; Seibel et Walsh, 2002). Ce système antioxydant a protégé les jeunes petites roussettes (*Scyliorhinus canicula*) contre les dommages oxydatifs malgré une exposition prolongée à l'acidification des océans pendant 9 mois, depuis le début de l'embryogenèse (Pegado et al., 2020).

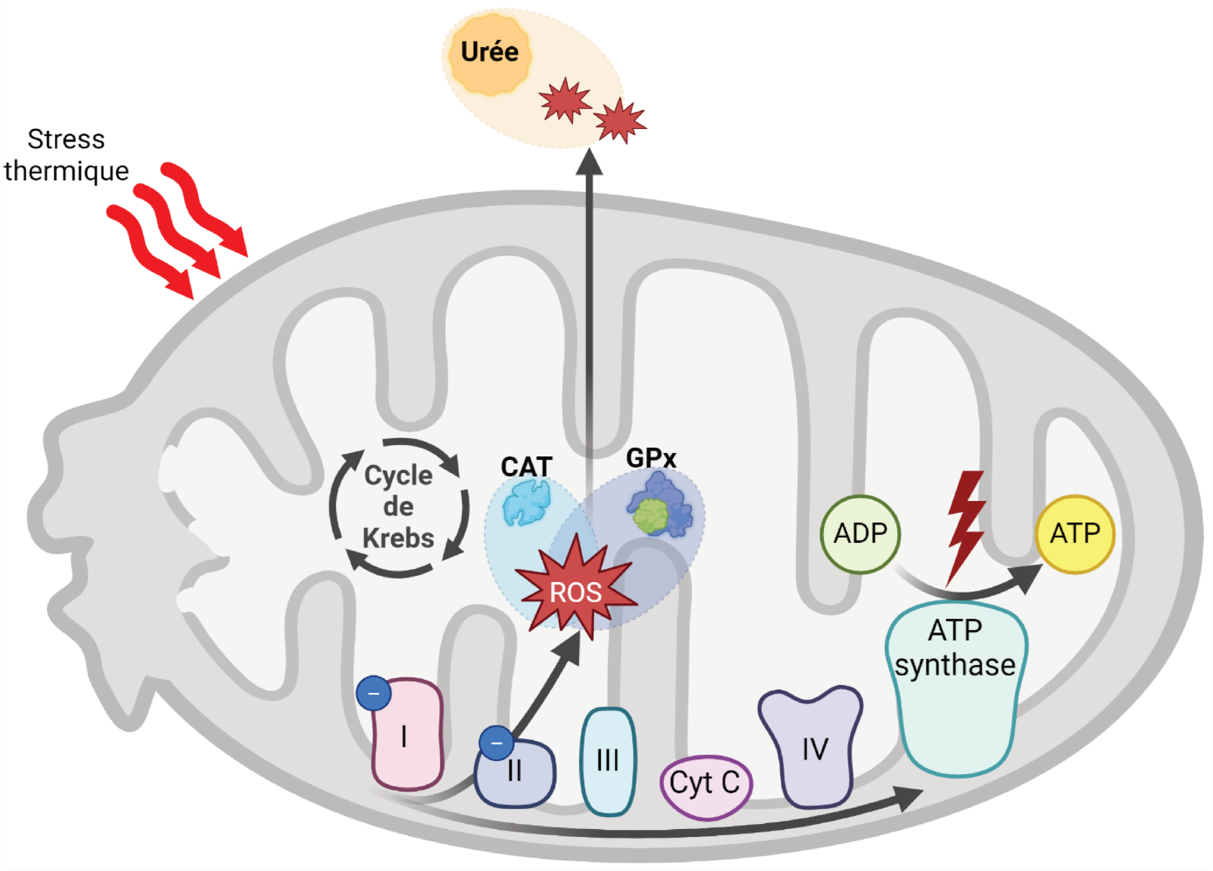

Figure 4 : Mécanismes de protection contre les espèces réactives de l'oxygène (ROS, Reactive Oxygen Species) chez les requins. En situation de stress thermique, les mitochondries produisent des ROS, qui sont neutralisées par des antioxydants enzymatiques tels que la catalase (CAT) et la glutathion peroxydase (GPx). Ces enzymes sont complétées par des piégeurs de ROS non enzymatiques, comme l'urée, assurant ainsi une protection contre le stress oxydatif. Créée avec Biorender.com

2. Des réponses (sub)cellulaires aux réponses physiologiques

Lorsque les stress thermiques sont trop importants, certains mécanismes de défense cellulaires peuvent devenir insuffisants pour prévenir les dommages, conduisant à des processus de mort cellulaire programmée (apoptose) ou non programmée (nécrose), avec des conséquences sur la fonction des tissus (Feder et Hofmann, 1999 ; Gabai et Sherman, 2002). Par exemple, des températures élevées ont entraîné l'apoptose des cellules sanguines chez une espèce de poisson globe asiatique, le *Takifugu obscurus* (Cheng et al., 2015 ; 2018) tandis que de faibles concentration en oxygène ont provoqué l'hyperplasie, la nécrose des cellules branchiales et des congestions des lamelles chez la dorade royale (*Sparus aurata*) (Araújo-Luna et al., 2018), compromettant ainsi les fonctions circulatoires et respiratoires. De plus, les stress thermiques peuvent provoquer une augmentation significative du stress oxydatif et de l'apoptose dans le foie, entraînant des lésions hépatiques graves, notamment des ruptures vasculaires, des infiltrations sanguines et des vacuolisations chez le sandre doré européen (*Sander lucioperca*) (Liu et al., 2022). De même, l'activation des réponses au choc thermique et antioxydante n'a pas atteint un niveau suffisant pour protéger efficacement contre les dommages oxydatifs et l'inflammation dans le foie des Labéo Rohita (*Labeo rohita*), ce qui a entraîné une mortalité partielle des individus qui y ont été soumis (Roychowdhury et al., 2021).

Pour faire face à ces stress cumulés, certains tissus subissent une réorganisation structurelle. Par exemple, chez le carassin commun (*Carassius carassius*) et le poisson rouge (*Carassius auratus*), lorsque les besoins en oxygène sont faibles, une masse cellulaire comble l'espace entre les lamelles branchiales. Cependant, en conditions d'hypoxie ou de températures élevées, cette masse cellulaire régresse par apoptose et inhibition de la mitose, permettant aux lamelles de se déployer (Sollid et Nilsson, 2006). Ce remodelage améliore l'apport en oxygène et en nutriments tout en facilitant l'élimination des déchets métaboliques. De manière similaire, les raies pastenagues de l'Atlantique (*Hypanus sabinus*), qui habitent les herbiers marins peu profonds, sont exposées à des cycles naturels d'hypoxie sévère durant les mois d'été. En laboratoire, la surface des branchies a augmenté de 1,7 fois, passant de 85 à 142 $mm^2.g^{-1}$, chez les raies exposées à des conditions hypoxiques (saturation en oxygène de 30 % pendant 7 heures, équivalent à environ 60 $µmol.L^{-1}$) par rapport à celles maintenues en conditions normales avec une saturation en oxygène de 80-90 % (≥190 $µmol.L^{-1}$) (Dabruzzi et Bennett, 2014). Bien que les poissons ne possèdent pas de tissu adipeux brun comme les mammifères, qui est spécialisé dans la production de chaleur par thermogenèse, ils peuvent moduler le stockage et la distribution de leurs réserves lipidiques pour soutenir leur métabolisme énergétique (Bruslé et al., 2017). Les poissons peuvent également ajuster leur métabolisme en diminuant l'activité de certains enzymes et en réduisant la taille et la fonction de certains organes digestifs, ce qui permet de réduire la demande énergétique globale et de minimiser la production de chaleur métabolique (Pörtner et al., 2014).

Ces adaptations peuvent néanmoins affaiblir considérablement le système immunitaire des poissons, les rendant plus vulnérables aux infections (Avtalion et al., 1973 ; Scharsack et Franke, 2022). Par exemple, une étude de 12 mois sur l'effet de la température a révélé que les morues exposées à des températures élevées développent des infections parasitaires, fongiques et bactériennes, avec les taux de mortalité les plus élevés atteignant 48 % à 14 °C, contre 12 % à 1 °C et 6 % à 7 °C (Magnadottir et al., 1999). De plus, des températures plus élevées peuvent également favoriser la croissance des parasites chez les poissons, surtout lorsqu'ils servent d'hôtes intermédiaires. Chez les épinoches (*Gasterosteus aculeatus*) infectées par un ténia dont les hôtes finaux sont des oiseaux piscivores (Dubinina, 1957 ; Smyth, 1946), des températures basses sont associées à une augmentation du nombre de leucocytes et à une croissance ralentie du parasite. À l'inverse, des températures plus élevées entraînent une diminution de l'activité des leucocytes, ce qui est corrélé à une croissance accélérée du parasite (Franke et al., 2017 ; 2019 ; Scharsack et al., 2021). Ces observations suggèrent que les réponses immunitaires adaptatives sont particulièrement sensibles à l'élévation des températures. En ce qui concerne les élasmobranches, leur système immunitaire diffère de celui des poissons osseux, et les impacts du changement climatique sur ce système demeurent encore peu explorés. Chez les requins dormeurs cornus (*Heterodontus francisci*) exposés à des températures de 15°C et 25°C, le nombre d'érythroblastes et de leucocytes est resté globalement stable, à l'exception d'une augmentation des neutrophiles (Neale et al., 1977). En revanche, une simulation de vague de chaleur, avec une élévation de 3°C, a conduit à une augmentation des leucocytes et des thrombocytes, ainsi qu'à une réduction du nombre et de la taille des érythrocytes chez la petite roussette (Pegado et al., 2020b).

3. Des réponses physiologiques aux réponses individuelles

Les poissons, en tant qu'ectothermes, ajustent leur métabolisme en fonction de la température ambiante, ce qui est souvent évalué en mesurant le taux métabolique standard (SMR, Standard Metabolic Rate) dans des conditions contrôlées (Chabot et al., 2016; Little et al., 2020). Cela est réalisé à l'aide de la respirométrie statique à flux intermittent, une méthode où les poissons sont placés dans une chambre fermée où l'eau est périodiquement renouvelée pour maintenir les niveaux d'oxygène tout en mesurant la consommation d'oxygène. Le SMR représente la consommation minimale d'oxygène nécessaire pour maintenir les fonctions physiologiques de base comme la respiration, la circulation sanguine et le maintien de l'équilibre ionique (Jobling, 1994).

$$SMR = \frac{VO_2}{masse}$$

Où SMR est le taux métabolique standard ($g.O_2.g^{-1}.h^{-1}$), VO_2 est le taux de consommation d'oxygène ($g.O_2.h^{-1}$), masse est la masse du poisson (g). Lorsqu'une élévation de la température de l'eau se produit, les réactions biochimiques et enzymatiques dans leurs cellules s'accélèrent. Selon la règle de Q_{10}, pour chaque augmentation de 10°C, la vitesse des réactions enzymatiques double, ce qui entraîne une augmentation exponentielle des processus métaboliques et du SMR.

$$Q_{10} = \frac{SMR_{T2}}{SMR_{T1}}$$

$$SMR\left(T_2\right) = SMR_{T1} \times Q_{10}^{\frac{(T_2 - T_1)}{10}}$$

Où T_2 est la température la plus élevée, T_1 la plus basse et Q_{10} le facteur de température qui exprime le changement relatif du taux métabolique pour chaque augmentation de 10°C. Les mesures du SMR en laboratoire permettent de quantifier les réponses métaboliques des poissons, offrant ainsi des indicateurs essentiels de leur capacité à maintenir l'homéostasie face aux variations de température (Chabot et al., 2016). Chez les élasmobranches, les SMR suivent généralement les fluctuations de la température environnementale (Rummer et al., 2022 ; Figure 5).

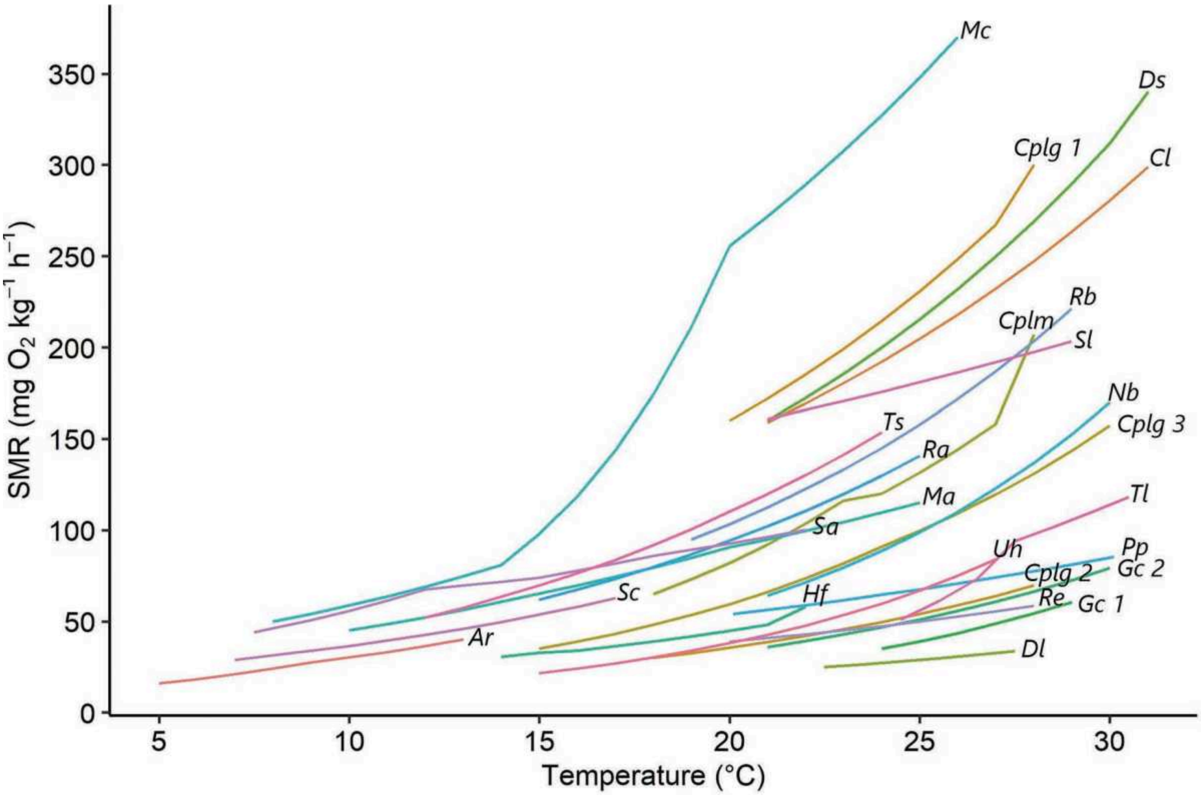

Figure 5 : Variation du taux métabolique standard (SMR, Standard Metabolic Rate) en fonction de la température. Les espèces sont indiquées à la fin de leurs tendances respectives, abrégées par les premières lettres du nom du genre et de l'espèce, comme suit : Ar, Amblyraja radiata (Schweiterman et al. 2019) ; Cl, Carcharhinus leucas (Lear et al. 2020) ; Cplg, Chiloscyllium plagiosum (1, DiSanto et Bennett 2011 ; 2, Chen et al. 2008 ; Tullis et Baillie 2005) ; Cplm, Carcharhinus plumbeus (Dowd et al. 2006) ; Dl, Dasyatis lata (Dale et al. 2013) ; Ds, Dasyatis sabina (DiSanto et Bennett 2011) ; Gc, Ginglymostoma cirratum (1, Lear et al. 2017 ; 2, Whitney et al. 2016) ; Hf, Heterodontus francisci (Luongo et Lowe 2018) ; Ma, Myliobatus aquila (Du Preez et al. 1988) ; Mc, Myliobatus californica (Hopkins et Cech 1994) ; Nb, Negaprion brevirostris (Lear et al. 2017) ; Pp, Pristis pristis (Lear et al. 2020) ; Ra, Rhinobatos annulatus (Du Preez et al. 1988) ; Rb, Rhinoptera bonasus (Neer et al. 2006) ; Re, Rostroraja eglanteria (Schweiterman et al. 2019) ; Sa, Squalus acanthias suckleyi (Giacomin et al. 2017) ; Sc, Scyliorhinus canicula (Butler et Taylor 1975) ; Sl, Sphyrna lewini (Lowe, 2001) ; Tl, Taeniura lymma (Dabruzzi et al. 2013) ; Ts, Triakis semifasciata (Miklos et al. 2003) ; Uh, Urobatis halleri (Silva-Garay et Lowe 2021). Figure extraite de Rummer et al., (2022).

Néanmoins, les mesures du SMR ne sont pas suffisantes pour évaluer pleinement la réponse métabolique d'un organisme aux facteurs de stress liés au changement climatique, car elles ne permettent pas de quantifier les taux d’O_2 nécessaires pour la recherche de proie, la reproduction ou bien encore les migrations (Clark et al., 2013). Le champ aérobique, défini comme la différence entre le taux maximal d'absorption d'O_2 lors d'un exercice (Sandblom et al., 2016) et le SMR, est une mesure couramment utilisée pour estimer cette capacité (Lefevre, 2016). La quantité d'O_2 et le temps requis pour récupérer après une activité stressante, telle qu'une exposition à des conditions hypoxiques ou à des pics de température, constituent également des indicateurs pertinents. Toutefois, il est important de souligner que bien qu'il soit relativement simple d'élever des poissons de petite taille dans des conditions simulant divers scénarios de changement climatique et de mesurer leurs taux métaboliques, cela devient particulièrement complexe pour les espèces de plus grande taille, surtout celles qui occupent des niveaux trophiques élevés, comme c'est le cas pour de nombreux élasmobranches. Par conséquent, les études sur les grandes espèces, telles que le requin à pointes noires (*Carcharhinus melanopterus*) et le requin gris (*Carcharhinus plumbeus*), se sont majoritairement concentrées sur les nouveau-nés ou les juvéniles, qui sont plus facilement maintenus en captivité et adaptés à des équipements expérimentaux comme les chambre de respirométries. Ces deux espèces ont montré des réponses métaboliques distinctes face aux variations de température. Par exemple, les nouveau-nés de requins à pointe noire n'ont pas présenté de différences significatives dans leurs taux métaboliques après une acclimatation à des températures supérieures de 3 °C aux conditions ambiantes pendant 2 à 4 semaines (Bouyoucos et al. 2020a, 2020c). Toutefois, la combinaison des températures élevées et de l'acidification a entraîné une augmentation du SMR chez certains individus (Bouyoucos et al., 2020c). À l'inverse, chez les juvéniles de requins gris, les taux métaboliques ont augmenté et la tolérance à l'hypoxie a diminué sous l'effet d'une élévation des températures de 24°C à 32°C (Crear et al. 2019). Bien que les réponses métaboliques aux augmentations de température aient varié entre ces études, l'activité des deux espèces, mesurée par l'accélération dynamique du corps à l'aide d'accéléromètres, n'a pas été affectée par les températures élevées (Bouyoucos et al. 2020c ; Crear et al. 2019).

L'accélération du métabolisme entraîne une augmentation des besoins en nutriments, essentiels pour soutenir les processus physiologiques intensifiés, tels que la maintenance cellulaire et la croissance somatique. Cela est particulièrement critique durant le développement embryonnaire des espèces ovipares, lors duquel les embryons dépendent entièrement des réserves énergétiques disponibles dans l'œuf. Chez les élasmobranches ovipares, l'augmentation des températures accélère la consommation du vitellus, entraînant des éclosions plus précoces et des nouveau-nés de plus petite taille (Rummer et al., 2022 ; Wheeler et al., 2020 ; 2021 ; Figure 6). Les nouveau-nés commencent également à se nourrir de manière exogène plus rapidement et consomment davantage de nourriture (Di Santo 2015 ; Rosa et al. 2014 ; Wheeler et al. 2021). De plus, l'acidification réduit leur taux de survie pendant 30 jours après l'éclosion chez le requin-chabot bambou (Rosa et al. 2014).

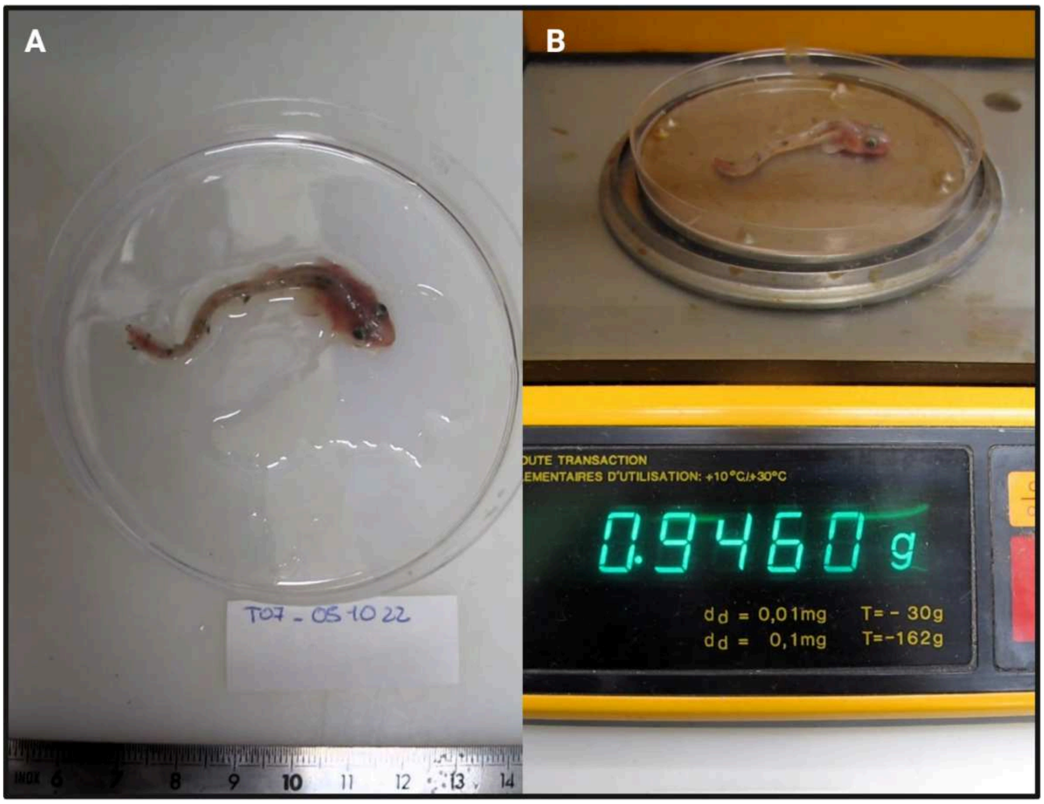

Figure 6 : Mesure de la A) taille et du B) poids d'un nouveau-né de petite roussette exposé à un scénario de « Fossil-fueled Development » pour 2100 durant l'embryogenèse. Un nouveau-né en bonne santé devrait mesurer 10,0 ± 0,5 cm et peser 3,8 ± 0,3 g. Photographies réalisées par Noémie Coulon.

Parallèlement, dans un environnement en changement, il peut devenir difficile de répondre aux besoins nutritionnels accrus des jeunes stades de vie des poissons. Par exemple, les proies riches en acides gras polyinsaturés oméga-3, dont l'assimilation est cruciale pour les poissons (Bowyer et al., 2013), peuvent voir leur abondance et leur valeur nutritive diminuer (Grieve, 2017 ; Pethybridge et al., 2015). Un exemple notable de ce phénomène est observé au sud de la mer de Norvège, où le copépode tempéré *Calanus helgolandicus* remplace progressivement *C. finmarchicus* (Montero et al., 2020). Or, le profil lipidique (diversité des acides gras), la charge lipidique (quantité totale de lipides) et la taille de *C. finmarchicus* sont mieux adaptés aux besoins nutritionnels des larves de morue que ceux de *C. helgolandicus*. Ce changement dans la disponibilité des proies pourrait compromettre la survie des larves de morue (Kattner et Hagen, 2009 ; Kristiansen et al., 2011). Bien que la modification du régime alimentaire ne conduise pas nécessairement à la mortalité des individus, elle peut cependant entraîner une réduction des taux de croissance et altérer la condition physique des poissons ayant dû adapter leurs habitudes alimentaires (Huang et al., 2021 ; McLeod et al., 2012). Depuis 2008, les sardines (*Sardina pilchardus*) subissent une dégradation significative de leur condition physique et une diminution de leur taille adulte (Brosset et al., 2016 ; Saraux et al., 2019). Ces altérations sont principalement liées à des changements dans le brassage des eaux et les apports en nutriments, qui ont favorisé le développement de petites espèces planctoniques dans le Golfe du Lion (Feuilloley et al., 2020). Or, ces espèces plus petites sont souvent moins nutritives (Zarubin et al., 2014). Ce phénomène reflète un effet ascendant, où une dépendance accrue à des proies planctoniques de moindre qualité nutritionnelle a probablement augmenté les coûts énergétiques associés à l'alimentation, et par conséquent la dépense énergétique quotidienne (Queiros et al., 2024). Bien que l'analyse des lipides et des acides gras ne soit pas encore largement répandue chez les élasmobranches, elle a été validée comme méthode efficace pour détecter les changements de régime alimentaire à court terme (Beckmann et al., 2013a ; 2013b). De plus, l'extraction des acides gras à partir de biopsies de tissus musculaires chez des individus vivants de raie manta (*Mobula birostris*), de requins-baleines (*Rhincodon typus*) et de requins blancs (Couturier et al., 2013 ; Pethybridge et al., 2014), ainsi que les prélèvements sanguins chez des requins à pointes noires, bouledogue (*Carcharhinus leucas*), nourrice (*Ginglymostoma cirratum*) et tigre (*Galeocerdo cuvier*) (Gallagher et al., 2017), ont fourni des informations cruciales sur leur écologie trophique. Cette méthode pourrait donc s'avérer particulièrement utile pour suivre les variations dans la composition des proies des élasmobranches en milieu naturel, notamment en réponse aux changements climatiques. Par ailleurs, les poissons et les requins entreprennent souvent des migrations de plusieurs milliers de kilomètres pour atteindre leurs zones de reproduction, accumulant des réserves de graisse pour soutenir ces longs déplacements (Del Raye et al., 2013 ; Goñi et al., 2010 ; Weber, 2009). Une carence en acides gras essentiels pourrait non seulement réduire les réserves énergétiques accumulées mais aussi affecter la condition physique des individus et leur flottabilité altérant ainsi leurs capacités migratoires. De plus, l'acidification de l'eau peut altérer la sensibilité olfactive et compromettre les comportements essentiels tels que la recherche de nourriture, la navigation et la détection des prédateurs (Heuer et Grosell, 2014). Chez les élasmobranches, de nombreux changements de comportement ont été observés (Rummer et al., 2022), mais les mécanismes sous-jacents à ces effets ne sont pas encore pleinement compris, et des effets contradictoires ont été rapportés. Par exemple, l'exposition à des conditions acides a modifié le comportement de nage nocturne des petites roussettes (Green et Jutfelt, 2014), tandis que les requins de Port Jackson ont mis plus de temps à trouver leur nourriture (Pistevos et al., 2015). En revanche, l'acidification n'a pas entraîné de changements significatifs dans les niveaux d'activité ou les comportements de recherche de nourriture chez le requin-chabot ocellé (Heinrich et al., 2015) ni chez les nouveau-nés du requin pointe noire, même en combinaison avec des températures élevées (Bouyoucos et al., 2020a ; 2020b).

4. Des réponses individuelles aux réponses populationnelles

Les œufs puis les larves de poissons constituent la fondation des cohortes, chacune d’entre elles correspondant à l’ensemble des individus nés au cours d'une même période de reproduction et donc globalement du même âge. La survie et la croissance de ces cohortes déterminent la part des individus qui contribueront à la population adulte lorsqu’ils atteignent leur maturité sexuelle. Une cohorte robuste, avec un taux de survie élevé et un développement sain, soutient une densité de population plus élevée et stable, tandis qu'une cohorte réduite ou affaiblie par des conditions environnementales défavorables peut entraîner une diminution significative de la densité future de la population. Les œufs et les larves de poissons sont particulièrement vulnérables à l'augmentation de la température, à l'acidification, à la désoxygénation et aux variations de salinité. Les températures élevées et les niveaux d'oxygène dissous insuffisants peuvent non seulement accélérer le développement embryonnaire, mais également entraîner des malformations (Vaquer-Sunyer et Duarte, 2008) et compromettre la viabilité des œufs en dépassant les seuils de tolérance spécifiques (Pepin, 1991). Chez les élasmobranches ovipares, au-delà d'une certaine température critique, située entre 3 °C et 5 °C au-dessus des températures observées au début du 21ème siècle, la survie jusqu'à l'éclosion diminue considérablement, de 30 % à 60 % (Di Santo, 2015; Gervais et al., 2016 ; Rosa et al., 2014 ; Vila Pouca et al., 2019). Par ailleurs, les effets combinés des températures élevées, de l'acidification et de la désoxygénation ont été observés chez le requin bambou à bandes brunes, la raie bouclée et la petite roussette, aggravant les impacts sur leur développement et leur survie. (Di Santo, 2015 ; Musa et al., 2020 ; Rosa et al. 2014 ; Varela et al., 2023).

Une fois éclos, les individus qui sont parvenus à survivre à ces conditions environnementales difficiles subissent souvent un ralentissement de leur croissance (Canosa et Bertucci, 2023 ; Niu et al., 2023). Les températures élevées, en particulier, peuvent perturber les cycles hormonaux essentiels à la reproduction. Ces perturbations hormonales affectent directement la maturation des gonades, entraînant des diminution de la taille et de la qualité des gamètes (Alix et al., 2020 ; Servili et al., 2020). Cette altération diminue les taux de fertilisation et peut entraîner une réduction du succès reproducteur global (Lema et al., 2024). Par exemple, l'augmentation de la température a un impact majeur sur la reproduction du poisson-clown bistré (*Amphiprion melanopus)*, réduisant significativement la performance reproductive à +1,5°C et l'arrêtant complètement à +3,0°C, tandis que l'élévation de la pCO_2 n'a qu'un effet minimal, principalement en réduisant la qualité des descendants lorsqu'elle est combinée à une température élevée (Miller et al., 2015). En raison de leur grande taille et de leur comportement migratoire, la plupart des élasmobranches, notamment les espèces vivipares, ne se reproduisent pas en captivité sans installations adaptées et périodes d’acclimatation prolongées. Ces contraintes logistiques compliquent la réalisation d’expériences en laboratoire visant à évaluer les effets potentiels du changement climatique sur leur reproduction. Les recherches actuelles montrent cependant que la température joue un rôle essentiel dans la stimulation et la régulation de la reproduction des élasmobranches (Elisio et al., 2019). Par exemple, le début de la saison de reproduction, ainsi que les modifications morphologiques et physiologiques associées, sont étroitement liés aux variations de température de l'eau chez l’émissole gatuso (*Mustelus schmitti*) (Elisio et al., 2019) et le requin-chabot ocellé (Heupel et al., 1999). De plus, les femelles vivipares peuvent ajuster leur température corporelle en se dirigeant vers des zones de nourriceries plus chaudes pour réduire la durée de gestation (Hight et Lowe, 2007 ; Speed et al., 2012 ; Sulikowski et al., 2016 ; Wallman et Bennett, 2006), tandis que les espèces ovipares déposent leurs œufs dans des frayères avec des eaux plus chaudes pour accélérer le développement *in ovo* (Salinas-De-León et al., 2018 ; Wheeler et al., 2020). Par conséquent, des températures élevées pourraient affecter non seulement la gamétogenèse mais aussi la recherche de partenaires, le développement post-zygotique, ainsi que les périodes de frai et de ponte, entraînant une désynchronisation temporelle entre les cycles reproductifs et les conditions environnementales optimales nécessaires à la reproduction dans ces zones fonctionnelles (Anderson et al., 2013 ; Cohen et al., 2018 ; Walsh et al., 2015). Une modification spatiale des zones fonctionnelles, souvent situées dans les eaux côtières peu profondes et les estuaires, particulièrement vulnérables aux impacts extrêmes du changement climatique est également à prévoir (Chin et al., 2010 ; Heupel et al., 2007 ; Matich et Heithaus, 2012 ; Matich et al., 2020). Par exemple, l'habitat favorable aux juvéniles de requins gris pourrait se réduire horizontalement tout en s'étendant verticalement au sein d'une même nourricerie (Crear et al., 2020). De même, des observations ont montré que le requin bouledogue a élargi la taille de sa nourricerie au cours des deux premières décennies du 21e siècle, en réponse à l'augmentation des températures (Bangley et al., 2018).

L’abondance au sein des populations peut non seulement diminuer, mais la distribution géographique de celle-ci peut également être modifiée (Last et al., 2011). Elles peuvent se replier dans des habitats historiques devenus suboptimaux ou s’étendre vers de nouvelles zones plus favorables. En général, les limites de répartition des populations se déplacent vers les pôles ou en profondeur en réponse au réchauffement des océans (Hastings et al. 2020). Ce phénomène semble déjà affecter un large éventail de taxons (Baudron et al., 2020 ; Gervais et al., 2021), y compris certaines espèces de requins (Bangley et al., 2018 ; Bennett et al., 2021 ; Hammerschlag et al., 2022 ; Sguotti et al., 2016). En conséquence, plusieurs études de modélisation prévoient un déplacement des habitats favorables pour certaines populations de requins pélagiques vers les pôles ou en profondeur, avec des réductions ou des expansions de leur aire de répartition globale selon les régions et les espèces (Andrzejaczek et al., 2018 ; Birkmanis et al., 2020a ; 2020b ; Diaz-Carballido et al., 2022 ; Hazen et al., 2013 ; Hobday, 2010 ; Robinson et al., 2015). Par ailleurs, l'expansion des zones à faible teneur en oxygène devrait également entraîner une compression de l'habitat vertical pour les espèces pélagiques, comme le requin peau bleu (*Prionace glauca*) (Vedor et al., 2021).

5. Des réponses populationnelles aux réponses communautaires

Comprendre la diversité génétique au sein des espèces est essentiel pour prédire quelles populations et espèces seront les plus vulnérables aux changements climatiques rapides (Bennett et al., 2019 ; McKenzie et al., 2021). Bien que la diversité génétique des élasmobranches soit encore insuffisamment explorée (Domingues et al., 2018 ; Stein et al., 2018), des recherches en laboratoire ont mis en lumière l'importance de la variation intraspécifique dans la réponse au changement climatique. Ces études ont démontré des réponses divergentes aux conditions climatiques changeantes parmi les populations localement adaptées de requins et d'espèces similaires. Par exemple, les requins de Port Jackson provenant des eaux plus froides d'Adélaïde, en Australie, ont montré une sensibilité accrue à la chaleur en termes de coût énergétique, comparativement à ceux originaires des eaux plus chaudes de Jervis Bay, en Australie (Gervais et al., 2021). De manière similaire, les juvéniles de raie hérisson (*Leucoraja erinaceus*) des régions méridionales de Georges Bank ont présenté une résistance supérieure aux facteurs de stress climatiques en termes de coûts métaboliques par rapport à leurs homologues des régions septentrionales du golfe du Maine (Di Santo, 2016). Ces résultats soulignent l'importance d'intégrer la diversité génétique dans les modèles de prévision des impacts climatiques pour mieux comprendre et anticiper les réponses adaptatives des populations marines. De plus, face à la vitesse des changements environnementaux et à la pression accrue des facteurs anthropiques, la capacité des espèces à cycle de vie lent à s'adapter à de nouvelles conditions environnementales pourrait largement dépendre de leur plasticité phénotypique (McKenzie et al., 2021). Par exemple, une adaptation locale rapide des raies tachetées (*Leucoraja ocellata*) à une élévation de la température de l'eau de 10°C sur une période évolutive relativement courte de 7000 ans a été principalement attribuée à des modifications épigénétiques plutôt qu'à des changements dans les fréquences des allèles (Lighten et al., 2016).

Les réponses des populations influencent profondément les dynamiques des communautés marines (Beaugrand et Kirby, 2018). Par exemple, les changements dans la répartition géographique des populations de poissons peuvent modifier les interactions interspécifiques, entraînant une restructuration des communautés marines (Beaugrand et al., 2003). Les espèces les plus sensibles aux perturbations environnementales risquent de voir leurs effectifs diminuer drastiquement, tandis que les espèces plus résistantes ou opportunistes peuvent prospérer, modifiant ainsi la composition spécifique des communautés (Lurgi et al., 2012). Par exemple, les espèces pélagiques à cycles de vie rapides, caractérisées par une reproduction massive et une maturation précoce, ont fortement diminué après une augmentation de la température de surface de la mer due à une phase de réchauffement de l'Oscillation Multidécennale Atlantique en Manche orientale, aggravée par la pression de pêche historique. En revanche, les espèces avec maturation tardive et un soin parental important ont vu leur abondance augmenter (McLean et al., 2018). Ces dynamiques modifient non seulement la composition des communautés marines, mais aussi leur fonctionnement, créant ainsi des scénarios complexes de réponse des écosystèmes aux changements climatiques et environnementaux (Chapman et al., 2020 ; Stefani et al., 2020 ; Murgier et al., 2021). Par exemple, ces transformations peuvent perturber les chaînes alimentaires et compromettre des processus essentiels comme la capture du carbone, surtout lorsque des espèces clés pour le fonctionnement des écosystèmes car possédant des traits bio-écologiques uniques (i.e. espèces fonctionnellement distinctes ; Violle et al., 2017) telles que les requins, voient leur répartition et leur abondance diminuer (Dedman et al., 2024 ; Ferretti et al., 2010). L'établissement dans de nouveaux habitats, qu'il soit permanent ou prolongé au cours de l'année, peut également intensifier la concurrence avec les espèces locales et exiger des adaptations dans les interactions biotiques, telles que les relations trophiques (Blois et al., 2013). Par exemple, entre 1982 et 2021, les estuaires de l'ouest du Golfe du Mexique ont connu une augmentation moyenne de 1,55°C des températures automnales de l'eau, accompagnée d'un retard progressif des fronts froids d'environ 0,5 jour par an. En conséquence, les migrations des requins-bouledogues vers les estuaires plus au nord ont été retardées, avec des départs repoussés de 25 à 36 jours en 2021 par rapport à 1982. Les jeunes requins ont prolongé leur séjour dans leurs estuaires d'origine lorsque les proies deviennent moins abondantes. Si le réchauffement des eaux se poursuit, les requins-bouledogues du nord-ouest du Golfe du Mexique pourraient cesser leurs migrations hivernales d'ici 50 à 100 ans, modifiant ainsi leur rôle écologique au sein des écosystèmes estuariens (Matich et al., 2024). Ces déséquilibres écologiques affectent non seulement les populations de poissons, mais aussi d'autres organismes dont la survie dépend de ces interactions, ainsi que les services écosystémiques qu'ils fournissent (Heuer et Grosell, 2014 ; Pecl et al., 2017 ; Wang et al., 2021). Face à ces défis, l'adoption d'une approche holistique qui intègre les facteurs socio-économiques devient essentielle. Cette approche, prenant en compte à la fois les risques biologiques et techniques pour les requins ainsi que l'impact sur les communautés humaines, permettrait non seulement d'améliorer la conservation des requins, mais aussi d'apporter des avantages concrets aux populations dépendantes des ressources marines (Booth et al., 2019 ; 2020).

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III- Les pressions exercées sur les poissons osseux et cartilagineux en Atlantique Nord-Est

1. Préambule

Les élasmobranches présentent une distribution mondiale, colonisant des habitats allant des zones côtières peu profondes aux environnements pélagiques et benthiques des grandes profondeurs océaniques (Compagno, 2001). Certaines espèces, comme le requin bouledogue, ont également démontré une tolérance aux milieux dulçaquicoles. Cette répartition globale illustre leur grande adaptabilité physiologique et écologique. La diversité spécifique des élasmobranches est remarquable, avec plus de 1 200 espèces recensées présentant une grande variété de formes, de tailles et de stratégies écologiques. Ces caractéristiques font d'eux des acteurs clés dans les réseaux trophiques marins, où ils jouent un rôle central dans la régulation des populations de proies et la structuration des communautés. Cependant, cette diversité fonctionnelle se révèle particulièrement vulnérable, car elle repose sur des espèces et des localisations géographiques uniques à l'échelle mondiale (Pimiento et al., 2023). Les zones côtières et les îles océaniques abritent une richesse fonctionnelle élevée, avec 18 hotspots distincts identifiés. Par ailleurs, certaines régions tropicales, telles que le Triangle de Corail et l'océan Indien occidental, ont été reconnues comme des foyers de biodiversité exceptionnels, hébergeant un nombre particulièrement élevé d'espèces endémiques (Lucifora et al., 2011).

Les élasmobranches font face à des pressions anthropiques croissantes, principalement liées à la surpêche, à la dégradation des habitats et aux changements climatiques. L'intensification des pêcheries industrielles et artisanales, associée à des captures accidentelles dans les engins de pêche non sélectifs, a conduit à une exploitation insoutenable de nombreuses populations (Dulvy et al., 2021). Depuis 1970, l'abondance mondiale des requins et des raies a diminué de plus de 50 %, une tendance alarmante alimentée par une demande persistante pour leurs nageoires, leur chair et d'autres produits dérivés (Pacoureau et al., 2021). Cette surexploitation est exacerbée par la faible résilience démographique des élasmobranches, caractérisés par une maturité sexuelle tardive, une faible fécondité et des cycles de vie prolongés. Le dernier rapport du groupe de spécialistes des requins de la Commission pour la sauvegarde des espèces (SSC) de l'UICN, publié en 2024, souligne que plus d'un tiers des espèces d'élasmobranches sont actuellement classées comme menacées sur la Liste rouge de l'UICN, dont 12 % en danger critique d'extinction. Ce constat témoigne d'une aggravation du risque d'extinction de 19 % au cours des dernières décennies (Finucci, 2024). Les principales recommandations de ce rapport incluent le renforcement des réglementations sur la pêche, la création d'aires marines protégées (AMP) spécifiques aux élasmobranches et la suppression des subventions favorisant la surpêche. Ces actions apparaissent essentielles pour atténuer le déclin des populations et garantir la pérennité des fonctions écologiques qu'elles remplissent dans les écosystèmes marins.

2. La zone FAO 27

La zone FAO 27, ou l'Atlantique Nord-Est, s'étend sur une vaste région océanique à l'est de l'océan Atlantique, englobant les eaux côtières et marines de l'Europe de l'Ouest, ainsi qu'une partie des eaux arctiques et subarctiques (Figure 7). Cette zone couvre un large territoire allant du nord de la Norvège et de l'Islande jusqu'aux côtes du Portugal, incluant la mer du Nord, la mer Baltique, la Manche, la mer d'Irlande, la mer Celtique et le golfe de Gascogne.

Les plateaux continentaux dominent une grande partie de cette zone, avec des profondeurs généralement inférieures à 200 mètres, bien qu'elles puissent atteindre 400 mètres dans certaines régions, comme le plateau des Hébrides, au large de l'Écosse. En s'éloignant des côtes, on rencontre des marges et des talus continentaux où la profondeur augmente rapidement, conduisant aux grandes plaines abyssales. La fosse de Rockall, située à l'ouest des îles Britanniques, est l'une des zones les plus profondes, atteignant plus de 4500 mètres. La température de l'eau fluctue selon la latitude, descendant en dessous de 0°C dans les régions arctiques, tandis qu'elle peut dépasser 20°C en été dans les eaux plus méridionales. Le courant de l'Atlantique Nord, prolongement du Gulf Stream, transporte des eaux chaudes et salées vers le nord-est, réchauffant les côtes de l'Europe occidentale et contribuant à un climat plus doux. En revanche, des courants de retour froids descendent vers le sud le long de la côte est du Groenland et à travers la mer de Norvège, amenant des eaux froides arctiques vers le sud. Des phénomènes d'upwelling, notamment le long des côtes du Portugal et de l'Espagne, sont fréquents en été, favorisant une forte productivité biologique dans ces régions. La salinité est généralement élevée, autour de 35 PSU (Practical Salinity Units), mais elle peut être localement influencée par l'apport d'eau douce des rivières, en particulier dans la mer Baltique ou les eaux arctiques, où la salinité est plus faible.

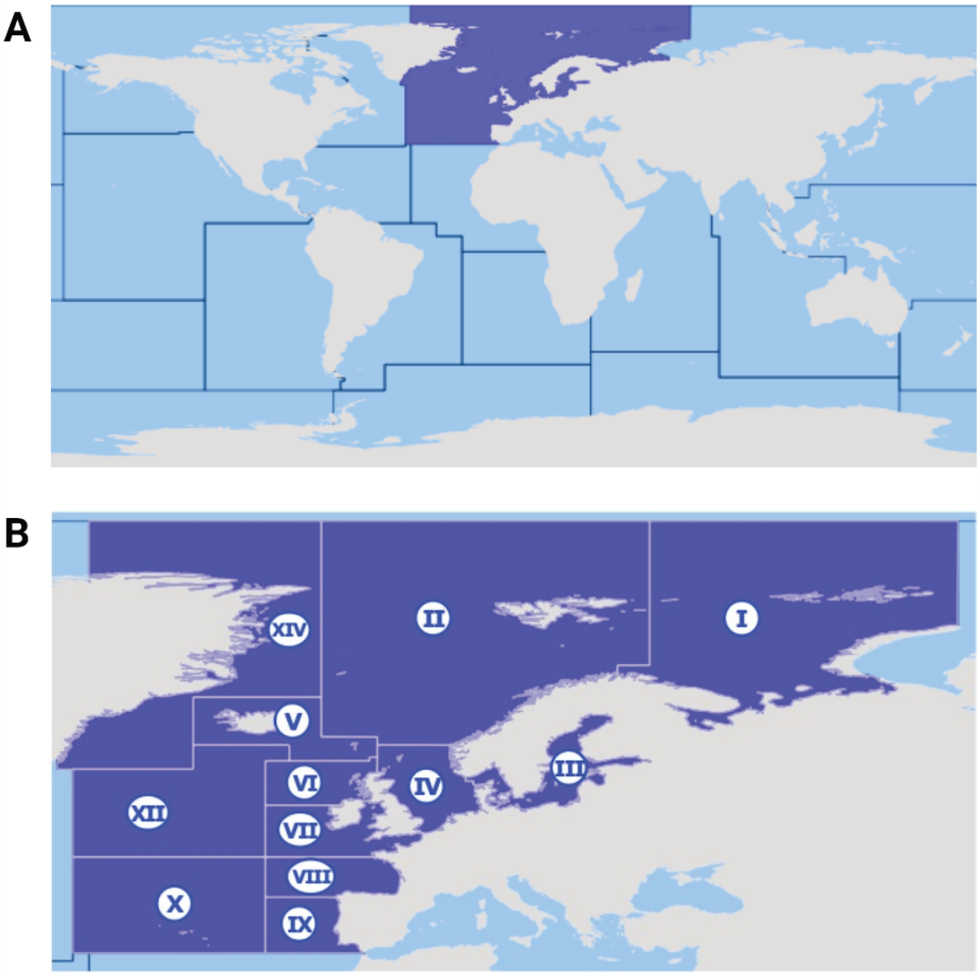

Figure 7 : La zone FAO 27 et ses sous-zones. I. Mer de Barents ; II. Mer de Norvège, Sptitzberg et île aux Ours ; III. Skagerrak, Kattegat, Sound, Belt et mer Baltique ; IV. Mer du Nord ; V. Eaux islandaise et féringienne ; VI. Rockall, côte nord-ouest de l'Écosse et nord de l'Irlande ; VII. Mer d'Irlande, ouest de l'Irlande, Banc de Porcupine, Manche orientale et occidentale, canal de Bristol, mer Celtique septentrionale et méridionale, et sud-ouest de l'Irlande ; VIII. Golfe de Gascogne ; IX. Eaux portugaises ; X. Banc des Açores ; XII. Nord des Açores ; XIV. Est du Groenland. Figure extraite de FAO (2023).

Ces caractéristiques environnementales font de l’Atlantique Nord-Est, une région riche en diversité se divisant en plusieurs provinces biogéographiques, chacune ayant des caractéristiques océanographiques, climatiques et écologiques uniques (Briggs et Bowen, 2011). Ces provinces sont essentielles pour comprendre la répartition des espèces et les dynamiques écologiques dans cette vaste région. La province Arctique couvre les eaux au nord de la Norvège, de l'Islande et du Groenland. Cette zone se caractérise par des températures extrêmement basses et une couverture de glace marine saisonnière. La biodiversité y est adaptée aux conditions polaires, avec des espèces endémiques telles que la morue arctique (*Boreogadus saida*) (Cohen et al., 1990) ou le requin du Groenland (*Somniosus microcephalus*) (MacNeil et al., 2012) et divers mammifères marins comme le narval (*Monodon monoceros*) (Jefferson et al., 1993). Plus au sud, la province Atlantique boréale englobe la mer de Norvège, la mer du Nord, les eaux autour de l'Écosse, et l'ouest de la Manche (Golikov et al., 1990). Cette province se distingue par ses eaux froides à tempérées, riches en nutriments, ce qui favorise une grande productivité biologique. Les espèces endémiques de cette région incluent le merlu (*Merluccius spp.*) (Grant et Leslie, 2001) et divers invertébrés, comme le copépode *C. finmarchicus* (Addison et Hart, 2005 ; Frederiksen et al., 2012 ; Wares et Cunningham, 2001), avec un taux d'endémisme de 20 à 25 % pour les poissons et les invertébrés (Briggs, 1974). La province Atlantique boréale-lusitanienne s'étend de la côte sud de l'Irlande jusqu'à la Manche et le golfe de Gascogne. Les eaux tempérées de cette région sont influencées par le courant de l'Atlantique Nord, qui apporte des eaux plus chaudes et plus salées. On y trouve des espèces telles que le bar commun (*Dicentrarchus labrax*), la plie (*Pleuronectes platessa*) et la limande commune (*Limanda limanda*) (van Hal et al., 2016). Enfin, la province Lusitanienne couvre le sud du Golfe de Gascogne et la côte nord-ouest de la péninsule Ibérique. Cette région bénéficie d'un climat plus chaud, renforcé par des phénomènes d'upwelling côtier créant des zones de haute productivité. La biodiversité y est typique des eaux tempérées à subtropicales, avec des espèces telles que le thon rouge (*Thunnus thynnus*) (Bañón et al., 2024).

En raison de cette diversité, la zone FAO 27 est soumise à une exploitation intensive par les pêcheries européennes, ce qui en fait une zone d'intérêt majeur pour la gestion durable des ressources marines et la conservation des écosystèmes marins (Fernandes et Cook, 2013 ; Kroodsma et al., 2018 ; Rousseau et al., 2019). Les petits poissons pélagiques, tels que le hareng (*Clupea harengus*), le maquereau (*Scomber scombrus*), et le chinchard (*Trachurus trachurus*), représentent une part importante des captures dans la zone FAO 27 (Kongsstovu et al., 2022). Les pêcheries de hareng et de maquereau sont particulièrement importantes en mer du Nord, dans les eaux autour des îles britanniques, ainsi que dans le golfe de Gascogne (Hannesson, 2013 ; Rybicki et al., 2020). Les poissons démersaux, comme l'églefin (*Melanogrammus aeglefinus*), et le lieu noir (*Pollachius virens*), constituent une autre composante majeure des pêcheries de la zone FAO 27 (FAO, 2019). Les pêcheries de coquilles Saint-Jacques (*Pecten maximus*) et de pétoncles (*Aequipecten opercularis ; Mimachlamys varia ; Chlamys islandica*) sont particulièrement importantes au large des côtes britanniques, en mer Celtique, et dans la Manche (Duncan et al., 2016). La gestion des pêcheries dans la zone FAO 27 est complexe en raison de la diversité des espèces et des pays impliqués. L'Union Européenne, par le biais de la Politique Commune de la Pêche, joue un rôle central en fixant des quotas, des tailles minimales de capture et des mesures de protection des habitats marins. Par exemple, la mise en œuvre de politiques visant à réduire la surpêche et à faciliter la reconstitution des stocks épuisés ou en voie d'épuisement a permis d’améliorer l'état des stocks et la durabilité de la pêche (Fernandes et Cook, 2013 ; Hilborn et al., 2021 ; Rindorf et al., 2020 ; Zimmermann et Werner, 2019). Toutefois, en 2018, environ 40 % des stocks faisaient encore l'objet d'une surpêche, environ 34 % des stocks étaient en dehors des limites biologiques de sécurité et environ 68 % des stocks étaient trop réduits pour produire des rendements maximaux durables (Froese et al., 2021). Par ailleurs, un déclin exceptionnellement marqué de la taille d'une population ne peut être attribué uniquement à une pression de pêche non durable, mais également à des conditions environnementales défavorables. Ces conditions peuvent augmenter la mortalité et entraîner des périodes de faible recrutement, en particulier lorsqu'elles affectent les premiers stades de vie. L'interaction entre une pression de pêche excessive et les fluctuations environnementales a été clairement démontrée par l'effondrement de pêcheries majeures, telles que celles du hareng (Dragesund et al., 1997) et des stocks de morue (Myers et al., 1997).

La surexploitation des populations de poissons ne menace pas uniquement les espèces ciblées, mais compromet également l'équilibre et la santé des écosystèmes marins dans leur ensemble. L'approche traditionnelle de la gestion des pêcheries, souvent axée sur des espèces spécifiques, révèle aujourd'hui ses limites face à la complexité des écosystèmes marins et les changements climatiques en cours (Crowder et al., 2008). En se concentrant principalement sur le maintien des stocks de poissons ciblés, cette méthode tend à négliger les interactions écologiques et les rôles fonctionnels essentiels que ces espèces jouent dans leur environnement. Pour garantir la durabilité des pêcheries à long terme, il est crucial de passer à une gestion écosystémique, prenant en compte non seulement les stocks de poissons, mais aussi les interactions entre les espèces, les habitats, et les processus écologiques (Holsman et al., 2020 ; Radinger et al., 2023). Une telle approche reconnaît l'importance de préserver la diversité des espèces, les réseaux trophiques, et les fonctions écosystémiques, comme le recyclage des nutriments. Elle souligne également la nécessité de protéger la diversité fonctionnelle des espèces, qui repose sur une variété de traits bio-écologiques (taille à maturité, régime alimentaire, habitat), aspect fondamental de la biodiversité (Naeem et al., 2012 ; Nash et al., 2017 ; Trindade-Santos et al., 2020). Les approches basées sur les traits bio-écologiques des espèces sont particulièrement utiles pour identifier les espèces les plus vulnérables aux pressions anthropiques directes, telles que la pêche (Cheung et al., 2005), ou indirectes tels que les changements climatiques (Jones et Cheung, 2018). Elles permettent de mettre en œuvre des mesures de protection ciblées, avant même que les espèces ne subissent des impacts irréversibles (Hare et al., 2016). De plus, ces approches aident à identifier les espèces fonctionnellement distinctes (Violle et al., 2017) dont la perte peut entraîner des conséquences graves sur la stabilité et le fonctionnement des écosystèmes, notamment si aucune autre espèce ne peut compenser les fonctions écologiques perdues (Carmona et al., 2021 ; Mouillot et al., 2013a, 2013b).

Le premier travail réalisé en amont de cette thèse, au sein du laboratoire Ressources Halieutiques de l'Unité Halieutique Manche Mer du Nord de l'IFREMER, a consisté à identifier les espèces fonctionnellement distinctes de l'Atlantique Nord-Est et à croiser leurs traits bio-écologiques avec leur risque d'extinction. Cette partie a fait l'objet d'un article scientifique publié dans la revue *Global Ecology and Biogeography* : **Coulon, N**., Lindegren, M., Goberville, E., Toussaint, A., Receveur, A., & Auber, A. (2023). Threatened fish species in the Northeast Atlantic are functionally rare. *Global Ecology and Biogeography, 32*, 1827–1845. https://doi.org/10.1111/geb.13731

3. Threatened fish species in the Northeast Atlantic are functionally rare

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Journal : *Global Ecology and Biogeography*

Résumé : Les critères utilisés pour définir les catégories de la liste rouge de l'Union internationale pour la conservation de la nature (UICN) sont essentiellement basés sur des paramètres démographiques au niveau de l'espèce, mais ils n'intègrent pas leurs traits bio-écologiques ni leur rôle dans les écosystèmes. Par conséquent, les mesures de protection actuelles basées sur les critères de l'UICN peuvent ne pas être suffisantes pour préserver le fonctionnement et les services des écosystèmes. Certaines espèces peuvent présenter une combinaison singulière de caractéristiques associées à des fonctions uniques. Ces espèces fonctionnellement distinctes sont de plus en plus reconnues comme un élément clé de la biodiversité car elles sont, par définition, fonctionnellement irremplaçables. L'objectif de cette étude est de déterminer si les espèces menacées sont également rares d'un point de vue fonctionnel et d'identifier les traits qui déterminent leur risque d'extinction. En utilisant des informations compilées sur les traits de 425 espèces de poissons marins recensés dans les eaux européennes, et plus de 30 ans de campagnes scientifiques de chalutage de fond, nous avons estimé la distinctivité fonctionnelle (= distinctiveness), la restriction (= scarcity) et la rareté (= rarity) de chaque espèce et les avons croisées avec leur statut de conservation de l'UICN. Dans les mers continentales européennes, 38 % des espèces menacées d'extinction (9 espèces sur 24) ont été identifiées comme étant les plus distinctes sur le plan fonctionnel. En cartographiant le risque d'extinction dans l'espace multidimensionnel des caractéristiques des espèces, nous avons montré que les espèces présentant le plus grand risque d'extinction ont une longue durée de vie et un niveau trophique élevé. Nous avons également constaté que ces espèces sont peu répandues (4 % de la superficie totale en moyenne) et ont une faible abondance (<1 % de l'abondance moyenne relative des espèces communes). Étant donné qu'une proportion substantielle d'espèces menacées sont fonctionnellement distinctes et peuvent donc jouer un rôle unique dans le fonctionnement des écosystèmes, nous soulignons que les caractéristiques des espèces - en particulier la rareté fonctionnelle - devraient devenir une étape indispensable dans l'élaboration des plans de gestion de la conservation.

Mots clés : distinctivité fonctionnelle, risque d'extinction, rareté fonctionnelle, UICN, espèces de poissons marins, trait, menacé d’extinction

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RESEARCH ARTICLE

Threatened fish species in the Northeast Atlantic are functionally rare

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Abstract

Aim: The criteria used to define the International Union for Conservation of Nature (IUCN) Red List categories are essentially based on demographic parameters at the species level, but they do not integrate species' traits or their roles in ecosystems. Consequently, current IUCN-based protection measures may not be sufficient to conserve ecosystem functioning and services. Some species may have a singular combination of traits associated with unique functions. Such functionally distinct species are increasingly recognized as a key facet of biodiversity since they are, by definition, functionally irreplaceable. The aim of this study is to investigate whether threatened species are also functionally rare and to identify which traits determine extinction risk.

Location: European continental shelf seas.

Time period: 1984–2020.

Major taxa studied: Marine fish.

Methods: Using newly compiled trait information of 425 marine fish species in European waters, and more than 30 years of scientific bottom trawl surveys, we estimated the functional distinctiveness, restrictedness and scarcity of each species and cross-referenced it with their IUCN conservation status.

Results: In European continental shelf seas, 38% of the species threatened with extinction (9 out of 24 species) were identified as the most functionally distinct. By mapping extinction risk in the multidimensional species trait space, we showed that species with the greatest risk of extinction are long-lived and of high trophic level. We also identified that the most functionally distinct species are sparsely distributed (4% of the total area on average) and have scarce abundances (<1% of the relative mean abundance of common species).

Main Conclusions: Because a substantial proportion of threatened species are functionally distinct and thus may play unique roles in ecosystem functioning, we stress that species traits—especially functional rarity—should become an indispensable step in the development of conservation management plans.

KEYWORDS
distinctiveness, extinction risk, functional rarity, IUCN, marine fish, species trait, threatened

1 | INTRODUCTION

Global changes and increasing anthropic pressures are causing a rapid and unprecedented loss of biodiversity (Ceballos et al., 2015; IPBES, 2019). This so-called '*biodiversity crisis*' not only threatens unique habitats and biota worldwide, but also the provisioning of key goods and services for human well-being (Halpern et al., 2008; Pecl et al., 2017). To ensure that biodiversity is preserved and that natural resources are used in an equitable and sustainable manner, the International Union for Conservation of Nature (IUCN) encourages and assists societies to preserve the integrity and diversity of nature. This includes providing assessments of the extinction risk of species across the globe to define the IUCN Red List used as a benchmark to support policymakers, government agencies, wildlife departments and nongovernmental organizations in the elaboration of conservation actions and priorities (Alaniz et al., 2019). Red List categories are defined according to quantitative thresholds using five criteria that incorporate the geographical range of the species and population size/trends, known for only a few well-monitored species (IUCN, 2022). The IUCN Red List does not currently integrate species traits that provide insights into their contribution to ecosystems through physiological, morphological, reproductive or behavioural characteristics (Tilman, 2001; Violle et al., 2017), making it difficult to integrate ecosystem functioning into conservation plans.

Traits provide a mechanistic understanding of species responses to environmental forcing and their effects on ecosystem functioning (Gagic et al., 2015; McGill et al., 2006). Trait-based indexes can detect community responses earlier than indexes based on taxonomic characteristics (McLean et al., 2019; Mouillot, Bellwood, et al., 2013; Pécuchet et al., 2017), allowing more efficient conservation plans. Moreover, trait-based approaches are helpful to anticipate which species are the most sensitive to climatic (Jones & Cheung, 2018), and/or anthropogenic (e.g. fishing; Cheun et al., 2005) pressures, to implement targeted protection measures, even before species are impacted (Hare et al., 2016). For example, the use of trait-based metrics has shown that seabirds with narrow habitat breadths, and fast reproduction strategies, are impacted by human-induced habitat degradation worldwide (Richards et al., 2021). Species traits can serve as a valuable tool in assessing species extinction risk (Carmona et al., 2021), especially when demographic data are lacking (Luiz et al., 2016; Walls & Dulvy, 2020). By incorporating species traits, it becomes easier to align species richness hotspots with functional concerns (Grenié et al., 2018), an approach more in line with a precautionary attitude (Dulvy et al., 2021; Lyons et al., 2005). This is especially evident for marine fish such as skates, classified as nonthreatened or data deficient species, but identified as highly sensitive to trawling based on their life-history parameters, body shape and habitat (Rindorf et al., 2020). Using different scenarios based on the IUCN species' extinction risk assessments, a recent study projected a global erosion of the functional spectra of larger species with slower pace of life (Carmona et al., 2021). Although considering functional trait information for more than 75,000 species worldwide, marine fishes were not included despite their important ecological and socio-economical roles and benefits to human health and well-being, from protein supply to climate regulation to recreation (Guerry et al., 2010). Many of these services rely—to some extent—on the presence of only a few functionally distinct species that provide pivotal functions within ecosystems (Bracken & Low, 2012; Dee et al., 2019; Leitão et al., 2016).

These key functions are generally achieved through a combination of traits that provide species-specific capabilities: while some combinations are widespread in marine ecosystems (e.g. invertivorous diet, demersal water-column position, diurnal active period, solitary behaviour and small-to-medium body size; McLean et al., 2021), other trait compositions are more distinct and supported predominantly by species with no functional equivalent; this results in low functional redundancy (Violle et al., 2017). The classical approach that consists of using biomass or total productivity as an indicator of ecosystem functioning, where dominant species are assumed to drive ecological processes and low-abundant species are assumed to contribute weakly (Grime, 1998), has led to disregarding low-abundant species that may be functionally distinct. Nevertheless, it is generally accepted that even when they are low in abundance, top predators can have a disproportionate impact on ecosystem functioning. Therefore, it should be acknowledged that the loss of species with unique functional traits (i.e. functionally distinct species; Violle et al., 2017), can have major impacts on ecosystem stability and functioning if no other species can compensate for the potentially lost functions (Mouillot et al., 2013a, 2013b). Shifts in energy and/or nutrient inputs in ecosystems or disequilibrium in the structure of trophic webs have already been documented in response to the loss of these species (Carmona et al., 2021; Colares et al., 2022; McLean et al., 2019).

Functionally distinct species are under-represented in the IUCN categories because of a lack of species trait information, including distinctiveness, in the classification (Loiseau et al., 2020), which may lead to mismatches between hotspots of functional fish distinctiveness and the implementation of protection measures such as marine protected areas (Grenié et al., 2018; Trindade-Santos et al., 2022). When functionally distinct species are also spatially restricted or poorly abundant, ecosystem stability may be even more fragile in the sense that stability depends on a few key species having disproportionate impacts on the ecosystem relative to their biomass (i.e. functionally rare species; Violle et al., 2017). For example, the giant moray eel (*Gymnothorax javanicus*) is a large sedentary nocturnal benthic specialized predator, with few potential challengers to this role in coral reef ecosystems (Mouillot, Bellwood, et al., 2013). This species is no longer just functionally distinct, it is also functionally rare within communities (Violle et al., 2017), as are most predators. Unfortunately, distinctiveness is thought to be an evolutionary response to a spatially and temporally stable environment, so functionally distinct species—especially species with specific dietary needs—may be more vulnerable to abrupt environmental and anthropogenic changes than those carrying more common traits (Clavel et al., 2011). Protecting functionally rare species is therefore crucial to maintaining the ecological integrity of ecosystems while helping to identify which sites to prioritize for conservation. It should also allow for the protection of a large assemblage of species, by focussing efforts on only a few, which can be a considerable advantage in establishing management plans (Astudillo-Scalia & de Albuquerque, 2019).

Based on approximately four decades of scientific bottom trawl surveys in European seas, we first identified which species are functionally distinct and what are the traits that characterize them. We then quantified to what degree threatened species are the most functionally rare by assessing their functional distinctiveness, restrictedness and scarcity. Finally, we argue for greater integration of traits in the assessment of species extinction risk, as the use of traits also allows the identification of functionally distinct species which, by definition, contribute to vulnerable functions performed by few species (Violle et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Study area and bottom trawl surveys

The study area covers most of the European continental shelf seas, including the Baltic Sea, the North Sea, the English Channel, the Scottish west coast, the Celtic Sea, Rockall and Porcupine Banks, the Irish Sea, Bay of Biscay and the Portuguese coast and is divided into 1° longitude by 0.5° latitude grid cells (hereafter 'rectangles') as defined by the International Council for the Exploration of the Sea (ICES) (Figure 1). Abundance data were collated from 20 scientific bottom trawl surveys (see Supporting Information Appendix S1—Table S1) during the last four decades, from 1984 to 2020. Sampling was carried out during daylight at an average speed of 4 knots for at least 20 min. Although gears and sampling schemes differ between surveys (see Supporting Information Appendix S1—Table S1), all captured individuals were identified at the finest taxonomic level possible and reported in a standardized number of individuals per species caught per hour of trawling, including potadromous species that may be caught in brackish water (Kawamura, 2008). The abundance dataset we used was obtained from the ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark. (https://datras.ices.dk) and includes 425 species across 536 standard ICES rectangles. Due to the absence of reporting on non-commercial species from Spanish surveys, we did not include these surveys. Since the total number of hauls per rectangle is spatially heterogeneous (from 3 to 1070; see Supporting Information Appendix S2—Figure S1a), we standardized sampling effort by means of species accumulation curves (SACs) (Chao, 1987) for each rectangle, considering each haul as a sampling unit, using the '*vegan*' R package (Oksanen et al., 2008). Nonlinear Michaelis–Menten curves were fitted to each of the SACs. When the total number of hauls was lower than the estimated number of hauls necessary to achieve 65% of the asymptotic species richness, we discarded the rectangle (59 rectangles out of 536) following the approach of Maureaud et al. (2019) (see Supporting Information Appendix S2—Figure S1b).

2.2 | Species traits and gap filling

We selected traits that reflect habitat use, life-history and trophic ecology of species expected to be implicated in the response of species to environmental changes and ecosystem functioning (see Supporting Information Appendix S1—Table S2 for reasoning; Beukhof, Dencker, Pecuchet, & Lindegren, 2019; McLean et al., 2019, Murgier et al., 2021). Among the selected traits, eight are continuous (trophic level, age at sexual maturity, length at sexual maturity, fecundity, offspring size, Von Bertalanffy growth coefficient K, maximum length and length infinity) and three are categorical (position in the water column, feeding mode and spawning type). Trait data for the 425 species were initially collected by extracting trait values from the North Atlantic and Northeast Pacific shelves dataset collated by Beukhof, Dencker, Palomares, and Maureaud (2019). Our obtained trait dataset had 38% missing trait values (1289 out of 3386), explained by the presence of missing data in Beukhof, Dencker, Palomares, and Maureaud (2019) and because some species we studied were not in Beukhof et al. (2019b). We filled missing values by following the procedure undertaken by Beukhof, Dencker, Palomares, and Maureaud (2019) and by using the predictive life-history model developed by Thorson et al. (2017).

Continuous traits were supplemented with information extracted from FishBase (Froese & Pauly, 2020) restricted to the Northeast Atlantic and completed by scientific literature as undertaken by Beukhof, Dencker, Palomares, and Maureaud (2019). For 'trophic level', 'offspring size' and 'fecundity' traits not available at the species levels, we averaged the trait values at the genus level or family level if genus was not available, following Beukhof, Dencker, Palomares, and Maureaud (2019). Additionally, 'age at maturity', 'size at maturity', 'Von Bertalanffy's growth coefficient K' and 'infinite size' traits were completed (171 values) using the data-integrated predictive life-history model (Thorson et al., 2017) made available in the '*FishLife*' R package. This model estimates life-history parameters by incorporating existing data and life-history correlations between related species into a multivariate random walk model. Three life-history traits per species must be known to accurately predict the remaining life-history variables. Predictions are more accurate for species with many measurements than those for which only a few measurements were made. Therefore, we were unable to predict all of the missing life-history traits and applied the note accompanying the FishBase 'Growth' table advising to keep species life-history parameters only when the predicted infinite size is not more or less than one-third different from the maximum reported size for the species. For categorical traits, missing traits were extracted from FishBase, completed by scientific literature and finally assigned according to the trait values of a species of the same genus or family when information was available. After completion, only 4% of the values (i.e. 139 of the 3386) were missing and scattered

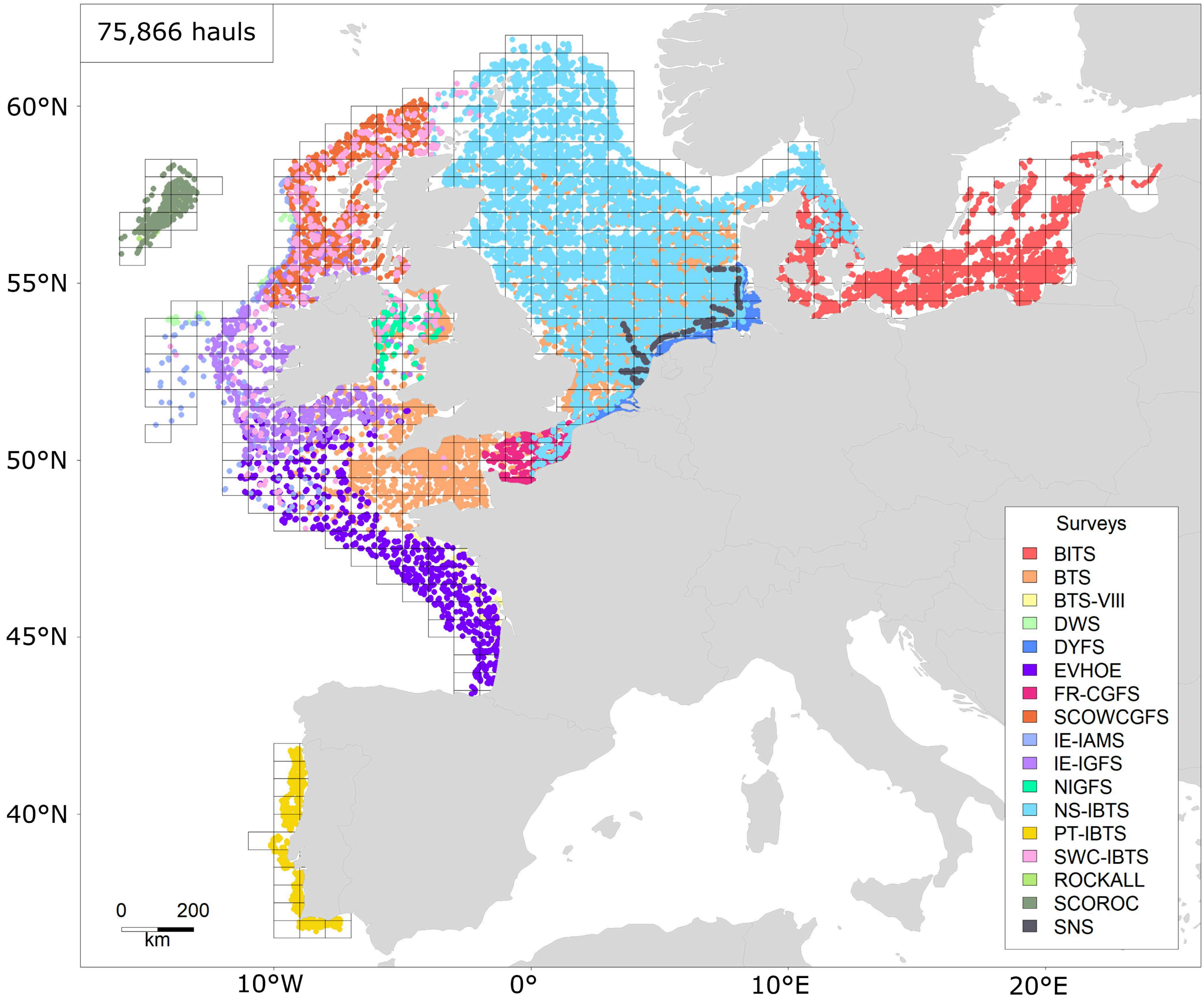

FIGURE 1 Map of the available bottom trawl surveys of demersal fish communities across northwest European continental shelf seas obtained from the International Council for the Exploration of the Sea data portal (https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx). Coloured dots locate the individual hauls, with one colour per survey. ICES rectangles (1° longitude by 0.5° latitude grid cells) are represented. See Supporting Informatioin Appendix S1—Table S1 for detailed information about bottom trawl surveys and their acronyms.

within the different trait types with less than 10% missing values, at most, per trait. Our final database contains 339 species fully informed. The resulting trait database is openly available at Figshare public data repository 10.6084/m9.figshare.19833304.v1 (see also Appendix 1—Data sources).

2.3 | Functional distinctiveness, restrictedness and scarcity

The functional rarity framework developed by Violle et al. (2017) provided a definition and quantification of functional rarity that considers both trait distinctiveness, species abundance and species distribution. According to this concept, functionally rare species have low abundances and are the most distinct and spatially restricted in local areas, while functionally common species have the highest abundances, common trait values and larger spatial distributions. The functional distinctiveness D_i of species i is an index calculated independently of species abundance, quantifying how a species i is functionally dissimilar to all other species in the community (Violle et al., 2017), considering one combination of traits:

$$D_i = \frac{\sum_{j=1, j \neq i}^{S} d_{ij}}{S-1} \tag{1}$$

with S the total number of species within the study area and d_{ij} the dissimilarity between species i and j. A species with a high D_i value is considered functionally distinct compared with the rest of the pool (Violle et al., 2017). Because identifying the relevant number of traits to correctly describe ecological functions is difficult and subjective

(Lepš et al., 2006; Petchey & Gaston, 2002), we computed an integrative version of the functional distinctiveness index (IntDi) that not only considers one combination of traits (i.e. the combination of all available traits) but all possible combinations of available traits. This index therefore provides a more robust assessment of species distinctiveness (see Supporting Information Appendix S1—Table S3) and a more objective ranking between species according to their functional distinctiveness; it ensures that a species has a high distinctiveness value not because of a single extreme trait value but because it has several uncommon trait values (Grenié et al., 2017). The R code is freely available at Figshare public data repository 10.6084/m9.figshare.22317643.v1 (see also Appendix 1—Data sources). We calculated the dissimilarity matrix (i.e. dissimilarities between species based on their traits) of each possible combination of traits among the 11 traits selected for this study, considering that a minimum of 4 is needed to characterize the difference between species (Petchey & Gaston, 2002). This procedure therefore provides a total of 1816 dissimilarity matrices. We then calculated the IntDi value of each species from the integrated dissimilarity matrix itself computed as the average between the 1816 matrices (see Supporting Information Appendix S2—Figure S2 for example). Additionally, to prevent any disproportionate contribution of categorical traits in dissimilarity matrices and thus on distinctiveness computation, we applied the approach developed by de Bello et al. (2021) using the '*gawdis*' package. Functional distinctiveness was standardized so that it ranges between 0 and 1. We followed the same procedure for the resulting trait database, the database with no missing data, and the database with missing data predicted with the R package '*missForest*' (Stekhoven & Buehlmann, 2012). We developed two linear models (Supporting Information Appendix S2—Figure S3; R_1^2=0.9954 & R_2^2=0.9982) and calculated the percentage of variation between the rankings to ensure the robustness of the ranking made from the integrated distinctiveness calculation (refer to Supporting Information Appendix S1—Table S4). The 425 species were then grouped on the basis of their IntDi values: the first group (D1, the most functionally common species) was defined according to the first decile of IntDi, while the last group (D10, the most functionally distinct species) was defined according to the last decile. This division into deciles was done a posteriori according to the number of groups allowing to best isolate the most functionally distinct species according to the distribution of distinctiveness values (Figure 2). We then performed Spearman correlation tests to assess the relationship between each continuous trait and species distinctiveness. For categorical traits, differences in functional distinctiveness between trait modalities were computed using Wilcoxon post hoc tests.

A Principal Coordinate Analysis (PCoA) was performed on the average dissimilarity matrix to summarize interspecific dissimilarities in a biplot referred to as a 'trait space'. We calculated the functional dissimilarity between the species of a functional distinctiveness group (e.g. D2) and all other species from all other groups (for this example: all groups without D2) to test for the difference between functional distinctiveness groups (D1 to D10 distribution deciles), according to their dissimilarities. We then tested whether this functional dissimilarity was lower or higher than expected by chance given the number of species in each functional distinctiveness group. The functional dissimilarity between the species of a functional distinctiveness group and all other species was calculated using the R function '*dissim*' of the package '*TPD*' (Carmona et al., 2019). It reflects the degree of functional dissimilarity between the probabilistic distributions of species in the trait space between the two assemblages and ranges from 0 (complete overlap) to 1 (no overlap). We used a TPD (Trait probability density; '*TPD*' package; Carmona et al., 2019) approach—estimation of the probabilistic distribution of the species within the trait space—by performing multivariate kernel density estimations. We divided the 2-dimensional space into 40,000 cells, that is, 200 per dimension. For each species, the kernel was a multivariate normal distribution centred in the coordinates of the species in the trait space and bandwidth was chosen using unconstrained bandwidth selectors from the '*Hpi*' R function in the '*ks*' package (Chacón & Duong, 2018). We then compared the

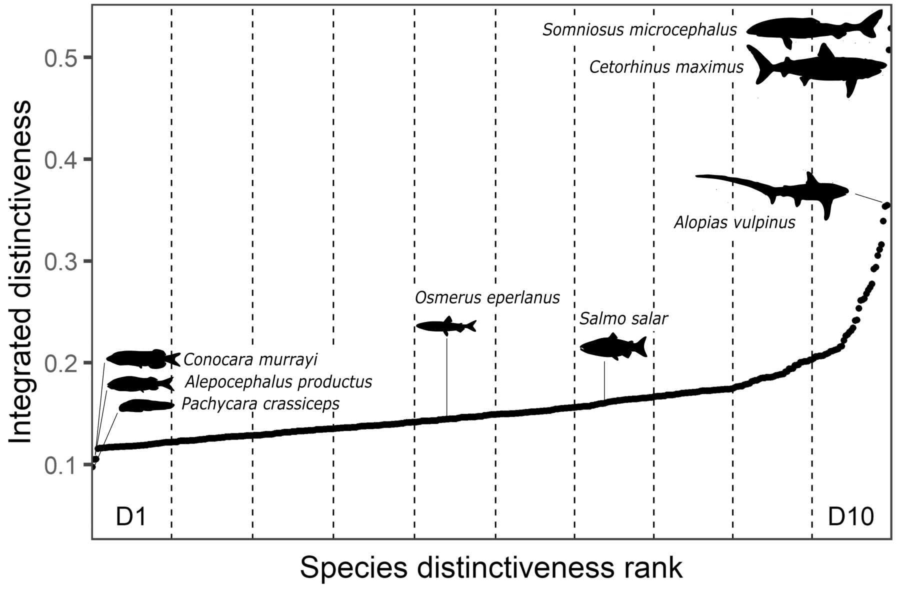

FIGURE 2 Integrated distinctiveness index per species showing that most species are rather functionally common and only a few are very distinct. The grey dotted lines separate species according to distinctiveness deciles, from D1 (the most functionally common species) to D10 (the most functionally distinct species).

observed functional dissimilarity to a null model where the functional distinctiveness groups were randomly assigned to species, keeping the number of species in each group constant. We drew 999 simulated assemblages and compared simulated and observed functional dissimilarities. We calculated standardized effect sizes (SES) as the difference between the observed value and the mean of the simulated values after standardization by their standard deviations: *p*-values higher (lower) than 0.975 (0.025) indicate that the observed functional dissimilarity is significantly lower (higher) than expected by chance (using a 5% threshold), given the number of species in each group.

We then turned to the complementary components of functional distinctiveness to define functional rarity, that is, the scarcity and spatial restrictedness of species in the study area. Although initially defined at local and regional spatial scales, the indexes can be calculated at the same study scale to capture both aspects of functional rarity: being low in abundance and being spatially poorly distributed (Grenié et al., 2017; Ricotta et al., 2016). This is because both range size and local abundance influence extinction risk; species with small ranges can avoid extinction if their local abundance is high, while species with low local abundance can avoid extinction if they are widespread; species with both small ranges and low local abundance should be at high risk (Johnson, 1998). For a given species, we compared its geographical range with the geographical extent of the entire study area. The spatial restrictedness R_i is an index between 0 and 1 based on species occurrence (Violle et al., 2017) (weakly impacted by gear selectivity) and is computed as follows:

$$R_i = 1 - \frac{K_i}{K_{tot}} \tag{2}$$

with K_i the number of ICES rectangles where species *i* occurs and *Ktot* the total number of ICES rectangles in the dataset. R_i nearly equals one when a species is present in a single site and 0 when the species is present in all sites (Grenié et al., 2017). Because there are differences in sampling effort between the 536 ICES rectangles, we computed the restrictedness to prevent under or overestimation. The restrictedness was computed for each grid cell by randomly selecting the minimum number of hauls to catch 65% of the asymptotic number of species with enough sampling effort (477 rectangles out of 536). For a given species, the procedure was repeated 100 times. The integrated restrictedness (IntRi) was calculated as the average of restrictedness values.

The scarcity index Sc_i, which ranges between 0 and 1, measures the relative abundance of species *i* in the community (Violle et al., 2017):

$$Sc_i = \left(-S \times \ln(2) \times Ab_i \right) \tag{3}$$

with *S* the total number of species in the study area and Ab_i the relative abundance of species *i* (i.e. the mean abundance of the species divided by the mean abundance of all species in the Northeastern community). A species with a low relative abundance will have a scarcity value close to 1, while dominant species will tend toward 0. Since scientific bottom trawl surveys are conducted with bottom trawls and not pelagic trawls, we also calculated the scarcity index excluding the 24 pelagic species. For both restrictedness and scarcity, a unilateral Welch's *t*-test was performed to compare the restrictedness/scarcity between the most functionally common and distinct species (D1 and D10, respectively). We also implemented two Generalized Linear Mixed Models (GLMM) using the *'lme4'* R package (Bates et al., 2015) using the restrictedness/scarcity index as a response, the deciles (D1 and D10) as predictors and the species family as a random factor.

2.4 | Relationship between extinction risk, functional distinctiveness and traits

Regional IUCN Red List statuses of species were obtained using the *'rredlist'* R package (Chamberlain & Salmon, 2018) and manually verified thanks to the IUCN Red List of Threatened Species (IUCN, 2022). Only species with IUCN status (and not 'Data Deficient' status; 362 out of 425 species) and complete trait information (294 out of 425 species) were selected for the rest of the study. We converted IUCN status into two threat categories: (i) 'not threatened', which grouped together 'least concern' (LC) and 'near-threatened' (NT) species, and (ii) 'threatened', that encompassed 'vulnerable' (VU), 'endangered' (EN) and 'critically endangered' (CR) species. A unilateral Welch's *t*-test was performed to assess whether species assigned as 'threatened' have a higher distinctiveness than 'non-threatened' species. We then mapped species conservation status in trait space using a trait probability density approach, following Carmona et al. (2021): we set up a Generalized Additive Model (GAM), using the species conservation status as a response, the corresponding position in the different dimensions of the trait space (PCoA axes) as predictors. Model predictions (i.e. the probability of species being threatened) were done for the different PCoA axes without extrapolation. By representing predictions on the different axis, we mapped the complete functional space and therefore offer a visualization of how extinction risk was distributed across trait combinations.

We finally performed a down-sampled Random Forest classification (RF; *'randomForest'* R package, Breiman, 2011), recommended when classes are unbalanced (Freeman et al., 2012) to assess the contribution of individual traits on species conservation status. Instead of a bootstrap sample from the entire dataset, each tree of the forest during down-sampling is built from a bootstrap sample from the rare class, along with a sub-sample of the same size from the more common class (Chen et al., 2004). Species threat (1: threatened, 24 species; 0: not threatened, 270 species) was the response variable, and species trait values were the predictors.

The flowchart of the methodology developed for our analyses is presented in Supporting Information Appendix S2—Figure S4.

3 | RESULTS

3.1 | Functionally rare species and their traits

Species rank based on distinctiveness is very robust to missing data, in particular for defining the ranks of the most common and distinct species (see Supporting Information Appendix S1—Table S4), but the absolute value of the distinctiveness decreases more for the most distinct species (see Supporting Information Appendix S2—Figure S3; $R_1^2 = 0.9954$ & $R_2^2 = 0.9982$). The integrated distinctiveness (IntDi; Figure 2; see SupportingInformation Appendix S1—Table S5) of Northeastern Atlantic marine fish ranges from 0.10 for *Pachycara crassiceps* to 0.51 and 0.53 for Basking Shark (*Cetorhinus maximus*) and Greenland Shark (*Somniosus microcephalus*), respectively, followed by Thresher Shark (*Alopias vulpinus*) with a IntDi value of 0.35. With a median integrated distinctiveness value of 0.14, most species of the European continental shelf are quite functionally common and only a few species are very functionally distinct. The first functional distinctiveness group (D1; 42 species), defined according to the first decile of the integrated distinctiveness indexes distribution, encompasses the most functionally common species with IntDi values ranging from 0.10 to 0.12. Almost all D1 species are 'non-guarder' (one value is missing) and 'demersal' (40 out of 43 species). They spawn a very large number of tiny eggs (median offspring size = 0.96 mm; median fecundity = 50,000) (see Supporting Information Appendix S2—Figure S5). On the opposite part of the distribution (Figure 2), D10 species (42 species, of which 41% are elasmobranchs with 16 sharks and one skate, and a significant number of deep-sea species) groups together the most functionally distinct species with IntDi values between 0.20 and 0.53.

Species that belong to D10 represent between 0 and 17% of the total number of species per ICES rectangle, the maximum number being observed on Porcupine Bank (see Supporting Information Appendix S2—Figure S6). They present particularly high restrictedness values (IntRi = 0.960 ± 0.097), indicating a spatial restriction with significantly more limitations than for D1 species (IntRi = 0.860 ± 0.219; unilateral Welch's *t*-test; $p = 0.003$; see Supporting Information Appendix S1—Table S5). At the scale of the European continental shelf seas, D10 species are present on average in 4% of the ICES rectangles, the most common species being present on average in 14% of the rectangles. Functionally distinct species (D10 species) also present very high scarcity values (Sci = 0.863 ± 0.278), which is significantly higher (unilateral Welch's *t*-test; $p = 0.011$; see Supporting Information Appendix S1—Table S5) than for functionally common species (D1 species; Sci = 0.590 ± 0.450): the relative mean abundance of functionally distinct species corresponds to 0.86% of the relative mean abundance of common species. When pelagic species are removed from the calculation of the scarcity index, the same conclusions are reached (unilateral Welch's *t*-test; $p = 0.003$). In addition, the variance of the family random effect is less than the residual variance of each GLMM showing that significant differences in restrictedness/scarcity between D1 and D10 species are not due to a family effect. In other words, this means that whatever the family, functionally distinct species are also scarce and geographically restricted, resulting in functionally rare species.

The first two axes of the PCoA (57.3% of the total variance; Figure 3a), and tests for the relationship between each trait and the species integrated distinctiveness (see Supporting Information Appendix S2—Figure S5), show that functionally rare species are mainly characterized by slow individual growth, large body size (i.e. length at infinity and maximal length), high trophic level, late sexual maturity, low fecundity and that they provide high parental investment to their progeny in comparison to functionally common species. These species are also mainly not demersal.

3.2 | Extinction risk and functional distinctiveness

Thirty species have not yet been assigned a European IUCN status and 33 species have a 'Data-Deficient' status. These species are distributed in each of the functional distinctiveness groups (see Supporting Information Appendix S2—Figure S7). Of the 294 species considered in this section, 24 are classified as 'threatened' (see Supporting Information Appendix S1—Table S5). Using a unilateral Welch's *t*-test to test whether 'threatened' and 'nonthreatened' species have distinct IntDi values, we show that 'threatened' species have a significantly higher distinctiveness ($p = 0.003$) than 'non-threatened' species (see Supporting Information Appendix S2—Figure S8). Indeed, 37.5% of the 'threatened' species are functionally rare species (D10 species) and this percentage increases further (58.3%) if we include D9 species, the second most functionally distinct group. These correspond to elasmobranchs (D9 and D10 species) classified as 'vulnerable', 'endangered' and 'critically endangered' on the IUCN Red List; European Sturgeon (*Acipenser sturio*) classified as 'critically endangered' (D10 species) and Beaked Redfish (*Sebastes mentella*) classified as 'endangered' (D9 species); 100% of the most common species (D1 species) are 'non-threatened' species. However, some threatened species are classified into the rather common functional groups (D2, D3 and D4 species): Sandy Ray (*Leucoraja circularis*; EN), Shagreen Ray (*Leucoraja fullonica*, VU), European Eel (*Anguilla anguilla*, CR), European Whitefish (*Coregonus lavaretus*, VU) and Roundnose Grenadier (*Coryphaenoides rupestris*, EN).

Species with the greatest risk of extinction belong to the group with the highest dissimilarity in trait space (SES = 0.78; Supporting Information Appendix S1—Table S6), a dissimilarity greater than that expected by chance (SES = 14.78, $p = 1$). The subspace they occupy is mostly characterized by slow pace-of-life species (i.e. slow individual growth, late sexual maturity, low fecundity, high parental care and larger offspring size; Figure 3b), large maximum size and high trophic levels with a piscivorous feeding mode. These traits are also the most important for assessing the risk of extinction of species according to the down-sampled random forest (error rate = 7.14%; see Supporting Information Appendix S2—Figure S9) with species in the 'threatened'

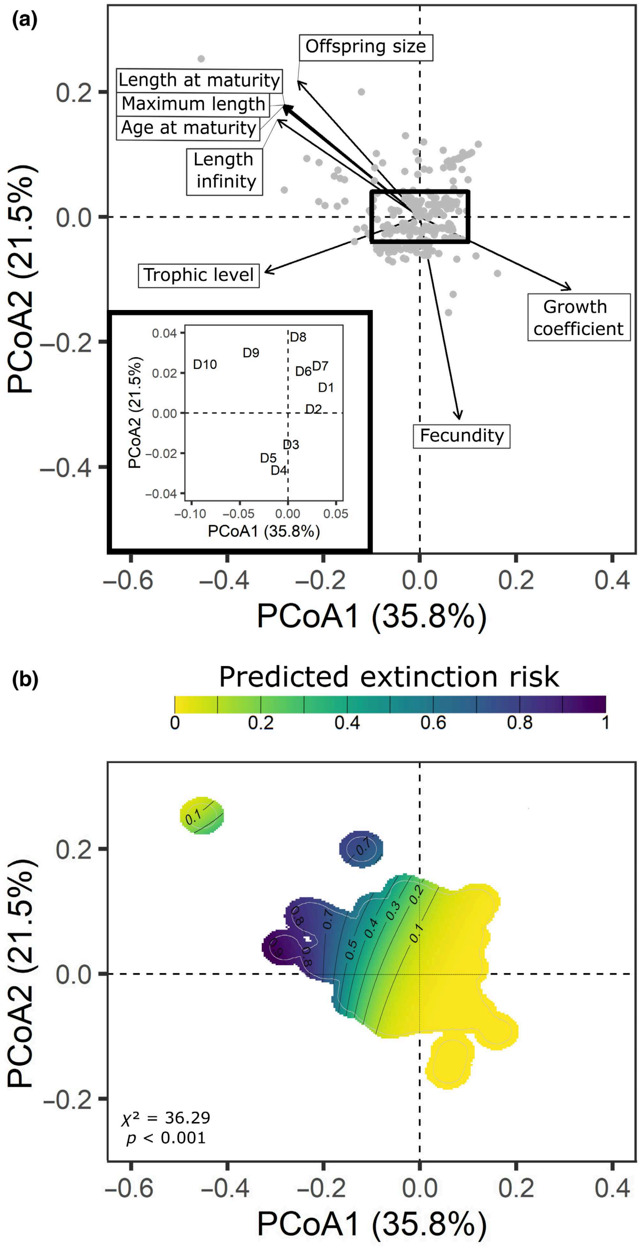

FIGURE 3 Sorting of species along the two principal axes of the principal coordinate analysis (PCoA) of the Northeastern Atlantic marine fish trait data. (a). Functionally rare species are long-lived species. Annotations from D1 (the most common species) to D10 (the most distinct species) refer to the centroids of each functional group. Categorical factors are not represented for convenience and given their low explanatory power. (b). Threatened fish species are functionally rare. Extinction risk in the trait space of the Northeastern Atlantic marine fish. Probability of species being classified as threatened according to the Generalized additive model (GAM) (with binomial distribution; χ^2 and p-values are shown), using the position of species in the functional space as predictors. Yellow tones indicate a low risk of extinction. Purple tones indicate a high risk of extinction. The grey line indicates the 0.99 quantile of the spectra of each group, considering only species with known extinction risk and traits (294 out of 425).

category having larger maximum length and much larger offspring size (see Supporting Information Appendix S2—Figure S10), followed by body size coefficients, fecundity and trophic level.

4 | DISCUSSION

Our aim was to evaluate whether threatened fish species are functionally rare and identify traits that make them vulnerable. To do so, we used IUCN species status, species traits and abundance data from bottom trawl surveys to define the functional rarity of 425 fish species in the European seas. Here we both demonstrate that (i) a substantial proportion (38%) of threatened fish are functional distinct, spatially restricted and present high abundance scarcity and (ii) that the functional distinctiveness of these species is primarily associated with slow pace-of-life strategies. Our results are analogous to similar studies on freshwater fishes (Su et al., 2019), or on terrestrial mammals and birds (Loiseau et al., 2020), demonstrating a general trend to devote efforts to protect species with unique functional traits and supporting key functions within ecological processes (Dee et al., 2019; Leitão et al., 2016; Mouillot, Bellwood, et al., 2013).

The most functionally distinct species identified in our analysis tend to occupy a higher trophic position in the food web to the extent that some, such as Porbeagle (*Lamna nasus*) that feeds mainly on teleost fish and cephalopods (Stevens, 2010), are known to be apex predators (Wallach et al., 2015). Because top predators exert top-down regulation (Barley et al., 2017a, 2017b; Ruppert et al., 2013), their decline or disappearance may destabilize ecosystems functioning through cascade reactions (Leitão et al., 2016; Mouillot, Graham, et al., 2013; Murgier et al., 2021; Violle et al., 2017). Top predators may also be linked to other ecosystem functions, such as transporting nutrients and carbon through the layers of the ocean (Atwood et al., 2018; Higgs et al., 2014; Williams et al., 2018). For example, Swordfish (*Xiphias gladius*) feed near the surface at night (0–90 m) and up to 650 m depth during the day on myctophid fish and squid (Chancollon et al., 2006). Species with a high trophic level may also facilitate the acquisition of organic matter for other species both during their lifetime through their feeding practices (e.g. bioturbation of skates; O'Shea et al., 2012) and after their death when the sinking of their carcass provides food for mobile scavengers over extended periods of time ranging from several weeks to months (e.g. Porbeagle or Thresher Shark; Higgs et al., 2014). Species, such as Turbot (*Scophthalmus maximus*), Brill (*Scophthalmus rhombus*) and Blue Shark (*Prionace glauca*), can also support ecosystem services including food supply (Simpfendorfer et al., 2011) and tourism (Cisneros-Montemayor et al., 2013; Gonzáles-Mantilla et al., 2022). Associating the extinction risk to the impact of a given species on the entire food web—like the complexity of its interactions with other species—would be relevant to move toward efficient ecosystem conservation plans.

Functionally distinct species (D10 species) also reach sexual maturity later, at a larger size, and carry few larger eggs or offspring to which they provide parental care, thus having an overall slower pace of life. Among these species, there are 16 external brooding and internal live-bearing sharks whose new-born pups are very large (28–175 cm), such as Blue Shark that has evolved placentae with gestation lasting from 9 to 12 months (Dulvy & Reynolds, 1997). The 'bearer' type (i.e. external brood and internal live-bearer type) occurs when the benefits of increased offspring survival outweigh the costs of reduced fertility, mobility and increased metabolic demands of carrying offspring through development (Goodwin et al., 2002). Two teleost species (Ribbonfish: *Trachipterus arcticus* and European Sturgeon), distinguished by very high fecundity in contrast to older ages at maturity are also among the most functionally distinct species. Similarly, by studying more than 75,000 species of vascular plants, mammals, birds, reptiles, amphibians and freshwater fish, Carmona et al. (2021) showed that species with long-lived functional strategies, living in stable environments in which investment in juvenile survival is more effective in maintaining the population, are more likely to be threatened with extinction.

Furthermore, we show that distinct species (D10 species) are mostly poorly geographically distributed and low in abundance. Unfortunately, species that have small population sizes, restricted geographical ranges (or habitat extent) and, often, narrow environmental niches, are especially vulnerable to extinction (Casey et al., 2021; Davies et al., 2004; Harnik et al., 2012; Johnson, 1998; Loiseau et al., 2020). Some of the most spatially restricted species (see restrictedness index) are evolving at great depths (e.g. *Melanostigma atlanticum*; *Maulisia microlepis*; *Benthocometes robustus*; *Normichthys operosus)*, including deep-sea sharks (e.g. sharpnose sevengill shark (*Heptranchias perlo)* and *Somniosus* sp.), therefore having a low probability of being encountered on the continental shelf due to biological constraints. Large pelagic species such as Thresher Shark and Swordfish rank among the least abundant species in European seas, as indicated by the scarcity index. By contrast, seven small pelagic fishes (out of a total of 29 pelagic species in our dataset) including European Sprat (*Sprattus sprattus)*, Atlantic Horse Mackerel (*Trachurus trachurus)*, Atlantic Mackerel (*Scomber scombrus)* and European Anchovy (*Engraulis encrasicolus*) are among the most abundant species. The International Bottom Trawl Survey (IBTS) has been previously shown effective for examining the temporal dynamics of both demersal and pelagic fishes (Hiddink & Ter Hofstede, 2008; McLean et al., 2018). Furthermore, bottom trawl surveys, including the IBTS surveys, are reliably used for pelagic stock assessment (HAWG, 2022; Heessen et al., 1997; ICES, 2007, 2022; Monnahan et al., 2021). Therefore, other species traits such as size and body shape or behaviour must be considered to further explain differences in abundance (Walker et al., 2017). What is certain is that less abundant species are less resilient to abrupt environmental changes (Bell & Gonzalez, 2011), and anthropogenic pressure such as habitat degradation and overfishing—that we can be related to the anthropogenic Allee effect; for example, Courchamp et al. (2006)—due to a limited supply of beneficial mutations and interspecific competition with more common species that have already undergone such beneficial mutation (Bell, 2017; van Eldijk et al., 2020) and competitive exclusion as they are less able to exploit their habitat (Segre et al., 2014). Here, we reveal that the abundance of the most functionally distinct species is low across the Northeast Atlantic, with maximum richness and abundance being found on the Porcupine Bank (see Supporting Information Appendix S2—Figure S5), although this region is one of the less well sampled of the European seas. Specific surveys conducted in this region between 2006 and 2009, O'Hea et al. (2020) sampled 21 species of deep-sea sharks (we counted seven deep-sea sharks in our datasets), the greatest number of individuals being constrained in deep habitats (~ 500 m depth). Porcupine Bank and adjacent areas support an important European demersal fishery, which makes these deep-sea species highly vulnerable to bottom trawl bycatch (Oliver et al., 2015), especially those for which abundance data do not support the implementation of management measures (ICES, 2021).

Our study reveals that the species facing the greatest risk of extinction are frequently functionally distinct species (D10 species), often contributing to unique niches and functions in the ecosystem (Hammerschlag et al., 2019). We showed that 38% of the species threatened with extinction according to the IUCN Red List in European seas (9 out of 24 species) are the most functionally distinct species (D10 species) with eight sharks belonging to both. If the second most functionally distinct group of species is added, the number of species increases up to 58% (14 species out of 24) and also includes one skate and one ray. Already alarming, this result is certainly underestimated because of the ‘Data Deficient’ classification of six D10 species (e.g. Forkbeard, *Phycis phycis*; Ocean Sunsfish, *Mola mola*; Arrowhead Dogfish, *Deania profundorum*; Sharpnose Sevengill Shark; Little Sleeper Shark, *Somniosus rostratus* and Atlantic Torpedo Ray, *Tetronarce nobiliana*) (Dulvy et al., 2021). Dulvy et al. (2021) estimated that one-third of chondrichthyan fishes worldwide were threatened with extinction, the largest sharks and rays being in the most peril, especially those living in shallow waters that are more accessible to fisheries, and more impacted by habitat degradation and pollution (Dulvy et al., 2021; Pacoureau et al., 2021). This risk is mainly related to their greater body size—a determining trait in the rate of extinction of animal species since the Pleistocene—(Cardillo et al., 2005; Carmona et al., 2021) and may result from a higher hunting pressure, a higher requirement for resources and a slower response to changes in conditions; nuances exist, however (see review by Chichorro et al., 2019). Moreover, sharks and skates are especially threatened in the Northeast Atlantic due to non-selective fishing techniques (Smith & Garcia, 2014; Walls & Dulvy, 2020) that may have led to local extinctions, such as occurred with Common Skate (*Dipturus batis*) (Brander, 1981) and angel sharks *Squatina* spp. (Lawson et al., 2020). If functionally rare species were to disappear, we could see significant changes in the functioning of ecosystems in connection with irreparable losses of functions (Carmona et al., 2021). Looking back to the unique functions already mentioned, such as highly specialized predation (Mouillot, Bellwood, et al., 2013), top-down trophic regulation (Barley et al., 2017a, 2017b; Ruppert et al., 2013), transfer of matter through the ocean layers (Atwood et al., 2018; Higgs et al., 2014; Williams et al., 2018), access facilitation to organic matter (Higgs et al., 2014; O'Shea et al., 2012), protein supply (Simpfendorfer et al., 2011) and ecotourism (Gonzáles-Mantilla et al., 2022), we realize that entire ecosystems are at stake, from coral reefs to abyssal plains to the continental shelves on which our marine resource exploitation relies. We also should highlight that several non-threatened species were functionally distinct, such as deep-sea lizardfish (*Bathysaurus ferox*), Alepocephaliformes, Stomiiformes, that can perform vertical migrations (e.g. *Vinciguerria poweriae*). Species expressing this behaviour influence ecological processes (e.g. grazing and predation pressure) in the upper water column by altering the composition of assemblages between day and night, and also participate in the organic matter transport from the surface to the seafloor (Angel & Pugh, 2000), thus enhancing the efficiency of the biological pump (Bianchi et al., 2013). Certainly ecologically unique—yet overlooked in conservation strategies—functionally distinct deep-sea species deserve greater attention for their conservation (Davies et al., 2007), especially in the context of climate change and carbon sequestration (Birch et al., 2016; De Stasio et al., 1993; Pinti et al., 2023).

The way we identify functionally distinct species is independent of species selectivity but can be influenced by both the selection of traits and the initial set of studied species (Legras et al., 2020). This means that whether a species is distinct or not is context and area dependent, conditioned by the regional species pool and their prevailing set of traits and adaptations. We therefore caution that our conclusions are limited to the spatial scale, species pool and trait combination we used. The inclusion of traits related to species' ecological versatility, such as thermal preference or range and vulnerability to acidification, could have been relevant to identifying species whose narrow ecological niches may make them particularly vulnerable to climate change (Jones & Cheung, 2018), with global declines observed in functionally distinct species predicted by niche theory (Clavel et al., 2011). For example, some functionally distinct but abundant and widely distributed species that were not identified as functionally rare in this study may become so if they exhibit increased sensitivity to environmental variation. Conversely, some species identified as low abundant and sparsely distributed but functionally common and therefore redundant in the ecosystem could become functionally rare if other species collapse. Second, highly specific life-history traits, such as amphidromy, could have been used to define distinct species (e.g. European Eel; European Whitefish; Salmon, *Salmo salar*), with amphidromic recruitment leading to movement of biomass from marine to freshwater systems, which may have important ramifications for riverine and estuarine trophic ecology and production (Jenkins et al., 2010). The inclusion of amphidromia would also be of particular interest as amphidromous species are at risk of extinction, mainly due to stream alteration (e.g. in-stream barriers, Cooney & Kwak, 2013; flow modifications, Kwak et al., 2013). Although there are many examples of very low abundance species having a disproportionate impact on their ecosystems (e.g. Canadian Beaver, *Castor canadensis*; bass, *Micropterus* spp.; gophers, *Geomys bursarius*, *Thomomys bottae* and Snow Geese, *Chen caerulescens*, as documented by Power et al., 1996), it should be noted that functionally distinct species are not always scarce. Neither are they always threatened, as evidenced for Brill (*Scophthalmus rhombus*): classified as a functionally distinct species (D10), Brill is present in over 38% of our study area, is one of the 100 most abundant species and belongs to the 'least concern' category. It is important to distinguish functional distinctiveness from functional rarity, which encompasses both the concept of functional distinctiveness and the notion of low abundance and spatial distribution. Lastly, we cannot reject a null effect of the selectivity of the trawling gears on scarcity results. The gears used during scientific surveys, primarily designed to sample commercial fish species, have varied over time with the improvement of fishing techniques; and they vary spatially at the scale of the different surveys, which may bias the assessment of spatial diversity patterns (O'Neill & Mutch, 2017).

Further research is needed to better understand the responses of functionally distinct species to past and current environmental changes and anthropogenic stressors. This will allow us to anticipate ecosystem responses and to develop management plans and strategies tailored to the responses of distinct species that will almost certainly determine future ecosystem structure and function. Such work should include understanding their responses to pressures in both recent (Osgood et al., 2021) and past periods (e.g. paleontological studies; Paillard et al., 2021; Stein et al., 2018). Identifying sustainable fishing strategies that reduce the impacts on functionally distinct species, for example, by limiting disturbance on critical life stages/areas, is also an essential prerequisite.

Our study highlights the importance of considering the conservation significance of functionally distinct species with unique combinations of ecological traits known to preserve ecosystem structure and function, a too often-overlooked facet of biodiversity. The life-history strategy of the most functionally rare species makes them particularly vulnerable to both natural variability and the drivers of global change, increasing the need for adaptive conservation efforts. In the context of the biodiversity crisis, there is an urgent need to complement the indicators used to guide species management and conservation policies, such as the IUCN Red List. Including the functional component of biodiversity would help better identify species that deserve special conservation attention due to their functional role, with respect to ecosystem functioning and balance.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The trait dataset that supports the fundings of this study is openly available at Figshare public data repository 10.6084/m9.figshare.19833304.v1. The abundance data that support the findings of this study are available on the ICES Database of Bottom Trawl Surveys (DATRAS) at https://datras.ices.dk. IUCN statutes that support the findings of this study are available on The IUCN Red List of Threatened Species (Version 2022–2) at https://iucnredlist.org. The R code used to calculate the integrated distinctiveness index that supports the fundings of this study is openly available at Figshare public data repository 10.6084/m9.figshare.22317643.v1.

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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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APPENDIX 1

DATA SOURCES

A.1 | THREATENED FISH SPECIES IN THE NORTHEAST ATLANTIC ARE FUNCTIONALLY RARE

Trait dataset

The sources used to build the dataset of traits for marine fish taxa observed during international scientific bottom-trawl surveys in the Northeast Atlantic are listed here. This dataset, which completes the one presented by Beukhof et al. (2019), is freely available at the Figshare public data repository (https://doi.org/10.6084/m9.figshare.19833304.v1).

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Abundance dataset

The Database of Trawl Surveys (DATRAS) is a repository for data collected primarily from bottom trawl fish surveys coordinated by ICES expert groups. These surveys cover a wide range of areas, including the Baltic Sea, Skagerrak, Kattegat, North Sea, English Channel, Celtic Sea, Irish Sea, Bay of Biscay, and the eastern Atlantic from the Shetlands to Gibraltar. The current dataset includes more than 45 years of continuous time series data, which is continuously updated by national institutions. Users can freely download both data products (such as CPUE) and raw data in accordance with the ICES Data Policy on the ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark, via the DATRAS website at https://datras.ices.dk.

IUCN statutes

The IUCN Red List Categories and Criteria were developed for assessing the extinction risk of species. This system provides information on a variety of factors, including range, population size, habitat and ecology, use and/or trade, threats, and conservation actions. This information can inform conservation decisions and actions. The IUCN Red List of Threatened Species provides free access to the latest IUCN Red List Categories and Criteria. Users can download the most recent version of the IUCN Red List at the following website: https://www.iucnredlist.org, Version 2022-2.

Integrated distinctiveness R code

The R code is freely available at Figshare public data repository https://doi.org/10.6084/m9.figshare.22317643.v1.

4. Les élasmobranches d’Atlantique Nord-Est face au changement climatique

En Atlantique Nord-Est 41 % des espèces les plus distinctes sur le plan fonctionnel sont des élasmobranches (Coulon et al., 2023). Parmi celles-ci, on trouve de grandes espèces pélagiques occupant une fonction de super prédateur telles que le requin renard (*Alopias vulpinus*), le requin taupe (*Lamna nasus*) et le requin peau bleue ou bien de filtreur spécialisé comme le requin pèlerin (*Cethorinus maximus*). De nombreuses espèces des grands fonds, appartenant aux familles des Centrophoridae (ex : *Daenia spp.*), Somnosidae (ex : *Centroscymnus spp. ; Somniosus spp.*), Dalatiidae (ex : squale liche, *Dalatias licha*) et Hexanchidae (ex : requin griset, *Hexanchus griseus*), figurent également parmi les espèces les plus fonctionnellement distinctes. Puis, figurent certaines raies de très grandes tailles comme les pocheteaux (ex : *Dipturus spp.*) ou de la famille de Torpedinidae (ex : *Torpedo spp.*) et Dasyatidae (ex : *Dasyatis spp.*). Enfin, des prédateurs démersaux de tailles moyennes telles que l’aiguillat commun, l’émissole tachetée (*Mustelus asterias*) et la grande roussette (*Scyliorhinus stellaris*) complètent ce tableau. Cependant, il est important de noter que tous les élasmobranches ne présentent pas un statut fonctionnel distinct dans l'Atlantique Nord-Est. A l'autre extrémité du spectre fonctionnel, parmi les espèces les plus communes, on trouve la petite roussette ainsi que plusieurs espèces benthiques de la famille des Rajidae, telles que la raie fleurie (*Leucoraja naevus*), la raie douce (*Raja montagui*), la raie lisse (*Raja brachyura*), et la raie bouclée (*Raja clavata*).

Dans l'Atlantique Nord-Est, la proportion d'élasmobranches menacés d'extinction, dont de nombreuses espèces fonctionnellement distinctes, a augmenté de 29 % à 41 % entre 1980 et 2015, principalement en raison de la surpêche (Coulon et al., 2023 ; Walls et Dulvy, 2021). En parallèle, des mesures de protection ont été progressivement mises en place dans les eaux de l'Union européenne : en 2006, l'interdiction de la rétention du requin pèlerin et du grand requin blanc (*Carcharodon carcharias*) ; en 2010/2011, l'interdiction de la rétention des anges de mer (*Squatina spp.*), des pocheteaux, de la raie blanche (*Rostroraja alba*), du requin taupe ; puis en 2020, la première limitation des prises de requins peau bleue. Toutefois, les raies et les requins représentent encore une part significative des captures en Atlantique Nord-Est. Par exemple, en 2022, les captures de raies et de requins en France ont représenté 6 % des prises totales de poissons marins, soit 13 677 tonnes d'élasmobranches contre 226 787 tonnes de poissons osseux marins (Eurostat, 2024). Les petites roussettes représentaient 22% du tonnage, les émissoles (*Mustelus spp.*) 23%, les raies fleuries 14%, les raies bouclées 13%, les raies lisses 10%, les grandes roussettes 5%

(Figure 8). À l'échelle mondiale, la surpêche constitue une menace directe majeure qui pourrait conduire à l'extinction des requins (Dulvy et al., 2021 ; Diaz et al., 2019).

Figure 8 : Photographies du débarquement de raies et de requins dans une criée en France.

Les élasmobranches ont survécu aux cinq grandes extinctions massives au cours des 450 derniers millions d'années, ce qui en fait l'un des groupes d'organismes marins les plus résilients aux changements environnementaux (Belben et al., 2017 ; Guinot et al., 2012 ; Guinot et Condamine, 2023 ; Kriwet et Benton, 2004 ; Sibert et Rubin, 2021). L'histoire évolutive des raies et des requins modernes a véritablement pris son essor après l'extinction massive de l'Ordovicien-Silurien, il y a environ 419 millions d'années. Lors de cette crise, les niveaux d'oxygène atmosphérique étaient supérieurs aux 21 % actuels, les températures mondiales étaient en phase de refroidissement, et les concentrations de CO_2 atmosphérique et aquatique étaient bien plus élevées qu'aujourd'hui, dépassant les 4000 ppm (Clack, 2007 ; Figure 9).

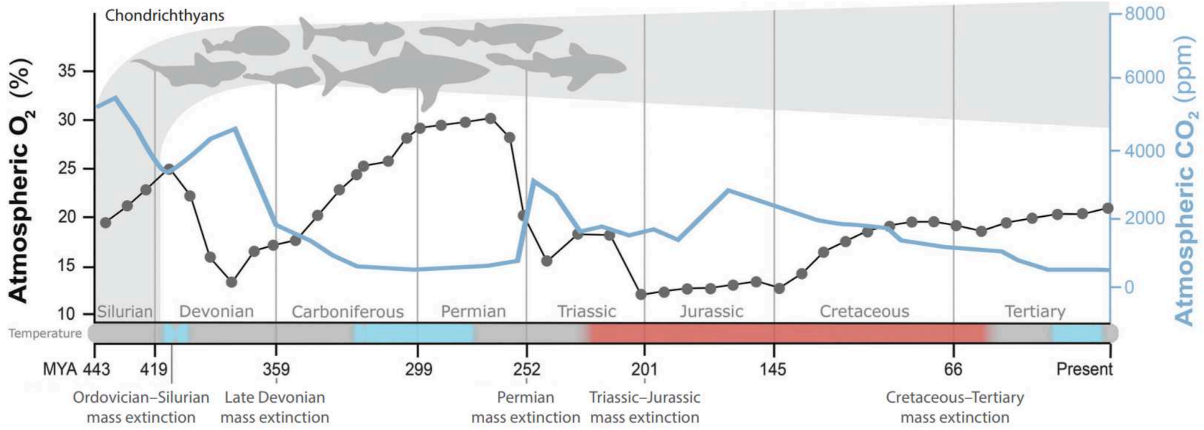

Figure 9 : Chronologie géologique (en millions d'années, MYA) retraçant l'évolution des Chondrichtyens (raies, requins et chimères). Les concentrations atmosphériques de dioxyde de carbone (CO_2) en parties par million (ppm) sont représentées sur l'axe des ordonnées de droite (en bleu), tandis que le pourcentage d'oxygène atmosphérique (O_2) est indiqué sur l'axe des ordonnées de gauche (en gris). Les périodes de réchauffement et de refroidissement planétaires sont signalées par des barres rouges et bleues le long de l'axe des abscisses. Figure extraite de Rummer et al., 2022.

De nombreux taxons de requins présents dans les archives fossiles du Cénozoïque, couvrant une période de -66 millions d'années (Ma) à aujourd'hui, ont encore des représentants vivants (Paillard et al., 2020 ; Pimiento et Benton, 2020). La diversité fonctionnelle des requins était particulièrement élevée au début du Cénozoïque, avec des pics au cours de l'Éocène et du Miocène, coïncidant avec des épisodes de réchauffement global, suivis d'un déclin progressif à partir de la fin du Miocène (Cooper et Pimiento, 2024). La diminution de la diversité fonctionnelle serait marquée par l'extinction de suceurs spécialisés (ex : *†Echinorhinus blakei*), de prédateurs de taille moyenne des grands fonds (ex : *†Dalatias sp.*), ainsi que de gigantesques prédateurs (ex : *†Otodus angustidens* et *†O. megalodon*). Bien que l'ère cénozoïque ait été marquée par des fluctuations environnementales, la tendance générale des 66 derniers millions d'années montre un refroidissement continu (Burke et al., 2018; Zachos et al., 2001). Cependant, les projections climatiques suggèrent que, sous des scénarios d'émissions non atténuées, les températures mondiales d'ici 2150 pourraient retrouver des niveaux similaires à ceux de l'Éocène, inversant ainsi une tendance au refroidissement vieille de 50 millions d'années en moins de 200 ans (Burke et al., 2018). Les raies et les requins de l'Atlantique Nord-Est seraient donc confrontés non seulement à la pression de la pêche, mais aussi aux effets des changements climatiques. Or, les connaissances sur les effets des changements climatiques sur les élasmobranches n'ont commencé à émerger dans la littérature scientifique qu'à la fin des années 2000 (Rummer et al., 2022). On pensait initialement que, puisque les requins et les raies avaient évolué durant des périodes où les niveaux de CO_2 atmosphérique étaient bien plus élevés qu'aujourd'hui, ils seraient naturellement résistants à l'augmentation en cours, rendant ces études moins pertinentes (Figure 9) (Chin et al., 2010 ; Rummer et Munday, 2022).

Pourtant, la dynamique de plusieurs espèces d'élasmobranches semble être étroitement liée aux modifications de la température de l'eau, en particulier dans la Manche et la mer du Nord, qui sont des zones particulièrement touchées par le réchauffement global (Dulvy et al., 2008 ; Simon et al., 2023). Au cours des 25 dernières années, la température de surface de la mer du Nord a augmenté de 1,6 °C (Dulvy et al., 2008 ; Hobday et Pecl, 2014). Ce réchauffement pourrait avoir contribué au déclin récent de la raie radiée (*Amblyraja radiata*), une espèce boréale associée aux eaux froides, ainsi qu'à l'augmentation de la raie bouclée, préférant les eaux plus chaudes (Sguotti et al., 2016). Bien que la surexploitation dans les années 1960 soit largement responsable du déclin de l'aiguillat commun (De Oliveira et al., 2013), le réchauffement global pourrait aussi jouer un rôle, cette espèce montrant une préférence pour les eaux plus fraîches (Sguotti et al., 2016). Parallèlement, les populations d’émissole tachetée et de petite roussette ont augmenté, passant d'occurrences limitées au début du XXe siècle à une présence bien établie au XXIe siècle. Leur expansion vers la mer du Nord suggère une immigration depuis la Manche. Ces deux espèces, aux affinités lusitaniennes (Engelhard et al., 2011), sont associées à des températures plus chaudes et semblent bénéficier du réchauffement global, avec des augmentations particulièrement marquées depuis les années 1990 (Sguotti et al., 2016). Des effets significatifs ont également été observés à l'échelle individuelle, notamment chez la petite roussette, une espèce modèle pour l'étude des raies et requins dans l'Atlantique Nord-Est. Le réchauffement, associé ou non à la désoxygénation, a eu des impacts notables sur la survie, le développement et le métabolisme des embryons de cette espèce (Brüggemann, 2013 ; Musa et al., 2020). Des résultats similaires ont été observés chez la raie lisse (*Raja microocellata*) (Hume, 2019). Sous l'effet de l'augmentation des températures, le comportement des embryons de petites roussettes apparaît également perturbé, diminuant leur capacité à stopper leur activité, y compris respiratoire (i.e. freezing) dans leur œuf pour échapper aux prédateurs (Kempster et al., 2013 ; Ripley et al., 2021). De plus, chez les adultes, il a été démontré que l'acidification de l’eau aurait modifié leur comportement nocturne de nage, qui est passé d'une alternance fréquente de départs et d'arrêts à une nage plus continue (Green et Jutfelt, 2014). Toutefois, aucune étude n’a encore évalué les impacts combinés du réchauffement et de l’acidification sur les élasmobranches de l’Atlantique Nord-Est.

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IV- Objectifs de la thèse

De nombreux élasmobranches d'Atlantique Nord-est présentent des traits bio-écologiques uniques pouvant soutenir des fonctions irremplaçables dans cet écosystème (Coulon et al., 2023) et sont confrontés à un risque élevé d'extinction, principalement en raison de la surpêche (Walls et Dulvy, 2021). Jusqu'alors, les effets des changements environnementaux en cours et à venir, susceptibles de renforcer cette pression, n'ont pas encore été pleinement évalués. Pourtant, l'exploitation des données de captures indépendantes de la pêche représente une opportunité précieuse pour mieux comprendre les impacts du changement climatique sur la distribution de ces espèces, l'abondance des populations et leurs compositions spécifiques et fonctionnelles. De plus, la taille modeste et le mode de vie de certaines espèces permettent de les étudier en milieu contrôlé sur des périodes prolongées. Cette thèse en écologie marine tire parti de ces deux observations et explore les effets du changement climatique sur les élasmobranches de l'Atlantique Nord-Est. Elle propose une approche intégrative, utilisant diverses méthodes complémentaires pour étudier les effets du réchauffement et de l'acidification de l'individu à l'assemblage des espèces (Figure 10).

Le premier chapitre de cette thèse explore l'impact du réchauffement et de l'acidification des océans sur la distribution spatiale de neuf espèces d'élasmobranches, chacune présentant des traits bio-écologiques variés. En analysant 24 années de données issues de campagnes scientifiques de chalutage de fond dans l'Atlantique Nord-Est (1997-2020), nous avons d'abord évalué la sensibilité de cinq espèces de raies (radiée, blonde, lisse, bouclée, fleurie) et de quatre espèces de requins (petite et grande roussettes, aiguillat commun, émissole tachetée) aux variations de pH et de température. Nous avons ensuite examiné si les conditions climatiques actuelles modifient l'adéquation à l'habitat de ces populations et, enfin, nous avons étudié l'évolution des traits bio-écologiques au sein de l'assemblage de raies et de requins. Cette partie a fait l'objet d'un article scientifique publié dans la revue *Global Change Biology* : **Coulon, N.,** Elliott, S., Teichert, N., Auber, A., McLean, M., Barreau, T., Feunteun, E., & Carpentier, A. (2024). Northeast Atlantic elasmobranch community on the move: Functional reorganization in response to climate change. *Global Change Biology, 30*, e17157. https://doi.org/10.1111/gcb.17157

Le deuxième chapitre se concentre sur les effets combinés du réchauffement global, incluant des variations mensuelles de température, et de l'acidification de l'eau sur les dix premiers mois de vie de la petite roussette, incluant les phases embryonnaires et juvéniles. Les températures et niveaux de pH utilisés correspondent aux projections pour 2100 selon deux scénarios climatiques du modèle CMIP6 du GIEC : SSP2, un scénario de type « Middle of the Road » et SSP5, un scénario de « Fossil-fueled Development. », (respectivement +2 et +4 °C et ΔpH = -0,2 et -0,4). Ces projections ont été comparées à une condition témoin, utilisant les données historiques de températures et de pH de la période 1995-2014. En utilisant une approche expérimentale axée sur les individus et les groupes expérimentaux, nous avons mesuré (i) la croissance des embryons, leur comportement de freezing et le métabolisme associé, (ii) le taux de succès d'éclosion, et (iii) la croissance des juvéniles. Cette partie, réalisée partiellement dans le cadre du stage de master 2 de Stanislas Pilet a fait l’objet d’un article scientifique publié dans la revue *Marine Environmental Research* : **Coulon, N.**, Pilet, S., Lizé, A., Lacoue-Labarthe, T., Sturbois, A., Toussaint, A., Feunteun, E., & Carpentier, A. (2024). Shark critical life stage vulnerability to monthly temperature variations under climate change. *Marine Environmental Research, 198*, 106531. https://doi.org/10.1016/j.marenvres.2024.106531

Le troisième chapitre évalue les réponses individuelles et démographiques potentielles de deux espèces phylogénétiquement proches, la petite roussette et la grande roussette, mais qui présentent des traits de vie et des aires de répartition distincts. Pour ce faire, nous avons développé un modèle bioénergétique basé sur la formulation du modèle Wisconsin, combiné avec un modèle matriciel de dynamique de population. Ces outils ont permis d’estimer l’impact des températures projetées pour la fin du siècle sur (i) la croissance individuelle, (ii) les traits d'histoire de vie, et (iii) la dynamique des populations des deux espèces. Cette partie réalisée partiellement dans le cadre du stage de master 1 de Emma Gousset a fait l’objet d’un article scientifique en préparation : **Coulon, N.**, Elliott, S., Barreau, T., Lucas, J., Gousset, E., Feunteun, E., & Carpentier, A. Elasmobranch vulnerability to global warming: insights from bioenergetic modelling of catsharks under climate scenarios.

Le dernier chapitre aborde un aspect jusqu'alors peu exploré : l’impact de la température sur la fertilité des raies et des requins. À travers une revue de la littérature, nous avons examiné comment les variations thermiques affectent divers aspects de la fertilité, notamment la gamétogenèse, la recherche de partenaires, le contact et le stockage des gamètes, ainsi que le développement post-zygotique et la production de juvéniles. Nous avons également évalué les conséquences écologiques et évolutives potentielles de la pression thermique et mis en lumière les lacunes et les incertitudes dans notre compréhension des processus affectant la fertilité, ainsi que les variations taxonomiques et géographiques susceptibles d'influencer ces effets. Cette partie a fait l’objet d’un article scientifique en préparation : **Coulon, N.**, **Lizé, A**., Feunteun, E., & Carpentier, A. The unexplored impact of global warming on elasmobranch fertility.

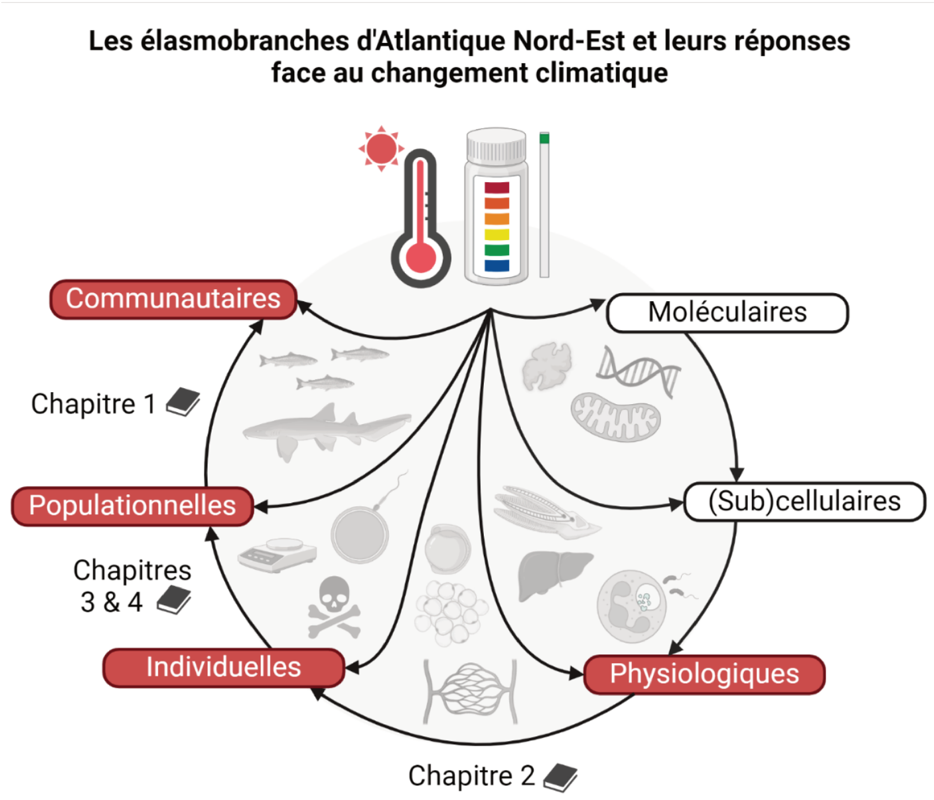

Figure 10 : Schéma illustrant les différents niveaux d'organisation biologique auxquels la température et le pH peuvent affecter les élasmobranches d'Atlantique Nord-Est. Inspirée de Rummer et al. (2022). Créée avec Biorender.com

CHAPITRE 1 : Réorganisation fonctionnelle de l’assemblage d'élasmobranches de l'Atlantique Nord-Est face au changement climatique

I- Expliquer et prédire la répartition des espèces

1. Concepts fondamentaux

Il est établi que trois conditions principales doivent être réunies pour qu'une espèce puisse occuper un site et y maintenir des populations viables (Guisan et al., 2017 ; Peterson et al., 2011 ; Soberón, 2007; Soberón et Nakamura, 2009) :

(i) L'espèce doit être capable d'atteindre le site, c'est-à-dire qu'elle doit avoir accès à la région et être en mesure de s'y disperser (Barve et al., 2011).

(ii) Les conditions environnementales abiotiques doivent être compatibles avec les exigences écophysiologiques de l'espèce (Austin et al., 2009).

(iii) Le contexte biotique, c'est-à-dire les interactions avec d'autres organismes, doit également être favorable à l'espèce.

Pour élaborer des modèles capables d'expliquer et de prédire la répartition des organismes, que ce soit dans des zones non échantillonnées ou au fil du temps en tenant compte des évolutions des paramètres environnementaux, il est essentiel que ces trois conditions soient remplies.

La première condition concerne la capacité de dispersion d'une espèce à partir de ses zones d'occupation antérieures. Cela inclut l'histoire biogéographique de l'espèce, intégrant tous les facteurs qui restreignent sa distribution depuis son lieu d'origine, tels que les obstacles à la migration et les vecteurs de dispersion biotiques et abiotiques. Un aspect crucial pour la modélisation de l'adéquation de l'habitat réside dans les effets de la spéciation allopatrique et sympatrique sur les schémas de distribution passés, présents et futurs des espèces. La spéciation allopatrique se produit lorsque des barrières géographiques interrompent le flux génétique entre populations d'une espèce ancestrale, menant à la formation de nouvelles espèces ou sous-espèces distinctes de part et d'autre de la barrière (Hoskin et al., 2005 ; Grant et Grant, 2009). Par exemple, l'élévation de l'isthme de Panama à la fin du Pliocène est souvent citée comme un facteur clé ayant contribué à la spéciation des requins-marteaux (famille des Sphyrnidés) entre les océans Pacifique et Atlantique (Lim et al., 2010). En revanche, la spéciation sympatrique se déroule au sein de l'aire de répartition originelle de l'espèce, souvent en réponse à une spécialisation écologique dans des conditions environnementales similaires. Un exemple de ce phénomène est la présence d'une espèce cryptique de requin-marteau dans l'ouest de l'Atlantique Nord, le requin-marteau de Caroline (*Sphyrna gilberti*) (Quattro et al., 2006 ; 2013 ; Fields et al., 2016), qui est par ailleurs actuellement menacée par l'hybridation avec le requin-marteau halicorne (*Sphyrna lewini*) (Barker et al., 2019). Ces deux processus jouent un rôle crucial dans la compréhension des distributions actuelles des espèces (Pearman et al., 2008) et ont des implications pratiques significatives. Par exemple, les changements de niche entre les aires de répartition indigènes et envahies peuvent influencer notre capacité à prédire et anticiper les invasions biologiques (Guisan et al., 2014). De même, la capacité des modèles à prédire la présence future des organismes dans le contexte du changement climatique peut être limitée si les niches écologiques sont incomplètement quantifiées. Ce biais survient lorsque les niches sont estimées uniquement à partir des conditions climatiques actuelles, sans prendre en compte que le changement climatique pourrait rendre accessibles des portions de la niche fondamentale actuellement inaccessibles aux espèces (Chevalier et al., 2024a).

La deuxième condition concerne l'adéquation de l'habitat abiotique pour l'espèce cible. En d'autres termes, la combinaison des variables environnementales abiotiques d'un site, souvent appelée adéquation environnementale, doit correspondre aux conditions nécessaires pour que l'espèce puisse croître et maintenir des populations viables. Cette adéquation reflète la niche environnementale de l'espèce (*sensu* Hutchinson, 1957) et forme la base de l'approche de modélisation de l'adéquation de l'habitat (Guisan et Zimmermann, 2000). Ces conditions sont dictées par les contraintes physiologiques des espèces par rapport aux gradients environnementaux. La réponse observée est généralement associée à une position optimale sur le gradient, où l'espèce atteint ses meilleures performances, appelée optimum physiologique. La performance de l'espèce tend alors à diminuer progressivement à mesure que l'on s'éloigne de cet optimum, que ce soit dans un sens ou dans l'autre. (Ellenberg, 1953 ; 1954 ; Hector et al., 2012). Ces réponses physiologiques peuvent être représentées par des courbes sigmoïdes ou unimodales (Figure 11), les courbes unimodales étant généralement dominantes. Par exemple, Lee et al. (2019) ont démontré que l'abondance mensuelle des requins bouledogues sur la côte sud-est de l'Australie suivait une distribution unimodale. Ces requins étaient présents lorsque la température de surface de la mer variait entre 20 et 26°C, avec un pic d'abondance observé à 24°C.

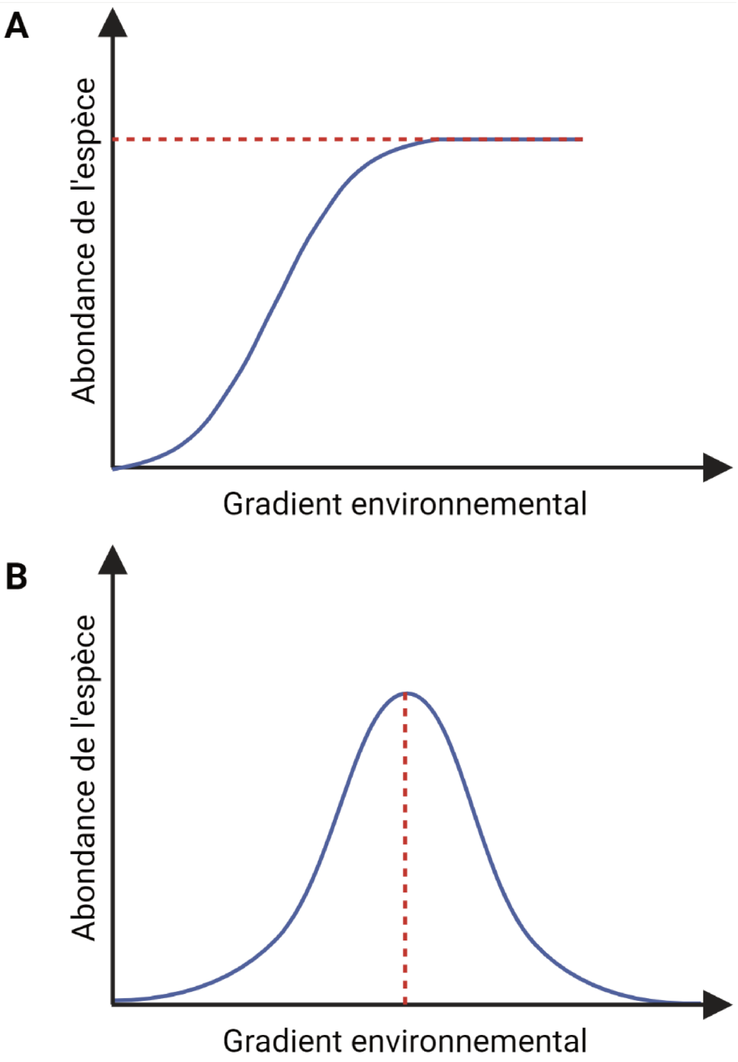

Figure 11 : Courbe de réponse fondamentale d'une espèce hypothétique le long d'un gradient environnemental hypothétique. A. Courbe de réponse sigmoïde typique, généralement attendue à la fin du gradient ou en réponse à une troncation d'une courbe unimodale. B. Courbe de réponse unimodale. D'après Guisan et al. (2017). Créée avec Biorender.com

Certaines variables pouvant atténuer ou amplifier les effets d'autres, il est essentiel d'analyser toutes les variables importantes conjointement. Les réponses physiologiques d'une espèce à plusieurs variables environnementales définissent un volume multidimensionnel, connu sous le nom de niche environnementale fondamentale de l'espèce (Hutchinson, 1957). En pratique, il est souvent difficile de mesurer la niche fondamentale uniquement à partir des observations sur le terrain dans des conditions naturelles. En effet, les interactions biotiques—qu'elles soient positives (comme le commensalisme ou le mutualisme) ou négatives (comme la compétition ou la prédation)—limitent ou augmentent davantage la distribution d'une espèce dans l'espace, dans le temps, ou le long des gradients environnementaux, constituant ainsi la troisième condition présentée précédemment (Anderson, 2016 ; Chevalier et al., 2024b ; Wisz et al., 2013 ; Figure 12). Ces interactions sont également influencées par l'environnement, qui façonne la dynamique des organismes au sein de la communauté. Par exemple, le registre fossile des Lamniformes et des Carcharhiniformes montre que leur évolution a été influencée non seulement par les variations du niveau de la mer et de la température, mais aussi par leur écologie alimentaire et la compétition associée (Bazzi et al., 2021 ; Condamine et al., 2019).

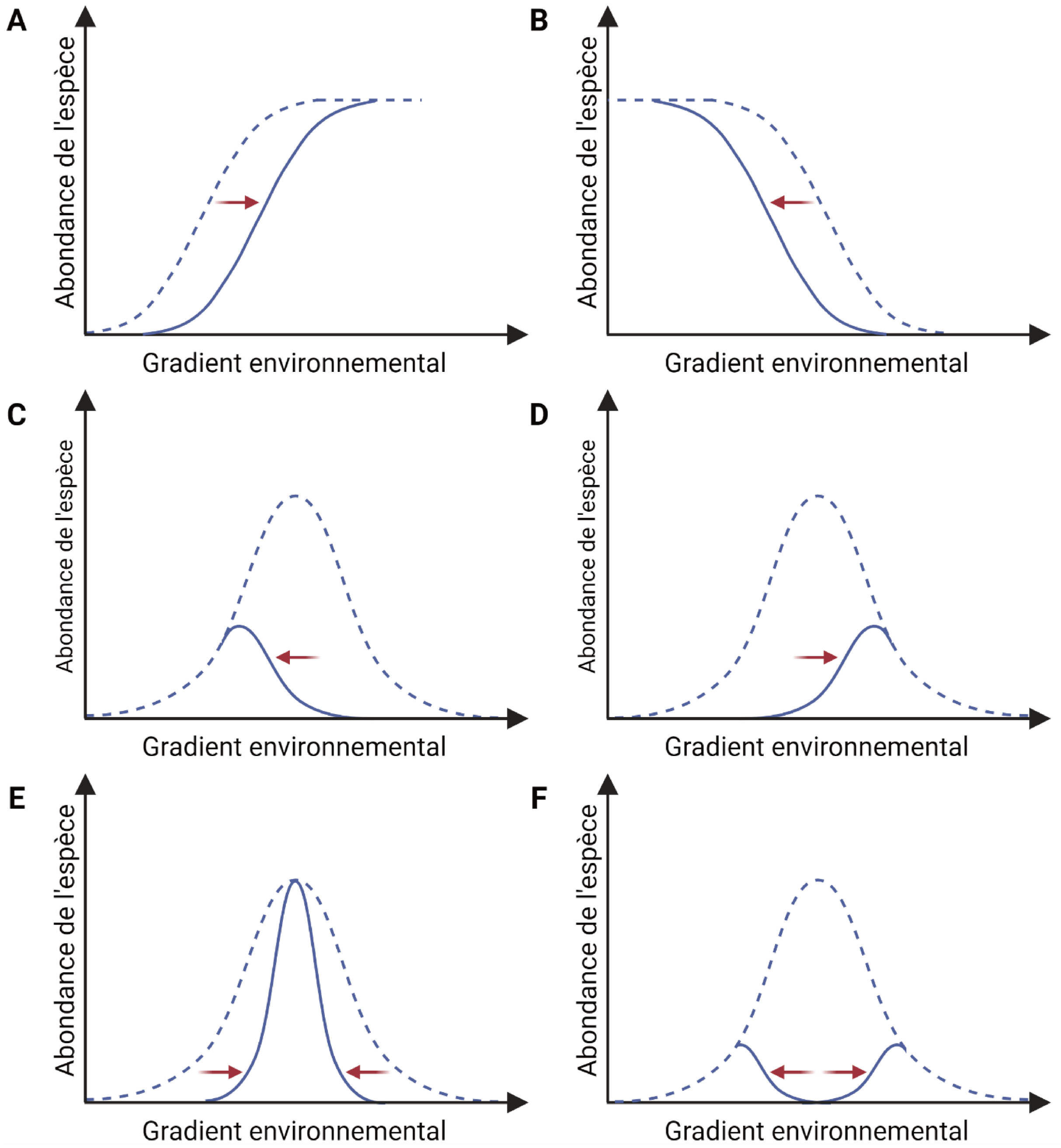

Figure 12 : Principales situations d'exclusion compétitive contraignant la courbe de réponse fondamentale d'une espèce hypothétique le long d'un gradient environnemental hypothétique à la courbe de réponse réalisée observée dans les systèmes naturels. Ces modifications comprennent le déplacement linéaire de la réponse (A, B), le déplacement optimal (C, D), le rétrécissement de la niche (E) et l'élimination optimale (entraînant une réponse bimodale) (F). D'après Guisan et al. (2017). Créée avec Biorender.com

Dispersion, niche environnementale et interactions peuvent être schématiquement représentées par des ensembles distincts, chacun défini par des conditions limites spécifiques (Soberón, 2007). Les conditions optimales pour une espèce, résultant de la combinaison de ces trois facteurs, se situent à l'intersection des trois ensembles (Figure 13, cas 1). Toutefois, des populations d'une espèce peuvent être présentes dans des situations sous-optimales (cas 2-4 dans la Figure 12), soit dans des environnements adéquats où l'espèce est normalement exclue par des interactions biotiques défavorables (Figure 13, cas 2), soit dans des environnements inadaptés, dits « puits », colonisés par une forte densité de propagules, conformément à la dynamique source-puits (Pulliam, 2000 ; Figure 13, cas 3). Enfin, l'espèce peut également être observée dans des environnements inadaptés, où les conditions abiotiques sont défavorables et les interactions biotiques sont négatives (Figure 13, cas 4). Ce dernier scénario représente cependant la situation la moins probable dans laquelle une espèce peut être présente. Une espèce peut également être absente d'un site pour des raisons autres que ces trois facteurs principaux, comme les perturbations naturelles ou anthropiques, ou encore la stochasticité intrinsèque de la population, qui peuvent entraîner des fluctuations spatiales et temporelles de la taille de la population, avec de possibles extinctions locales temporaires dans certaines zones (Pulliam, 2000). Par exemple, depuis le milieu du 20e siècle, le requin de récif *Carcharhinus galapagensis* a disparu localement de l'archipel des Rochers de Saint-Paul en raison de la surpêche (Luiz et Edwards, 2011). Toutefois, la présence occasionnelle de *Carcharhinus falciformis*, une espèce sympatrique autrefois fréquente sur les mêmes récifs que *C. galapagensis*, indique que cette espèce océanique continue d'immigrer dans la région. Ce phénomène laisse penser que *C. galapagensis* pourrait recoloniser ces eaux si la pression de pêche venait à diminuer, étant donné que des conditions écologiques favorables semblent encore exister.

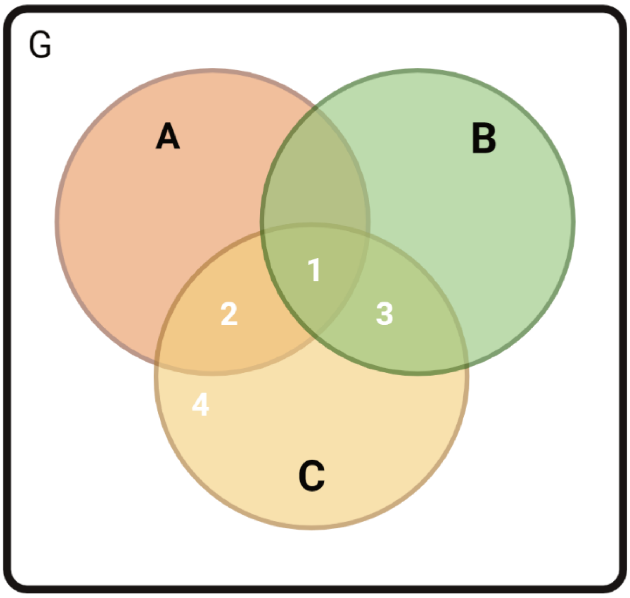

Figure 13 : Les trois principaux facteurs déterminant l'aire de répartition des espèces. G : zone géographique étudiée ; A : milieu abiotique adéquat (niche) ; B : milieu biotique adéquat ; C : aire de colonisation. Les observations sur le terrain peuvent résulter de quatre situations, classées de la plus probable à la moins probable : 1. Niche réalisée, adaptée aux trois aspects. 2. Milieu abiotique favorable mais conditions biotiques défavorables, par exemple en raison d'une forte concurrence. 3. Colonisation en dehors du milieu adéquat, potentiellement facilitée (puits écologique). 4. Puits écologique dans des conditions abiotiques et biotiques inadaptées, possiblement en raison d'un effet historique. D'après Guisan et al. (2017). Créée avec Biorender.com

Néanmoins, il est généralement admis que les espèces sont fortement influencées par le déterminisme environnemental. Par conséquent, la quantification de leurs niches environnementales devrait fournir des informations cruciales pour prédire leur distribution. À très grande échelle, la répartition de la majorité des espèces semble être principalement déterminée par des facteurs abiotiques, en particulier par les conditions climatiques. Les questions clés à aborder pour établir le lien entre la répartition des espèces et les conditions d'habitat reposent principalement sur l'inclusion des gradients environnementaux proximaux, c'est-à-dire ceux qui ont des effets directs sur les espèces, ainsi que sur la prise en compte de leurs variations. Un autre aspect essentiel des interactions entre les espèces et leur environnement réside dans le fait que ces relations peuvent également varier en fonction de la résolution spatio-temporelle de l'analyse. Par exemple, la température joue un rôle crucial dans les mouvements horizontaux et verticaux des raies et des requins, influençant leur comportement sur diverses échelles temporelles. À court terme, elle peut affecter la thermorégulation comportementale, essentielle pour optimiser la recherche de nourriture : les températures plus chaudes en surface favorisent des niveaux d'activité accrus, tandis que les températures plus fraîches en profondeur améliorent l'efficacité métabolique, un phénomène souvent décrit comme « chasser au chaud, se reposer au frais » (Matern et al., 2000 ; Sims et al., 2006). À des échelles temporelles plus longues, comme les saisons ou les années, la température peut également signaler le début des migrations (Heupel, 2007) ou prédire la résidence saisonnière dans des zones spécifiques (Kessel et al., 2014).

2. Des modèles d'adéquation de l'habitat monospécifique aux modèles de distribution conjointe des espèces

Les communautés écologiques peuvent être étudiées en modélisant individuellement chaque espèce qui les compose à l'aide de modèles de distribution des espèces (SDM, Species Distribution Models), également appelés modèles de niche ou modèles d'adéquation de l'habitat. Les SDM établissent des relations statistiques entre l'abondance ou la présence d'une espèce et son environnement biotique et abiotique (Franklin, 2009 ; Guisan et al., 2017 ; Peterson et al., 2011). Toutefois, ces modèles ne modélisent pas directement les processus d'assemblage des communautés, mais plutôt les patrons de distribution résultant de ces processus (Elith et Leathwick, 2009 ; Ovaskainen et al., 2017). Il est également possible d'appliquer les modèles de distribution monospécifiques pour modéliser simultanément les distributions de plusieurs espèces, une approche connue sous le nom de modélisation de la distribution d'espèces empilées (SSDM, Stacked Species Distribution Modelling). Cette méthode consiste d'abord à ajuster séparément les SDM pour chaque espèce, puis à combiner leurs prédictions pour obtenir une vue d'ensemble de la distribution des communautés (Calabrese et al., 2014 ; Guisan et Rahbek, 2011).

En revanche, les modèles de distribution conjointe des espèces (JSDM, Joint Species Distribution Models) intègrent les données de plusieurs espèces pour analyser leurs distributions conjointes en prenant en compte les interactions entre elles.. Cette approche permet non seulement d'identifier des patrons à l'échelle de la communauté concernant la manière dont les espèces réagissent à leur environnement (Clark et al., 2014 ; Ovaskainen et Soininen, 2011 ; Ovaskainen et al., 2017), mais aussi de relier ces patrons aux traits bio-écologiques et aux relations phylogénétiques des espèces qui sont inclus dans les données d'entrées des modèles (Pollock et al., 2012). De plus, les JSDM quantifient les cooccurrences entre espèces, révélant ainsi de potentielles interactions écologiques qui seraient invisibles dans une analyse monospécifique (Ovaskainen et al., 2010 ; Ovaskainen et al., 2016 ; Pollock et al., 2014).

Ces deux approches, SSDM et JSDM, représentent respectivement les stratégies « prédire d'abord, assembler ensuite » et « assembler et prédire ensemble » (Ferrier et Guisan, 2006). Le cadre de la modélisation hiérarchique des communautés d'espèces (HMSC, Hierarchical Modelling of Species Communities) s'inscrit dans cette dernière stratégie, cherchant à modéliser les communautés de manière holistique. C’est cette dernière approche qui a été sélectionnée pour décrire les modifications spécifiques et fonctionnelles de l’assemblage d’élasmobranches dans ce chapitre.

3. Aperçu de la modélisation hiérarchique des communautés d'espèces

La modélisation HMSC est une méthode statistique avancée utilisée pour analyser les données écologiques des communautés (Ovaskainen et al., 2017). Contrairement aux modèles mécanistes, qui intègrent des descriptions détaillées des processus d'assemblage et de dynamique des communautés (Franklin, 2010), le modèle HMSC se concentre principalement sur les corrélations entre les variables. En d'autres termes, HMSC ne fournit pas d'explications sur les mécanismes par lesquels les individus interagissent avec leur environnement ou avec d'autres individus, ni sur les dynamiques énergétiques ou trophiques au sein des communautés. Il ne traite pas des interactions alimentaires spécifiques ni de la circulation de l'énergie et des ressources au sein du réseau d'espèces en interaction.

Dans la terminologie statistique, le modèle HMSC est un modèle linéaire généralisé mixte multivarié utilisant l'inférence bayésienne (Ovaskainen et Abrego, 2020). La première étape de la configuration d’un tel modèle consiste à prendre plusieurs décisions clés, basées sur une compréhension approfondie de la physiologie et de l'écologie des organismes. Certaines concernent la structure même du modèle, comme l'intégration d'effets aléatoires, tandis que d'autres portent sur la sélection des prédicteurs, tels que les covariables environnementales et les traits spécifiques des espèces à inclure (Araújo et Guisan, 2006 ; Austin et Van Niel, 2011). Il est donc recommandé de rapporter ces choix de manière rigoureuse afin de permettre une évaluation précise des modèles publiés, en tenant compte des données, des procédures de modélisation et de l'incertitude associée (Feng et al., 2019 ; Zurell et al., 2020). Ensuite, pour ajuster le modèle HMSC aux données, on utilise l'inférence bayésienne combinée avec les méthodes de Monte Carlo à chaîne de Markov (MCMC, Markov Chain Monte Carlo) (Gamerman et Lopes, 2006). L'inférence bayésienne commence par définir des distributions *a priori* pour les paramètres du modèle, reflétant les connaissances préalables avant d'examiner les données. La fonction de vraisemblance évalue comment les données observées sont générées en fonction de ces paramètres. En intégrant les distributions a priori avec la vraisemblance, on obtient la distribution *a posteriori*, qui représente nos connaissances actualisées sur les paramètres après avoir pris en compte les données. Comme cette distribution peut être complexe, les méthodes MCMC sont employées pour échantillonner efficacement cette distribution *a posteriori*. Ces méthodes génèrent une séquence d'échantillons en construisant une chaîne de Markov, permettant ainsi de représenter les paramètres du modèle de manière probabiliste. Après un nombre suffisant d'itérations, les échantillons obtenus permettent d'estimer les paramètres du modèle. La deuxième étape consiste à vérifier si la convergence MCMC est satisfaisante. Si ce n'est pas le cas, les échantillons fournis par la chaîne MCMC peuvent donner des estimations de paramètres biaisées entraînant une vision erronée de la quantité d'incertitude dans les estimations de paramètres. Le modèle doit alors être réajusté. La convergence MCMC peut être examinée à l'aide d'une inspection visuelle des tracés MCMC ou à l'aide de diagnostics plus formels, tels que la taille effective de l'échantillon et le facteur de réduction d'échelle potentiel (Brooks et Gelman, 1998 ; Gelman et Rubin, 1992). La troisième étape consiste à évaluer l'adéquation du modèle, ainsi qu'à comparer plusieurs modèles pour sélectionner celui qui sera utilisé comme modèle final. Le pouvoir explicatif du modèle est déterminé en évaluant dans quelle mesure celui-ci prédit les données utilisées pour son ajustement, tandis que son pouvoir prédictif est évalué en examinant la capacité du modèle à prédire des données de test indépendantes qui n'ont pas été utilisées lors de l'ajustement (Araújo et Guisan, 2006 ; Roberts et al., 2017 ; Santini et al., 2021). Par ailleurs, les modèles HMSC ont démontré une très bonne performance dans la prédiction des occurrences d'espèces rares, en tirant parti des données de cooccurrence avec des espèces plus communes qui partagent des préférences environnementales similaires (Ovaskainen et Soininen, 2011 ; Zhang et al., 2020). La quatrième étape consiste à analyser les estimations des paramètres du modèle. Les paramètres clés comprennent les niches environnementales des espèces, qui mesurent la manière dont les occurrences ou les abondances des espèces sont influencées par les variations abiotiques. De plus, contrairement à d’autres modèles, le HMSC permet d’intégrer des informations sur les traits bio-écologiques des espèces ainsi que leurs relations phylogénétiques dans les données d’entrée. Cela permet d'évaluer comment les niches des espèces dépendent de leurs traits bio-écologiques et de leurs relations évolutives, facilitant ainsi l'identification des traits de réponse et la détection de signaux de conservation des niches (Ovaskainen et Abrego, 2020). La cinquième étape consiste à utiliser le modèle pour réaliser des prédictions. Celles-ci peuvent être effectuées pour des zones où les co-variables environnementales sont connues, mais où la présence des espèces n'a pas encore été étudiée. Cette approche permet de générer des cartes de distribution des espèces, de richesse spécifique, ou encore de répartition des traits. Cependant, la transférabilité du modèle diminue à mesure que la distance géographique s'accroît et que le degré d'extrapolation environnementale augmente (Elith et al., 2010 ; Rousseau et Betts, 2022).

Les modèles bayésiens peuvent être visualisés à l'aide d'un graphe acyclique dirigé (DAG, Directed Acyclic Graph), qui montre comment les paramètres du modèle sont reliés entre eux et aux données (Ovaskainen et Abrego, 2020 ; Figure 14). La composante à effets fixes du modèle HMSC (voir la partie gauche de la Figure 14) traite du filtrage environnemental, c’est-à-dire comment l'interaction entre les niches des espèces et la variabilité environnementale influence leur occurrence et leur abondance. Les paramètres β du modèle représentent les niches des espèces et indiquent comment les variations environnementales affectent la présence de chaque espèce. Chaque espèce a ses propres paramètres β, reflétant sa niche spécifique. Ces niches dépendent des traits bio-écologiques de réponse, dont la dépendance est capturée par les paramètres γ. Les traits de réponse non mesurés peuvent également présenter un signal phylogénétique, reflété par le paramètre ρ dans le modèle HMSC. La composante à effets aléatoires du modèle HMSC (Ovaskainen et Abrego, 2020 ; voir la partie droite de la Figure 14) modélise le filtrage biotique, c'est-à-dire comment les interactions entre les espèces influencent leur occurrence, notamment leurs co-occurrences. Un paramètre crucial de cette partie est la matrice d’association espèce-espèce Ω, qui indique les paires d'espèces observées ensemble plus ou moins fréquemment que prévu par hasard. Cependant, dans ce contexte, « par hasard » signifie que la partie à effets fixes du modèle HMSC, qui gère le filtrage environnemental, est prise en compte. Ainsi, lorsque deux espèces se retrouvent ensemble « plus souvent que par hasard », cela suggère une co-occurrence plus fréquente que ce que l’on pourrait attendre compte tenu de la similarité de niche. Ainsi, la matrice Ω capture la cooccurrence résiduelle, c'est-à-dire la cooccurrence qui n'est pas expliquée par le filtrage environnemental (Dormann et al., 2018). La composante à effets aléatoires du modèle prend également en compte la limitation de la dispersion. En particulier, lorsque des effets aléatoires spatialement explicites sont inclus, un paramètre α mesure l’échelle spatiale de la variation aléatoire inexpliquée, et est donc lié à l’échelle spatiale de la dispersion.

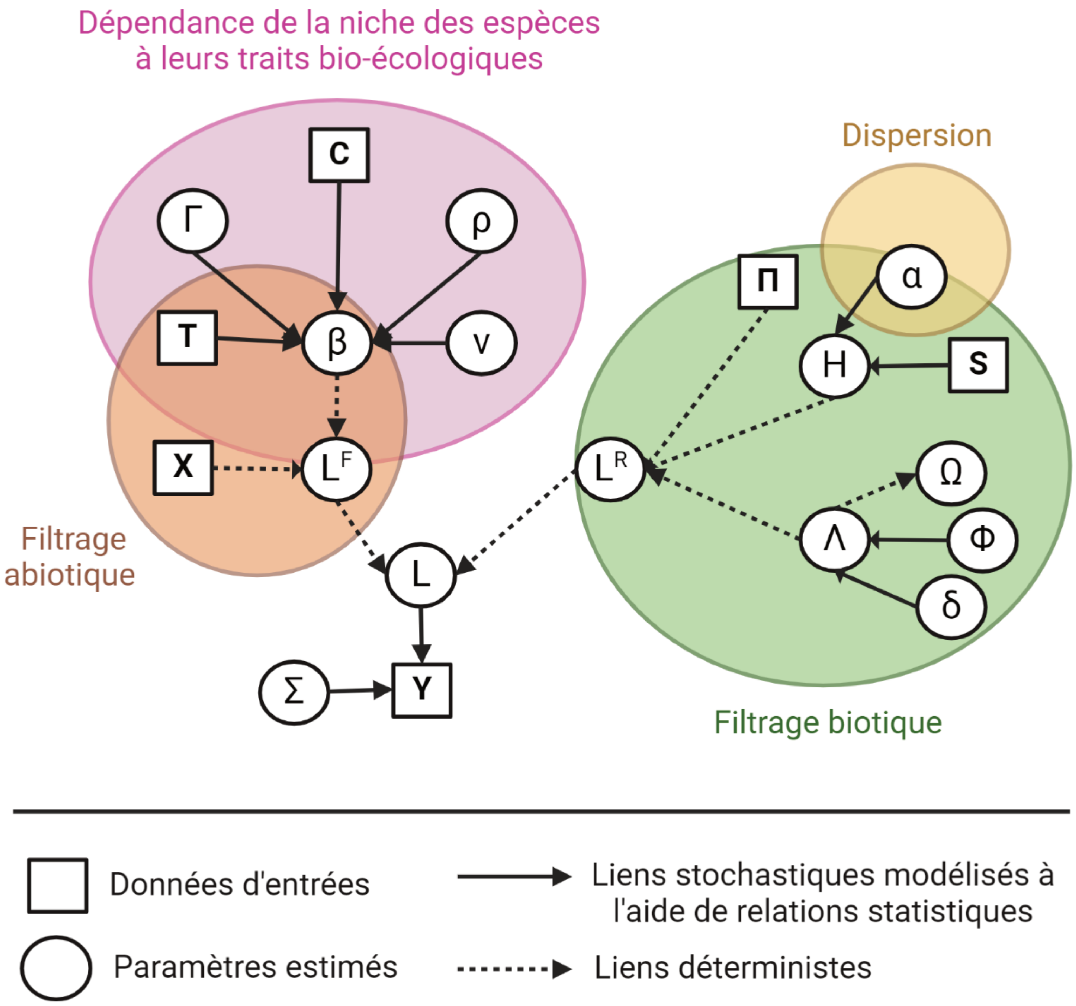

Figure 14 : Graphique acyclique dirigé (DAG) du modèle HMSC et liens entre la théorie de l'écologie des communautés et la structure statistique du HMSC. Les données d'entrée sont représentées par des carrés, tandis que les paramètres estimés sont indiqués par des cercles (voir Tableau 1 et Tableau 2 pour la signification des lettres). Les flèches pleines symbolisent les liens stochastiques modélisés à travers des relations statistiques, tandis que les flèches en pointillés représentent les liens déterministes. Les zones colorées illustrent les différents processus d'assemblage des communautés. Adaptée de Ovaskainen et Abrego (2020). Créée avec Biorender.com

Tableau 1: Matrices de données dans le modèle HMSC. Adapté de Ovaskainen et Abrego (2020).

Matrice de données	Explication
Y	Données de la communauté
X	Données environnementales
T	Traits bio-écologiques des espèces
C	Données phylogénétiques
Π	Design de l'étude
S	Coordonnées spatiales

Tableau 2 : Paramètres et leurs interprétations dans le modèle HMSC. La colonne catégorie indique si le paramètre est lié à l'effet fixe (F), à l'effet aléatoire (R) ou au modèle de données (D) de HMSC. Adapté de Ovaskainen et Abrego (2020).

Catégorie	Paramètre	Interprétation
F	L^F	Prédicteur linéaire des effets fixes
F	β	Niches d'espèces
F	ρ	Signal phylogénétique dans les niches des espèces
F	Γ	Influence des caractéristiques sur les niches
F	V	Covariance résiduelle des niches d'espèces
R	L^R	Prédicteur linéaire d'effets aléatoires
R	H	Chargements du site
R	α	Échelle spatiale des charges du site
R	Λ	Charges d'espèces
R	Ω	Associations d'espèces
R	Φ	Rétrécissement local des charges d'espèces
R	δ	Rétrécissement global des charges d'espèces
D	L	Prédicteur linéaire
D	Σ	Residual variance

Dans ce chapitre, la modélisation HMSC est utilisée pour explorer l'impact du réchauffement et de l'acidification des océans sur la distribution spatiale de neuf espèces d'élasmobranches de l'Atlantique Nord-Est, chacune présentant des combinaisons différentes de traits bio-écologiques. L'étude examine également l'évolution de l'assemblage de ces traits au sein de cet assemblage d'espèces.

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II- Northeast Atlantic elasmobranch community on the move: Functional reorganization in response to climate change

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Résumé : Alors que des modifications de la distribution spatiale ont été documentées chez de nombreux poissons marins soumis au changement climatique, les réponses des élasmobranches ont rarement été étudiées, ce qui peut avoir conduit à une sous-estimation des menaces potentielles supplémentaires qui pèsent sur eux. Compte tenu de leur rôle irremplaçable dans les écosystèmes et de leur risque élevé d'extinction, nous avons utilisé une série chronologique de 24 ans (1997-2020) de chalutage scientifique de fond pour examiner les effets du changement climatique sur la distribution spatiale de neuf espèces d'élasmobranches dans les eaux de l'Atlantique Nord-Est. En utilisant une modélisation hiérarchique des communautés d'espèces, appartenant aux modèles conjoints de distribution des espèces, nous avons constaté que la surface des habitats appropriés a augmenté en moyenne d'un facteur de 1,6 pour quatre espèces et, pour six espèces, se sont déplacés vers le nord-est et/ou vers des eaux plus profondes au cours des deux dernières décennies. En intégrant les traits des espèces, nous avons montré que les changements dans l'adéquation de l'habitat ont entraîné des changements dans la composition des traits des assemblages d'élasmobranches. Ces derniers se sont par ailleurs déplacés vers des eaux plus profondes et leur niveau trophique moyen a diminué. Nous notons également une augmentation de la taille moyenne à maturité des assemblages, concomitante d'une diminution de la fécondité. Les raies et les requins étant fonctionnellement uniques et dangereusement vulnérables à la fois au changement climatique et à la pêche, nous plaidons pour une prise en compte urgente des traits bio-écologiques des espèces dans les mesures de gestion. Leur utilisation permettrait de mieux identifier les espèces dont la perte pourrait avoir des impacts irréversibles sur l'équilibre des écosystèmes.

Mots clés : changement climatique ; communauté ; déplacement de l'aire de répartition ; élasmobranche ; modélisation conjointe de la distribution des espèces ; traits des espèces

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RESEARCH ARTICLE

Northeast Atlantic elasmobranch community on the move: Functional reorganization in response to climate change

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Abstract

While spatial distribution shifts have been documented in many marine fishes under global change, the responses of elasmobranchs have rarely been studied, which may have led to an underestimation of their potential additional threats. Given their irreplaceable role in ecosystems and their high extinction risk, we used a 24-year time series (1997–2020) of scientific bottom trawl surveys to examine the effects of climate change on the spatial distribution of nine elasmobranch species within Northeast Atlantic waters. Using a hierarchical modeling of species communities, belonging to the joint species distribution models, we found that suitable habitats for four species increased on average by a factor of 1.6 and, for six species, shifted north-eastwards and/or to deeper waters over the past two decades. By integrating species traits, we showed changes in habitat suitability led to changes in the elasmobranchs trait composition. Moreover, communities shifted to deeper waters and their mean trophic level decreased. We also note an increase in the mean community size at maturity concurrent with a decrease in fecundity. Because skates and sharks are functionally unique and dangerously vulnerable to both climate change and fishing, we advocate for urgent considerations of species traits in management measures. Their use would make it better to identify species whose loss could have irreversible impacts in face of the myriad of anthropogenic threats.

KEYWORDS
climate change, community, elasmobranch, joint species distribution modeling, range shift, species traits

1 | INTRODUCTION

Climate change is an intensifying pressure affecting all marine organisms that may lead to irreversible ecological transformations such as biodiversity loss, decreased ocean productivity, and altered food webs (Henson et al., 2021; Hoegh-Guldberg & Bruno, 2010; Worm & Lotze, 2021). Increasing temperatures are responsible for shifting the distribution of marine species to more offshore, deeper, or colder waters (Dulvy et al., 2008; Punzón et al., 2016), as well as to higher latitudes (Cheung et al., 2013). Furthermore, ocean acidification is known to have turned calcified coastal habitats into non-calcified ones, reducing benthic complexity and reshaping nursery communities (Cattano et al., 2020; Zunino et al., 2019). While climate change effects on teleost fishes have been extensively documented (Pörtner

& Peck, 2010), fewer studies have been carried out in elasmobranchs (sharks, rays, and skates; Rummer et al., 2022), whose lineage includes more than three times as many species threatened with extinction (IPBES, 2019; Stein et al., 2018). Since elasmobranchs had lived in periods with higher atmospheric CO_2 concentrations than today, it was thought that they should be able to tolerate such conditions in the future (Rummer & Munday, 2017). However, since the late 2010s, a growing number of experimental studies show that elasmobranchs are sensitive to ocean acidification and warming (Rummer et al., 2022). Population-level changes in response to climate change have also been observed in recent decades, such as changes in the range and/or migratory timing of the Tiger Shark (Hammerschlag et al., 2022), or increased use of breeding habitat by the Bull Shark (Bangley et al., 2018) and White Shark (Tanaka et al., 2021). Future shifts are also expected for the 21st century, with both gains and losses of suitable habitats depending on the species (e.g., Grieve, et al., 2020, and requiem and mackerel sharks, Birkmanis et al., 2020; Diaz-Carballido et al., 2022; Lezama-Ochoa et al., 2023).

Climate change may equally exacerbate fisheries-related risks by increasing the strength and frequency of extreme events (Cheung et al., 2021; Yan et al., 2021). For example, the risk of extinction of the Short-tailed Nurse Shark (*Pseudoginglymostoma brevicaudatum*) increased in the southwestern Indian Ocean due to the combination of overfishing, destructive fishing practices, rising temperatures, and increased frequency and severity of coral bleaching (Pollom et al., 2022). This is of particular concern in the Northeast Atlantic, where the English Channel and North Sea have been identified as hot spots for global warming (Dulvy et al., 2008; Simon et al., 2023) and where bycatch, habitat loss, and degradation are driving almost half of sharks and their relatives to extinction (56 out of 136 species, Dulvy et al., 2021; Walls & Dulvy, 2021). Shallow-distributed, slow-growing, low reproductive capacity species are the most likely to experience a decline in status (Coulon et al., 2023; Pimiento et al., 2023; Stein et al., 2018; Walls & Dulvy, 2021).

Elasmobranchs contribute to ecosystem functioning with unique combinations of physiological, morphological, reproductive, or behavioral traits (Tilman, 2001) that have no functional equivalent (i.e., functionally distinct species; Coulon et al., 2023; Leitão et al., 2016; Mouillot et al., 2013; Violle et al., 2017). They are known for exerting top-down regulation (Barley et al., 2017a, 2017b; Ruppert et al., 2013) but they are also linked to other ecosystem functions such as promoting energetic connectivity between neritic, oceanic, and deep-sea ecosystems (Shipley et al., 2023). Simulated extinction scenarios within various taxonomic groups (e.g., vascular plants, mammals, birds, reptiles, amphibians, and freshwater fish) revealed extensive changes in species trait composition within communities when functionally distinct species were lost (Carmona et al., 2021; Colares et al., 2022; McLean et al., 2019). Consequently, coupled with the human-induced reduction in population size, elasmobranch range shifts in the Northeast Atlantic could lead to profound and irreversible ecosystem reorganizations.

Using 24 years (1997–2020) of scientific bottom trawl surveys in the Northeast Atlantic, we first evaluated the sensitivity of five skate and four shark species to pH and temperature gradients. Then, we investigated whether the habitat suitability of these populations has been altered by ongoing climate change. Lastly, we studied how the trait composition of the elasmobranch community has changed over the last three decades.

2 | MATERIALS AND METHODS

2.1 | Study area and bottom trawl surveys

The study area covers the Greater North Sea, Celtic Seas, and Bay of Biscay (Figure 1). Spanning 24 years (1997–2020), the dataset is part of the time series of scientific bottom trawl surveys collated by the International Council for the Exploration of the Sea (ICES) expert groups conducted to examine changes in fish stock abundance and distribution (Appendix S1—Table S1). Species abundance data were downloaded from ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark.

Only fishing gear types with homogeneous spatiotemporal coverage and hauls made in the first 200 m depth were used to reduce spatiotemporal capture bias. All abundance data were converted to presence–absence to reduce biases of gear catchability. Only species present in more than 2% of the total number of trawls were

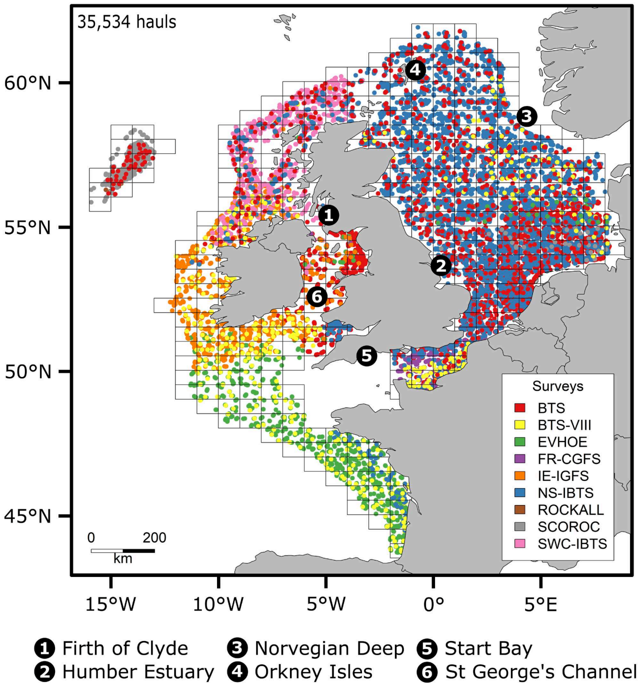

FIGURE 1 Map of the available bottom trawl surveys of elasmobranch communities across northwest European continental shelf seas obtained from the International Council for the Exploration of the Sea data portal (https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx). Colored dots locate the individual hauls, with one color per survey. ICES rectangles (1° × 0.5° grid cells) are represented. Table S1 for detailed information about bottom trawl surveys and their acronyms. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

selected (minimal thresholds defined according to model prediction accuracy). This was to reduce the imbalance between presence and absence data that can limit the model's ability to effectively learn the characteristics of the minority class (i.e., the class of presences), leading to biased predictions and reduced accuracy in identifying suitable habitats (Appendix S1—Table S1 and Appendix S2—Figures S1–S4). Some parts of our study area (e.g., the North Sea) are sampled at multiple seasons (i.e., quarters) within a year which implies a greater number of presences per year in these subareas. Therefore, the study area was gridded with cells of 0.111° × 0.134° in which only one species occurrence per year was kept to limit bias model training (Feng et al., 2019; Appendix S2—Figure S5).

The final selected community is composed of four sharks (Spurdog, *Squalus acanthias*; Large-spotted Dogfish, *Scyliorhinus stellaris*; Small-spotted Catshark, *Scyliorhinus canicula*; Starry Smooth-hound, *Mustelus asterias*) and five skates (Spotted Ray, *Raja montagui*; Thornback Ray, *Raja clavata*; Blonde Ray, *Raja brachyura*; Cuckoo Ray, *Leucoraja naevus*; Thorny Ray, *Amblyraja radiata*).

2.2 | Environmental drivers

Depth (positive values) and slope, descriptors of relief and complexity were obtained from GEBCO Bathymetric Compilation Group (2020) and "MARSPEC: ocean climate layers for marine spatial ecology" (Sbrocco & Barber, 2013), respectively (Appendix S2—Figure S6). Habitat types were obtained from the EUSeaMap 2021–EUNIS 2019 habitat types (European Marine Observation and Data Network) and grouped into seven broader categories based on their grain size composition (Appendix S1—Table S2), then used to calculate a Shannon substrate diversity index, reflecting habitat diversity.

A wide range of parameters may be affected by climate forcing and are likely to restrict sharks and skates distribution (e.g., temperature, dissolved oxygen, chlorophyll *a*, pH; Rummer et al., 2022; Schlaff et al., 2014). To correctly estimate species' responses to environmental variables, we built the most parsimonious model possible (Merow et al., 2014). We retained only temperature and pH that were not highly correlated with all the other variables (i.e., were unique in terms of signal; $R^2 < .75$). For example, we did not include dissolved oxygen because it was strongly correlated with temperature, meaning that the oxygen signal was already included in the temperature variable. While temperature influences key metabolic and physiological processes in ectothermic species and drives seasonal (Dunbrack & Zielinski, 2003; Hopkins & Cech, 2003; Vaudo & Heithaus, 2013) and diurnal movements (Matern et al., 2000; Papastamatiou et al., 2015; Vaudo et al., 2016), pH can markedly affect organismal physiology and behavior (Green & Jutfelt, 2014; Rummer et al., 2020) and enhanced temperature-induced effects (Rummer et al., 2022). Moreover, the effects of pH on the distribution of species remain unclear. Surface parameters were used in preference to bottom parameters, as bottom pH data were not available and most of the study area is relatively shallow, resulting in a close relationship between surface and bottom parameters (Young & Holt, 2007). Similarly, the monthly summer maximum of sea surface temperature (SST) and surface pH were selected in preference to winter values or annual averages. In addition, summer values are more likely to exert pressure on species that reach the upper limit of their thermal niche. For example, some oviparous species spawn during summer along the coast (e.g., *Scyliorhinus canicula*, Ellis & Shackley, 1997). Data were obtained from E.U. Copernicus Marine Service Information for each year (Appendix S1—Table S2). Monthly Atlantic Multidecadal Oscillation (AMO) indexes were obtained from the NOAA-PSL and averaged per year (Enfield et al., 2001; Appendix S1—Table S3) to disentangle the effects of ongoing climate change and the potential effects of long-term natural climate oscillations (Edwards et al., 2013; Faillettaz et al., 2019).

All drivers were downloaded at the finest resolution, then scaled down to presence–absence data cells (i.e., 0.111° × 0.134°) and kept in the absence of strong correlations (threshold = 0.85; Appendix S2—Figure S7).

2.3 | Species traits

We selected six species traits reflecting trophic ecology, life history, and ecological versatility that are expected to be implicated in the species' response to environmental changes (McLean et al., 2018; Murgier et al., 2021) and geographic range shifts (Albouy et al., 2015; Sunday et al., 2015; Appendix S1—Table S5 for reasoning). Species traits were collected by extracting traits values from Coulon et al. (2023) and Ocean Biodiversity Information System (OBIS, 2022). From the OBIS data, the geographic range was calculated as the difference between the highest and lowest latitudes in the distribution, given the spatial extent of the study area and after removing the first and last percentiles of the latitude distribution, to limit false presences due to species misidentification. The depth preference was calculated as the mean value of the depth distribution (Appendix S1—Table S5).

2.4 | Joint species distribution modeling

We used an hierarchical modeling of species communities (HMSC; Ovaskainen et al., 2017), belonging to the joint species distribution models (jSDM) class (Warton et al., 2015) to model species-specific changes in response to environmental variations and capture changes in species trait composition (Maioli et al., 2023; Montanyès et al., 2023; Weigel et al., 2023), using the "*Hsmc*" R package (Tikhonov et al., 2020; version 3.0-1). Each grid cell (29,193) was considered as a sampling unit (matrix S). We included species occurrence as a response variable in the HMSC analysis (matrix Y) and modeled presence–absence with a probit link function (Ovaskainen & Abrego, 2020), assuming the default prior distributions. Six continuous environmental drivers were included (matrix X), estimating a second-order polynomial term for sea surface temperature and pH (Appendix S2—Figure S8). We also included six species traits (matrix T) and a phylogenetic tree of elasmobranch species from VertLife.org (matrix C; Stein et al., 2018). Finally, we included a random effect to account for spatially structured samplings (i.e., fishing gears- types and quarters; matrix Π) and potential year-to-year variation not captured by the climatic covariates (i.e., years).

Two Markov Chains Monte Carlo (MCMC) simulations were run to generate 1000 posterior samples using a thinning interval of 50 following a burn-in period of 25,000 (Jönsson et al., 2022; Ovaskainen & Abrego, 2020). The effective sample sizes were very close to the actual sample sizes (mean difference < 6%), indicating that there is very little autocorrelation between consecutive samples. The potential scale reduction factors were very close to one (mean difference < 0.3%), which indicates that the two chains gave consistent results, as was also suggested by visual inspection of the trace plots (Appendix S3). The model was evaluated using area under the receiver operating curve (ROC) score (AUC = 0.83 ± 0.05; Appendix S1—Table S6), and examining the positive predictive value (PPV = 0.98 ± 0.04; Appendix S1—Table S6) and negative predictive value (NPV = 0.04 ± 0.07; Appendix S1—Table S6) using a random subset of 75% of the dataset used for parameter estimation and the remaining 25% of observations for validation (Elliott, Carpentier, et al., 2020). Thresholds were defined per species to maximize the Percentage of Correct Classification (PCC) using the R function "*optimal. threshold*" in the "*PresenceAbsence*" R package (Cantor et al., 1999; Manel et al., 2001; Wilson et al., 2004).

2.5 | Species responses to pH and temperature

We evaluated the species sensitivity to pH and temperature gradients by estimating second-order polynomial terms following Antão et al. (2022). Species were considered nonresponsive if the calculated range of probability (referred to as the posterior distribution) for a species' response included zero with more than 10% probability. Nonzero responses were then classified as positive, negative, or bell-shaped, depending on the sign of the derivative. A positive response corresponds to a species at the lower end of its niche (i.e., occurrences increasing along the environmental gradients), a bell-shaped response (derivative is positive or negative over at most 60% of the environmental gradient; Antão et al., 2022) corresponds to a species at the optimum of its niche (i.e., occurrences peaking within the gradients), and a negative response corresponds to a species at the upper end of its niche (i.e., occurrences decreasing along the gradients) (Antão et al., 2022).

2.6 | Shift in habitat suitability

We determined habitat suitability-weighted areas using annual jSDM projections from 1997 to 2020, calculating the sum of the cell areas weighted by the habitat suitability of each species (from 0 to 1), subsequently referred to as habitat suitability areas (A_{Hs}), as follows:

$$A_{\mathrm{Hs};j} = \sum_{i=1}^{N} a_{\mathrm{Hs};i} \times \mathrm{Hs}_i \tag{1}$$

where j is the year considered, $a_{\mathrm{Hs};i}$ is the area of the spatial cell i in km^2 calculated using the *"area"* function of the *"raster"* R package, Hs_i is the habitat suitability in the cell, and N is the total number of cells. This weighted calculation limits threshold selection bias and is a more conservative approach, given the different range of habitat suitability between species (Lezama-Ochoa et al., 2023; Rubenstein et al., 2023).

Along the same lines, we calculated habitat suitability-weighted centroids (C) and centroids of the first and last decile of the habitat suitability based on longitudinal, latitudinal, and depth components for each species, subsequently referred to as centroids, as follows:

$$C_{X,j} = \frac{\sum_{i=1}^{N} X_i \times \mathrm{Hs}_i}{\sum_{i=1}^{N} \mathrm{Hs}_i} \tag{2}$$

where j is the year considered, X_i is the latitude, longitude, or depth at the center of spatial cell i, Hs_i is the habitat suitability in the cell i, and N is the total number of cells (Weinert et al., 2016).

Then, we looked for trends in changes in habitat suitability-weighted areas, centroids, and habitat suitability in each cell for each species over time, based on Kendall's tau using the *"trend"* R package (Hipel & McLeod, 1994; Mann, 1945; Sen, 1968).

2.7 | Temporal change in species traits composition

Community weight mean (CWM) provides information about the average value of a species trait within the community, considering species abundance. Rather than assigning a weight to each species based on its abundance per cell, we assigned a weight to each species corresponding to the rate of change in the habitat suitability to examine changes in species trait composition for each trait in each cell over time. CWM values provide an overview of temporal changes but do not allow the strength and direction of the factors behind their variation to be quantified. For example, CWM increases when (i) the habitat suitability of species with higher species traits than the community increases, and (ii) the habitat suitability of species with lower species traits than the community decreases, while the CWM decreases when the opposite occurs. Therefore, we also decomposed the four underlying processes that cause CWMs to change (McLean et al., 2021). We calculated the difference between each species' traits and the mean of the community, multiplied this value by each species' change in habitat suitability, and took the sum of the resulting values for all species within each process (McLean et al., 2021):

$$\mathrm{PS}_{k,i} = \sum_{s=1}^{N} \left(\mathrm{ST}_s - \mathrm{CWM}_{k,i}\right) \times \Delta\,\mathrm{Hs}_i \tag{3}$$

where ST is the mean trait value of the species s, CWM is the community-weighted mean of the trait k in the cell i in all years, ΔPresence is the species' change in presence (i.e., Sen's slope), and N the total number of species. We evaluated the accuracy of this approach by comparing the value of the process strengths to the rate of change in CWM for each grid cell and for each trait (McLean et al., 2021; Appendix S2—Figure S9).

3 | RESULTS

3.1 | Species responses and pH & temperature

The three factors having the greatest influence on habitat suitability according to jSDM are SST (mean variance explained = 28.7), quarters and gears (mean variance explained = 24.8), and pH (mean variance explained = 18.4). Seafloor parameters (Appendix S2—Figure S10), and AMO had the lowest influence (mean variance explained = 0.1). The random effect of quarters and gears is spatiotemporally structured and reflects the different environmental conditions in the study area as well as the different distribution of species. While temperature explained more than 50% of the variance in habitat suitability for *L. naevus*, *R. montagui*, and *S. acanthias*, pH explained more than 50% in habitat suitability for *M. asterias* and more than 40% for *S. stellaris* (Appendix S2—Figure S10).

By estimating a second-order polynomial term for pH and temperature, we were able to state that all species, with the exception of *S. stellaris*, were in the optimal part of their pH niche from 1997 to 2020 (Figure 2; Appendix S1—Table S7), with no change over time. While four species (*A. radiata*, *M. asterias*, *R. clavata*, *S. stellaris*) were in the optimal part of their thermal niche, five (*L. naevus*, *R. brachyura*, *R. montagui*, *S. canicula*, *S. acanthias*) were at the higher end (Figure 2; Appendix S1—Table S7), meaning that during the warming period of 1997–2020, these species were present in temperature conditions in which their habitat suitability decreases when temperature increases.

3.2 | Shift in habitat suitability

Four of the nine species habitat suitability area increased with an annual rate of 2620 km^2 for *M. asterias* ($p < .001$), 1886 km^2 for *R. clavata* ($p < .01$), 1419 km^2 for *R. brachyura* ($p < .001$), and 1410 km^2 for *S. stellaris* ($p < .001$) (Appendix S1—Table S8). It extended approximately to 6% of the study area for *M. asterias*, 4% for *R. clavata* and *R. brachyura*, and 3% for *S. stellaris* from 1997 to 2020.

This extension is correlated with a centroids northward shift for *M. asterias* and *R. clavata* (respectively, 0.3 km decade^{-1}; $p < .02$ and .5 km decade^{-1}; $p < .05$) as well as deepening (0.02 m decade^{-1} and 0.03 m decade^{-1}; $p < .001$) (Appendix S1—Table S9). While the depth range of *M. asterias* has narrowed, with a deeper upper limit and a shallower lower limit, *R. clavata* upper longitudinal range extends to the east (Appendix S1—Table S10). Although the habitat suitability areas for *S. canicula* and *A. radiata* have not changed in size over time (Appendix S1—Table S8), their centroids have shifted

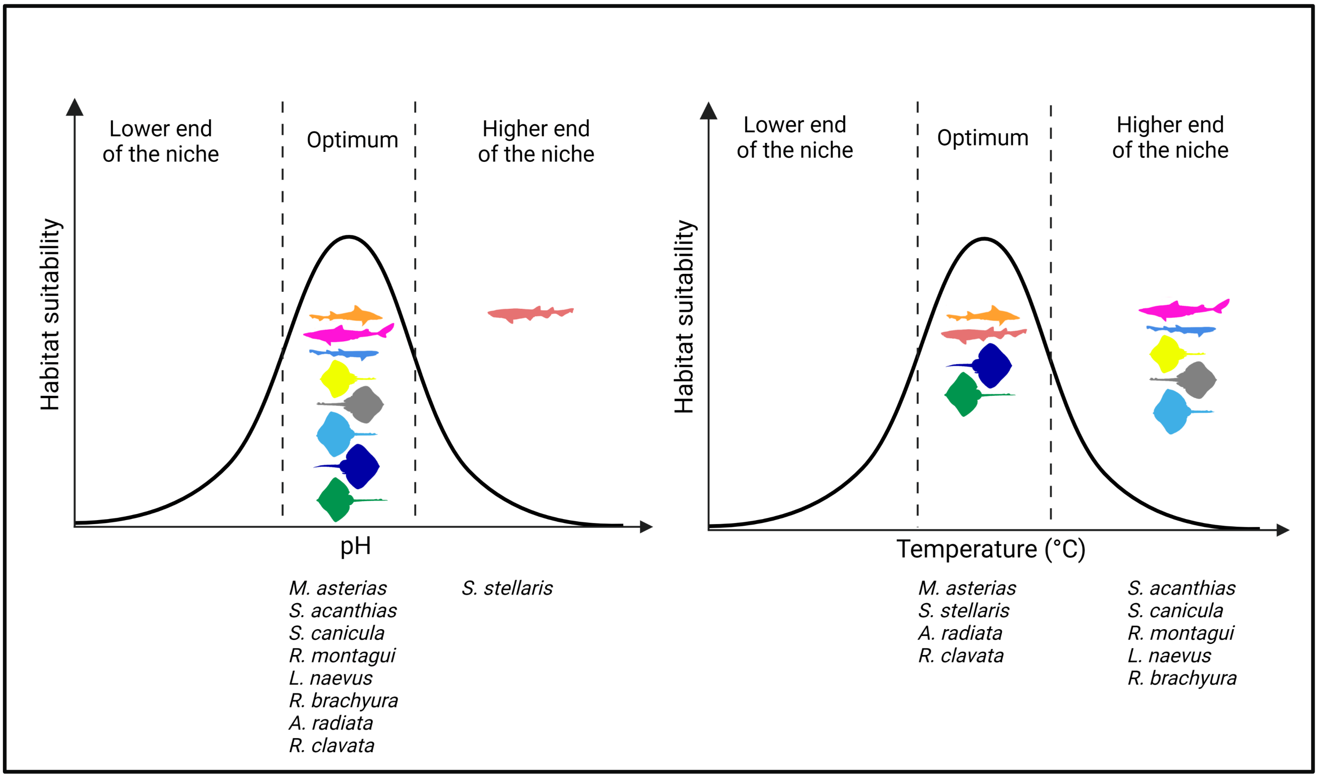

FIGURE 2 Species at the lower, optimal, or upper end of their pH and thermal niche with at least 90% posterior support for the effect of pH in the joint species distribution models between 1997 and 2020. Non-zero responses were classified as “bell-shaped,” “increasing” or “decreasing” based on the sign of the derivative of the response over the observed pH gradient. The colors refer to the different species studied. Created with BioRender.com.

northward (0.1 km decade^{-1}; $p < .01$), and in depth (0.01 m decade^{-1}; $p < .03$) for *S. canicula* and westward (0.5 km decade^{-1}; $p < .01$) for *A. radiata* (Appendix S1—Table S9). Although no change in the centroids for *R. brachyura* could be detected, the upper and lower limits of its range have shifted eastwards and extended northwards (Appendix S1—Table S10). *R. montagui* has also expanded eastwards (Appendix S1—Table S10).

L. naevus occupied the northwestern part of the study area to the North Channel (Appendix S4) and its habitat suitability decreased in the Irish Sea, English Channel, and the southern North Sea (Figure 3). *R. montagui* habitat suitability increased moderately in the Irish Sea, St. George's Channel, Scottish Sea, and around the Orkney Isles (+ 9% decade^{-1} cell^{-1}, Figure 3). *A. radiata* and *S. acanthias* are closely associated with deeper and cooler waters (50–200 m; Appendix S4) with increased habitat suitability along the Norwegian Deep (+5% and +4% decade^{-1} cell^{-1}, respectively, Figure 3), and along the continental shelf north of the British Isles and in the trough of the Firth of Clyde though. The habitat

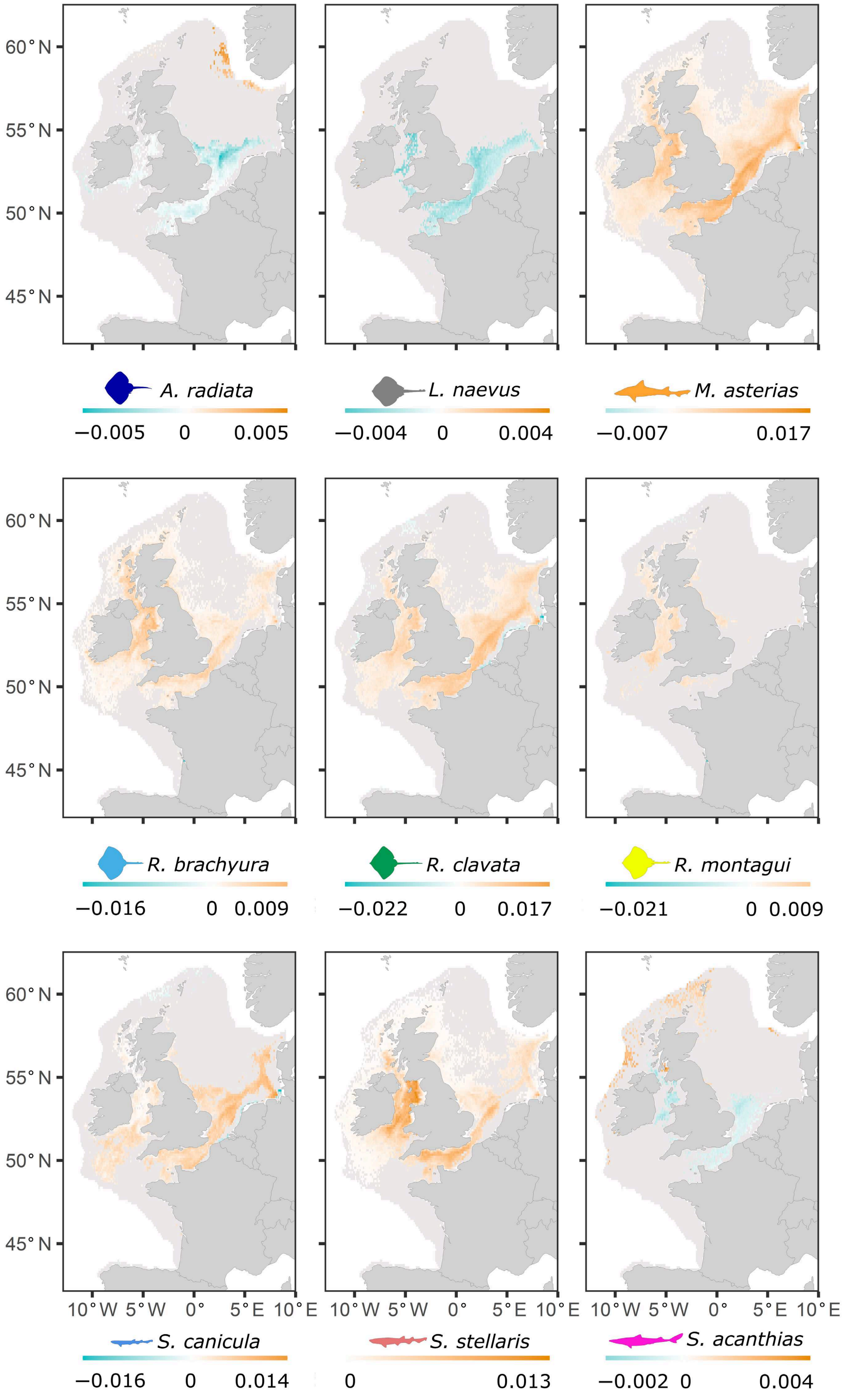

FIGURE 3 Estimates of the habitat suitability regression coefficient over time in each cell (0.111°×0.134°) based on Kendall's tau. Gray cells show no trend in the variation of the habitat suitability while orange tones indicate an increase in habitat suitability, and light blue tones a decrease ($p < .05$). Each map depicts trends for one species. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

suitability of *R. clavata* and *S. canicula* increased in the Western Channel, the southern and eastern North Sea reaching a rate of +10% and +20% decade^{-1} cell^{-1}, respectively, and to a lesser extent in the Irish Sea and the Celtic Sea (Figure 3). In contrast, the decrease in their habitat suitability is maximal along the German, Dutch, and Belgian coasts (both at a rate of −20% decade^{-1} cell^{-1}, Figure 3). Habitat suitability of *M. asterias* and *S. stellaris* has increased sharply in the Irish Sea, St George's Channel, in the southern and eastern North Sea, reaching rates of +20% decade^{-1} cell^{-1} and +10% decade^{-1} cell^{-1}, respectively (Figure 3). For *R. brachyura*, habitat suitability increased in the Irish Sea and west of Scotland up to 10% decade^{-1} cell^{-1} (Figure 3).

3.3 | Changes in species traits composition

The CWM of trophic level has decreased in the southern North Sea, especially in the Dogger Bank due to increased habitat suitability for low trophic level species (Figure 4) (e.g., *M. asterias*; Figure 3). The CWM length at maturity increased (+6 cm decade^{-1} cell^{-1}) due to an increase in the habitat suitability of late maturing species (Figure 4) (e.g., *M. asterias*, *R. brachyura*; Figure 3) and this was true up to the southern and eastern North Sea. Meanwhile, a decrease in the CWM fecundity was also detected in the Eastern English Channel, the Irish Sea and St. Georges Channel (up to −4 offsprings decade^{-1} cell^{-1}) due to an increase in the habitat suitability of low fecundity species (Figure 4) (e.g., *M. asterias*, *S. stellaris*; Figure 3). Finally, the CWM latitudinal range around the British Isles has decreased (−0.3° decade^{-1} cell^{-1}) due to an increase in the habitat suitability of species with a narrow latitudinal distribution (Figure 4) (e.g., *R. montagui*; Figure 3). In the North Sea, the British Isles, and in the western part of Celtic Sea, the CWM depth preference decreased (i.e., became shallower) by −4 m decade^{-1} cell^{-1} due to an increase in the habitat suitability of shallow water species (Figure 4; e.g., *M. asterias*, *R. clavata*; Figure 3). These changes mainly took place in areas of greater depth, which ultimately translates into a shift of shallow communities toward deeper waters.

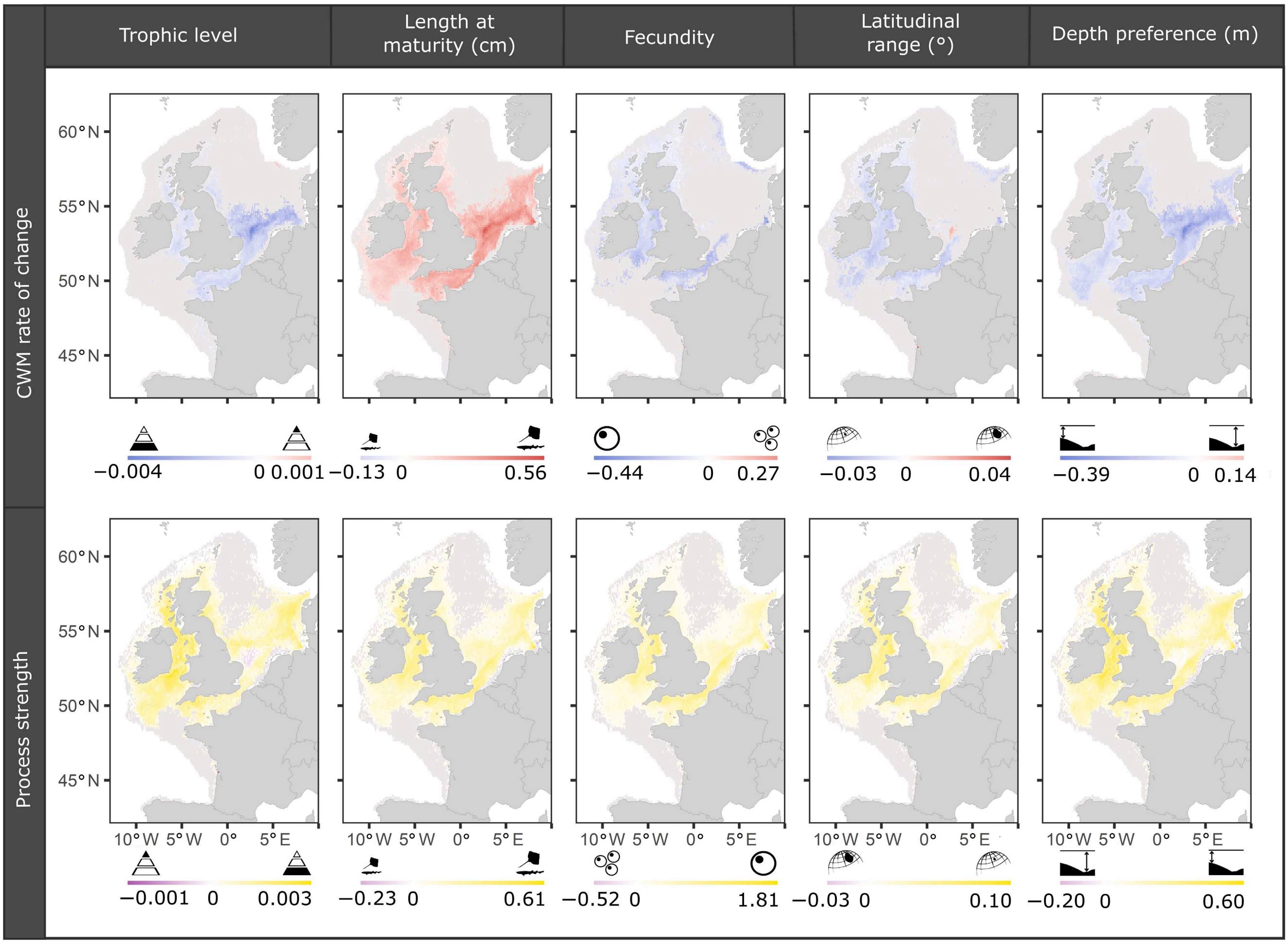

FIGURE 4 Rate of change in community-weighted mean (CWM) of trophic level, length at maturity, fecundity, latitudinal range, and depth preference for the period 1997–2020 in each cell (0.111° × 0.134°) and strengths of the processes leading to changes in the CWMs. Gray cells show no trend in the variation of the CWMs ($p > .05$). Red tones indicate a positive CWM rate of change, while dark blue tones indicate a negative. Yellow tones indicate a process with a positive force, while violet tones indicate a process with a negative force. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

4 | DISCUSSION

Despite a relatively short period of survey (1997–2020), it appears that climate change has contributed to change in elasmobranch communities in the Northeast Atlantic. Our results are analogous to similar studies conducted in the Northeast Atlantic on teleost fishes (Gordó-Vilaseca et al., 2023), cephalopods (Oesterwind et al., 2022), zooplankton (Ratnarajah et al., 2023), and diatoms (Edwards et al., 2022), demonstrating that the ongoing climate changes are affecting all marine organisms without exception. We found that, of the nine species of skates and sharks studied, five are at the upper limit of their thermal niche. Furthermore, six of the nine species experienced a change in their habitat suitability through an increase in size and/or a shift northward, eastward, or deeper. We found that the changes in the species' suitable habitat led to changes in the species trait assemblage. We detected a decrease in the mean trophic level, as well as an increase in size at maturity, correlated to a lesser extent with a decrease in fecundity. Communities have also been altered by the shift of species habitat suitability toward deeper waters. Finally, species with low latitudinal distribution experienced a shift in their suitable habitat to tight areas defined by high depths.

Although *L. naevus* and *R. montagui* were at their upper thermal limit, there was no change in their habitat suitability areas over time, despite the measured sea warming. Since *L. naevus* occupied the northwestern part of the European sea shelf and its habitat suitability decreased with increasing temperature, it is therefore questionable whether the species is currently undergoing a shift or whether the study area is not suitable for detection, knowing *L. naevus* has previously undergone deep-sea shifts in response to warming (Perry et al., 2005; Poulard & Blanchard, 2005). This dataset covers the European continental shelf and is not representative of the time series available worldwide (Maureaud et al., 2021). This raises concerns about the ability to monitor deep-sea and offshore species and justifies the need to adopt a precautionary approach to the exploitation of the ecosystems in which they depend (e.g., deep-sea mining and offshore fishing).

Within more coastal areas, we detected increased habitat suitability of *R. montagui* off the Humber Estuary and Start Bay but not throughout the Greater North Sea (Ellis et al., 2004; Sguotti et al., 2016). It could be hypothesized that although remaining adults could currently withstand the environmental conditions faced in estuaries (Ashcroft, 2010), eggs and juveniles may not have the same ability (Di Santo, 2015; Elliott, Bearup, et al., 2020; Musa et al., 2020; Rosa et al., 2014), thereby impeding the recolonization process that has been underway since the 1990s (Amelot et al., 2021). This also highlights the importance of long-term monitoring of spawning and nursery sites (Kinney & Simpfendorfer, 2009; McLean et al., 2018).

We show that *A. radiata* and *S. acanthias* are closely associated with deeper and cooler waters. While their habitat suitability at the southern edge of their distribution decreased, it increased in the north and on the continental slope. Although *A. radiata* shift was expected because it is already at the edge of its distribution (Ellis et al., 2004; Sguotti et al., 2016; Townhill et al., 2023), changes in the habitat suitability of *S. acanthias* were not expected (Ellis et al., 2004), suggesting a greater sensitivity to temperature increased and potential concomitant factors that have led to a sharp decline in its abundance since 1980 in the southern North Sea (Murgier et al., 2021; Sguotti et al., 2016). Continental slope can currently provide a climate change refuge for these species (Ashcroft, 2010; Morelli et al., 2016), but it is a restricted habitat and the dispersal capacity and population dynamics of these species limit their ability to adapt and colonize new potentially suitable areas.

The habitat suitability of *S. canicula* and *R. clavata* increased in the western English Channel, southern and eastern North Sea while it decreased along the German, Dutch, and Belgian coasts. We depicted the continuous northward shift pattern of *S. canicula* previously stated in several studies (Ellis et al., 2004; Rindorf et al., 2020; Sguotti et al., 2016; Townhill et al., 2023), coupled with a shift in depth. Before population depletion in the 1990s (Amelot et al., 2021), *R. clavata* was historically widespread around the British Isles (Ellis et al., 2004) and across the southern North Sea (Sguotti et al., 2016). After the 2000s, abundance increased in the North Sea (Rindorf et al., 2020) and in the eastern English Channel (Elliott, Bearup, et al., 2020), particularly with the fisheries ban on Undulate Ray (*Raja undulata*; 2009–2015), since *R. undulata* has a similar niche as *R. clavata* (Elliott, Bearup, et al., 2020; Elliott, Carpentier, et al., 2020). Therefore, while the decrease in the *R. clavata* habitat suitability could be mostly attributed to environmental changes, its increase could be attributed both to the current suitable environmental conditions and to the beneficial effects of *R. undulata* fishery regulation (Elliott, Bearup, et al., 2020).

Concerning *M. asterias*, the pH is the first factor explaining the variance in its occurrence. The direct effect of acidification on elasmobranchs is limited to oviparous species (Rummer et al., 2022) with the exception of the Blacktip Reef Shark (*Carcharhinus melanopterus*) neonates (Bouyoucos et al., 2020; Bouyoucos & Rummer, 2020; Rummer et al., 2020). Because experimental studies are limited by available facilities, we propose studying in situ behavior (e.g., foraging, activity levels) or physiological (e.g., hematology, metabolic rates, hypoxia tolerance) responses of viviparous sharks with a wide distribution (e.g., *C. melanopterus*), including areas where seawater is naturally more acidic due to volcanic carbon dioxide vents (e.g., coral studies, Comeau et al., 2022; Hall-Spencer et al., 2008). We also stress the need to consider the indirect effects caused by the increased sensitivity of calcifying benthic invertebrates on which benthivorous species such as *M. asterias* depend (Ellis et al., 1996; Marshall et al., 2017), whose habitat has greatly increased toward the northeast of the North Sea. While there were limited historical records of *Mustelus* spp. in the southern North Sea until the 1980s (Ellis et al., 2004), their abundance then increased exponentially after 2000 in close relation to warming surface (Rindorf et al., 2020).

Finally, we showed an increase in the habitat suitability of *S. stellaris*. This trend can reflect the potential increase in the abundance of *S. stellaris* as reported by Rindorf et al. (2020) and ICES (2022) but can also be attributed to improved identification of *S. stellaris* in scientific surveys, as suggested by the increase in landings that is mainly due to the improved species identification in fish markets in recent years (ICES, 2022). We therefore insist on eliminating misidentifications that may currently limit studying the responses of some species that look similar but have very different species traits (e.g., *Dipturus* spp. complex; Iglésias et al., 2010), and the need to be very careful with species identification when working with time series. *S. stellaris* trend can also be explained by the colonization of the southwestern part of the North Sea at depths of 20–50 m while it was very rare from 1967 to 2002 (Ellis et al., 2004). We found that *R. brachyura* was at the upper limit of its thermal niche, with habitat suitability increasing northward. Therefore, the contraction of its habitat to the south could be expected in the future.

Since we detected a decrease in the trophic level of the elasmobranch communities, which includes some of the highest trophic level species in the Northeast Atlantic (Coulon et al., 2023), food web dynamics under environmental change, from primary producers to top predators, should be investigated to detect potential food web imbalances (Albouy et al., 2014; Halouani et al., 2016; Nagelkerken et al., 2020; Sagarese et al., 2017). Similarly, the community deepening, a direct response to climate change (Dulvy et al., 2008; Punzón et al., 2016), may have altered ecosystem functioning, particularly in the southern North Sea (Murgier et al., 2021) and Celtic Sea. We also noted that species redistribution may currently be limited by depths beyond 50 m in the North Sea due to recruitment failure (Nicolas et al., 2014). Although linear trends are currently being observed, a threshold could be expected, with an abrupt change in community composition (Couce et al., 2020; Monaco & Helmuth, 2011; Townhill et al., 2023). Concerning life-history traits, we found an increase in size at maturity associated, to a lesser extent, with a decrease in fecundity. While in the Irish Sea, this is mainly attributed to the increased habitat suitability of *S. stellaris*, which is also the main species that led to the decrease in the mean latitudinal range of the communities, the dynamics are less clear in the Celtic and North Sea, where we can however reasonably attribute a strong effect of the presence of *M. asterias*. Since elasmobranchs have a slower pace of life compared to most teleost fishes, large-bodied endemic species (e.g., *D. intermedius*, Garbett et al., 2023) are even more vulnerable to climate change (Jones & Cheung, 2018). Nonetheless, some species such as *M. asterias* may currently benefit from ongoing changes (Sguotti et al., 2016). Furthermore, we cannot exclude a time lag between observed climate changes and their effects on communities, given their long lifespan and slow population turnover (Thompson & Ollason, 2001). As a result, a decline could occur in the decades to come, notably due to a failure of reproduction or recruitment.

The trends currently observed could be found in sympatric species and/or species sharing common traits (Barnett et al., 2019; Coulon et al., 2023), especially endangered species. This means that species found along the continental shelf, such as the Sandy Ray (*Leucoraja circularis*) and the Shagreen Ray (*Leucoraja fullonica*), can respond at least as much as *L. naevus* and therefore deserve special conservation attention. Similarly, it is reasonable to argue that coastal species such as the Small-eyed Ray (*R. microocellata*) and *R. undulata* have also been impacted by ongoing climate change in some way because of their lower ecological versatility than most of the species studied. It would be interesting to study a larger number of species, including teleost fishes with numerous and diverse traits, to identify the most sensitive combinations of traits to climate change. This will allow us to focus our conservation efforts without the need for individual species assessments.

We chose pH and temperature to study changes in habitat suitability over time. Additional drivers likely to be affected by climate forcing (e.g., dissolved oxygen) were not included in the model because they were highly correlated with temperature and/or depth. We acknowledge that they may have concomitantly contributed to the modification of species habitat suitability. For example, some studies showed that dissolved oxygen could influence the distribution of elasmobranchs over small spatial and temporal scales (Carlisle & Starr, 2009; Coffey et al., 2017; Drymon et al., 2013) and be responsible for increased mortality in the *S. canicula* embryos (Musa et al., 2020). Furthermore, we focused on maximum temperatures in summer because we were concerned with the upper limit of the species' thermal niche. However, losses of suitable habitat in summer could potentially be offset by gains in suitable habitat in winter and/or spring. These environmental changes are likely to cause phenological changes (e.g., in spawning periods, Rogers & Dougherty, 2019). For migratory species (e.g., *Mustelus asterias*), modifications in spatial sex differentiation during circannual migration could also be expected (Brevé et al., 2016, 2020).

We emphasize caution, since although the habitat suitability of species is related to the environmental parameters, it is not synonymous with presence probability. Changes in presence probability may be constrained by changes in environmental conditions but also by biotic interactions (Elliot et al., 2016; Preston et al., 2008), such as prey availability (Aebischer et al., 1990; Frederiksen et al., 2006). While we can consciously consider that interspecific relationships have been intrinsically taken into account where sampling has been conducted, we cannot reject that they may limit the probability of species presence where sampling has not. Fishing activity is also one of the main concerns in the Northeast Atlantic (Pimiento et al., 2023; Walker et al., 2019). In the Greater North Sea, the three main landed Rajidae species are *R. clavata*, *L. naevus*, and *R. montagui* (Amelot et al., 2021); hence, we cannot neglect an effect of fishing that we could not test in this study given the temporal range and spatial resolution of the fishing data available. Furthermore, our study did not test the possible degradation of essential habitats due to human pressures (e.g., the effect of bottom trawling on the productivity of marine fish; Collie et al., 2017). We can only stress the potential concomitant effects of climate change, fishing and habitat degradation. It is crucial to consider this new factor when implementing management measures, knowing species' sensitivity to both overfishing and climate change is higher at their range boundaries (Fredston-Hermann et al., 2020; Predragovic et al., 2023; Yan et al., 2021).

Long neglected in environmental matters, a growing number of studies, including this one, tend to demonstrate the vulnerability of elasmobranchs to climate change in addition to their vulnerability to anthropogenic pressures. As they are keystone species for ecosystem functioning, it is urgent to review our operating modes, from our habits to the management measures in place. These changes would then allow the necessary rebound of elasmobranchs to converge toward more resilient ecosystems.

AUTHOR CONTRIBUTIONS

Noémie Coulon: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft. **Sophie Elliott:** Conceptualization; methodology; supervision; validation; writing – original draft. **Nils Teichert:** Conceptualization; methodology; supervision; validation; writing – review and editing. **Arnaud Auber:** Methodology; resources; validation; writing – review and editing. **Matthew McLean:** Methodology; software; validation; writing – review and editing. **Thomas Barreau:** Methodology; resources; validation; writing – review and editing. **Eric Feunteun:** Funding acquisition; project administration; supervision; validation; writing – review and editing. **Alexandre Carpentier:** Conceptualization; funding acquisition; project administration; supervision; validation; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The abundance data that support the findings of this study are openly available on the ICES Database of Bottom Trawl Surveys (DATRAS) at https://datras.ices.dk. Species traits were collected by extracting traits values from Coulon et al. (2023) openly available on https://doi.org/10.6084/m9.figshare.19833304.v1 and using occurrence data from Ocean Biodiversity Information System (OBIS, 2022) openly available on https://obis.org/. Depth and slope data are openly available on the GEBCO Bathymetric Compilation Group 2019 (2019). The GEBCO_2019 Grid—a continuous terrain model of the global oceans and land. British Oceanographic Data Centre, National Oceanography Centre, NERC, United Kingdom (doi: 10.5285/836f016a-33be-6ddc-e053-6c86abc0788e). The relief and complexity data are openly available on MARSPEC: ocean climate layers for marine spatial ecology. https://doi.org/10.1890/12-1358.1. Seabed habitat data are openly available on European Marine Observation Data Network (EMODnet) (https://emodnet.ec.europa.eu/en/seabed-habitats). The pH and temperature data are openly available on E.U. Copernicus Marine Service Information (https://doi.org/10.48670/moi-00058; https://doi.org/10.48670/moi-00059). The Atlantic Multidecadal Oscillation data are openly available on the NOAA PSL (https://www.psl.noaa.gov/data/timeseries/AMO/). Phylogeny subset is openly available on the Global Phylogeny of Sharks (https://vertlife.org/sharktree/). The R code used for this study is openly available on https://github.com/ncoulon9/Coulon-et-al.-2024.

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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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III- Conclusion

Bien que la période d'étude soit relativement courte (1997-2020), elle suffit à montrer la sensibilité des assemblages d'élasmobranches dans l'Atlantique Nord-Est au changement climatique. Parmi les neuf espèces de raies et de requins analysées, cinq se trouvent désormais à la limite supérieure de leur niche thermique observée dans la zone d’étude. De plus, six de ces espèces ont vu l'adéquation de leur habitat se modifier, avec une augmentation de leur aire de distribution, un déplacement vers le nord ou l'est, ou une migration vers des eaux plus profondes, parfois très étroites comme le plateau des Hébrides ou la fosse norvégienne. Ces changements d'habitat ont entraîné des altérations notables dans l'assemblage des traits bio-écologiques des espèces. Nous avons observé une diminution du niveau trophique moyen des assemblages, associée à une augmentation de la taille à maturité des espèces, et, dans une moindre mesure, à une diminution de leur fécondité.

Dans le premier chapitre de cette thèse, nous avons également mis en évidence une diminution de l'adéquation des habitats estivaux, notamment le long des côtes belges, néerlandaises et allemandes. Bien que ces changements environnementaux puissent entraîner des modifications phénologiques, comme un décalage des périodes de frai, d'autres contraintes biotiques et abiotiques pourraient limiter ces ajustements, forçant ainsi les espèces à pondre dans des habitats inadaptés. Par conséquent, dans le deuxième chapitre de cette thèse, nous nous concentrons sur l'impact de l'élévation des températures et de l'acidification sur le développement embryonnaire des espèces ovipares, qui comprennent 7 des 59 espèces de requins et l'intégralité des Rajiformes (25 espèces) présents dans les eaux de France métropolitaine (Bisch et al., 2024). Contrairement aux espèces vivipares, dont les embryons bénéficient de la protection de la matrice maternelle, les espèces ovipares déposent leurs œufs dans des environnements où les embryons sont directement exposés aux conditions environnementales. Cette exposition directe rend les embryons ovipares particulièrement vulnérables aux variations de température et d'acidité, ce qui peut avoir des répercussions significatives sur leur développement et, par conséquent, sur la survie des jeunes individus.

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CHAPITRE 2 : Vulnérabilité des embryons et juvéniles de petite roussette aux variations mensuelles de température dans le contexte du changement climatique

I- Illustration du dispositif expérimental

1. La petite roussette : une espèce modèle

La petite roussette (*Scyliorhinus canicula*) est un requin de petite taille appartenant à la famille des Scyliorhinidae et à l'ordre des Carcharhiniformes. Elle est largement répandue et abondante dans l'Atlantique Nord-Est, des côtes norvégiennes jusqu'aux îles Canaries, et occupe principalement des habitats démersaux sur les plateaux continentaux et les pentes, pouvant descendre jusqu'à 800 m de profondeur. Cette espèce montre une grande tolérance écologique, s'adaptant à une variété d'environnements, tant en termes de profondeur que de température et de salinité. La petite roussette est ovipare, les femelles pondent des œufs qui sont ancrés aux macroalgues, aux herbiers ou aux invertébrés sessiles érigés tels que les porifères et les bryozoaires, ou bien encore à des infrastructures artificielles comme les pontons ou les cordages. La période de ponte s'étend tout au long de l'année, avec un pic durant les mois de juin et juillet (Ellis et Shackley, 1997). La fécondité des femelles dans l'Atlantique Nord-Est varie de 29 à 62 œufs par an, un taux relativement élevé pour une espèce de requin, ce qui peut contribuer à sa résilience dans des environnements soumis à des pressions anthropiques. Son cycle de vie relativement long, sa maturité sexuelle relativement tardive et son rôle dans les écosystèmes benthiques en font un modèle d'étude clé dans le contexte des recherches sur les effets des changements climatiques et des perturbations environnementales sur les élasmobranches ovipares.

La petite roussette peut être maintenue en captivité dans des infrastructures spécialisées, disponibles dans plusieurs stations marines et aquariums à travers l'Europe, comme la Station Biologique de Roscoff et l'Aquarium Marin de Trégastel. Cependant, malgré ces infrastructures, la durée relativement longue du cycle de vie de cette espèce limite la possibilité de contrôler son cycle de vie en laboratoire. Il n'existe pas encore de programmes d'élevage à long terme pour la petite roussette. Ainsi, l'obtention d'embryons à des fins de recherche repose majoritairement sur la capture de reproducteurs dans les populations sauvages, qui sont ensuite maintenus en captivité pour la ponte.

2. Infrastructure et conditions expérimentales

La Station marine du Muséum national d'histoire naturelle à Dinard dispose d'une plateforme dédiée à l'expérimentation animale sur les poissons. Cette infrastructure comprend une salle photo-thermorégulée, où se sont déroulées les expérimentations de cette thèse sur une période de 10 mois. Cette salle est équipée de neuf aquariums, chacun doté de son propre système de filtration, de thermorégulation, et de contrôle du pH (Figure 15).

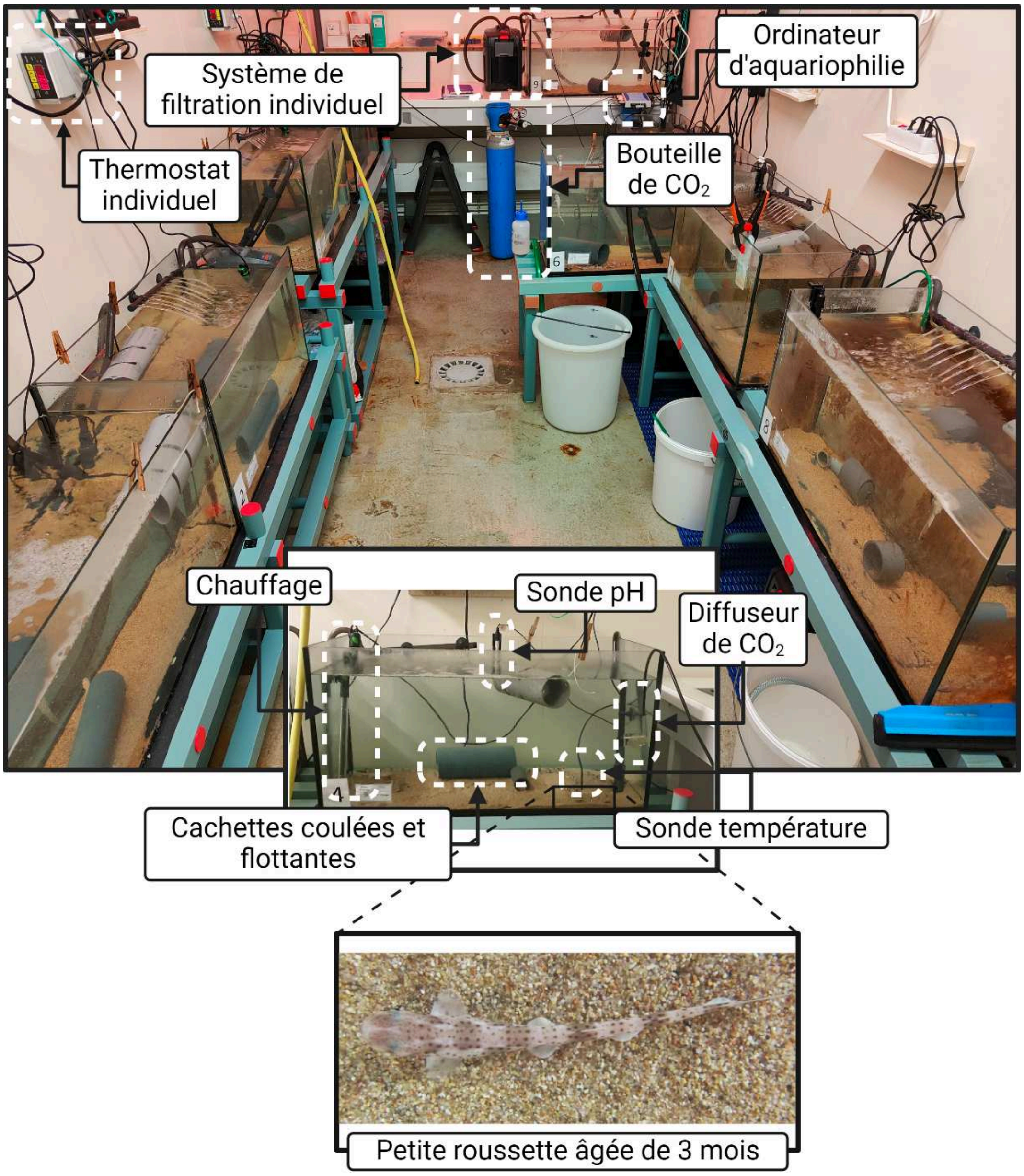

Figure 15 : Photographie de la salle expérimentale photo-thermorégulée et de ses différents équipements. Créée avec Biorender.com

Le contrôle de la température et du pH a permis d'exposer les embryons de petite roussette à trois conditions expérimentales distinctes : les conditions climatiques observées historiquement entre 1995 et 2014 pour l'Europe occidentale et centrale, ainsi que les conditions potentielles pour 2100 selon deux scénarios de changements socio-économiques mondiaux, tels que définis dans le sixième rapport d'évaluation du GIEC et téléchargés à partir de http://interactive-atlas.ipcc.ch (Gutiérrez et al., 2021 ; Iturbide et al., 2021).

Les scénarios communément appelés *Shared Socioeconomic Pathways* (SSP) sont des narratifs traduits en hypothèses socio-économiques décrivant les trajectoires possibles des sociétés futures (Figure 16). Les scénarios SSP1 et SSP5 offrent des visions relativement optimistes pour le développement humain, avec des investissements significatifs dans l'éducation et la santé, une croissance économique rapide et des institutions efficaces. Cependant, leur distinction principale réside dans leurs orientations : le SSP1 repose sur une transition vers des pratiques durables, tandis que le SSP5 s'appuie sur une économie très énergétivore et fortement dépendante des combustibles fossiles. À l'opposé, les SSP3 et SSP4 présentent des perspectives bien plus pessimistes. Le SSP3 envisage un monde fragmenté, où les pays privilégient leur sécurité régionale au détriment de la coopération internationale. Le SSP4, lui, met en avant des inégalités marquées à la fois au sein des pays et entre eux, rendant ces sociétés particulièrement vulnérables face au changement climatique. Entre ces extrêmes, le SSP2 propose une trajectoire intermédiaire, où les tendances actuelles se prolongent sans changements majeurs. Le GIEC a évalué la réponse du climat à cinq scénarios socio-économiques : deux avec des émissions de GES élevées (SSP3-7.0 et SSP5-8.5), un scénario intermédiaire (SSP2-4.5), et deux avec des émissions faibles à très faibles (SSP1-1.9 et SSP1-2.6). Nous n'avons pas retenu le SSP4, car il n'était pas utilisé pour les projections climatiques, ni les scénarios SSP1-1.9 et SSP1-2.6, qui supposaient un respect des accords de Paris, une hypothèse déjà jugée improbable en 2021. Finalement, nous avons sélectionné deux scénarios suffisamment contrastés, permettant de couvrir une large gamme de réponses aux changements environnementaux :

- Le **SSP2** « Middle of the road » représente un monde où les tendances sociales, économiques et technologiques suivent des modèles historiques, avec une croissance inégale entre les pays et des progrès lents vers les objectifs de développement durable. Les émissions de CO_2 restent stables jusqu'en 2050 avant de diminuer, sans toutefois atteindre la neutralité carbone d'ici 2100 (Fricko et al., 2017 ; scénario SSP2-4.5).

- Le **SSP5** « Fossil-fuelled Development » envisage un monde axé sur les marchés compétitifs, l'innovation, et un développement rapide du capital humain, soutenu par une exploitation intensive des combustibles fossiles. Cela entraîne une forte croissance économique mondiale, mais aussi un triplement des émissions de CO_2 d'ici 2075 (Kriegler et al., 2017 ; scénario SSP5-8.5).

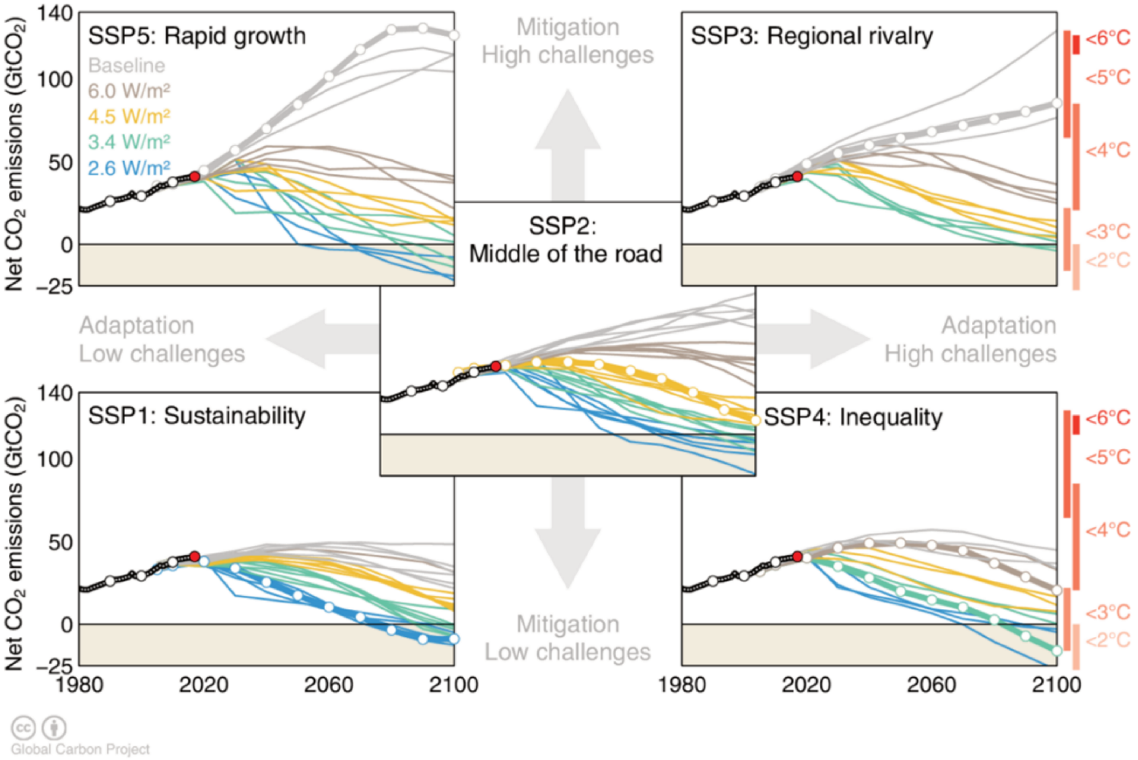

Figure 16 : Émissions globales de CO_2 séparées par SSP (Shared Socioeconomic Pathways). Graphique réalisé par Glen Peters, Robbie Andrews et le Global Carbon Project.

3. Suivi individuel des embryons

Le suivi embryonnaire sur plusieurs mois d'une espèce de grande taille, dans le cadre de scénarios de changement climatique, présente un certain nombre de contraintes. Elles découlent d'un nombre restreint de sujets expérimentaux et d'une variance accrue en raison des variations interindividuelles marquées (Araujo et Frøyland, 2005). Ces difficultés ont cependant encouragé le développement de nouvelles approches, alliant l'analyse des réponses à l'échelle des groupes expérimentaux à celle des réponses individuelles face au changement climatique.

Les 125 embryons de petite roussette ont été identifiés individuellement (date de ponte connue à un jour près) et intégrés au dispositif expérimental à la 4^{e} semaine après la ponte, une fois qu'il était possible de confirmer la fécondation des œufs. Par la suite, un suivi hebdomadaire individualisé de la croissance a été effectué. Chaque œuf a été transféré dans un support étroit et transparent, conçu pour le maintenir en position verticale tout en assurant une immersion constante. L'observation de l'intérieur des capsules a été facilitée par la technique de *candling*, qui utilise un éclairage à haute intensité pour permettre une observation par transparence (Figure 17a). Chaque œuf a été photographié pour mesurer la surface du vitellus et la longueur totale de l'embryon. Ces mesures ont été réalisées à l'aide du logiciel TPSDig, spécialisé dans la morphométrie géométrique (Rohlf, 2015 ; Figure 17b ; c). Pour garantir la précision et la cohérence des mesures, le même nombre de points de référence a été utilisé à chaque fois. Cela assure que toutes les mesures sont effectuées avec une précision constante, indépendamment du positionnement de l'embryon. Les mesures de longueur totale ont permis de calculer des taux de croissance ($cm.semaine^{-1}$) de consommation du vitellus ($cm^2.semaine^{-1}$). Les sept stades embryonnaires décrits par Musa et al. (2018) ont également été identifiés à partir des photographies (Figure 18) ; Tableau 3).

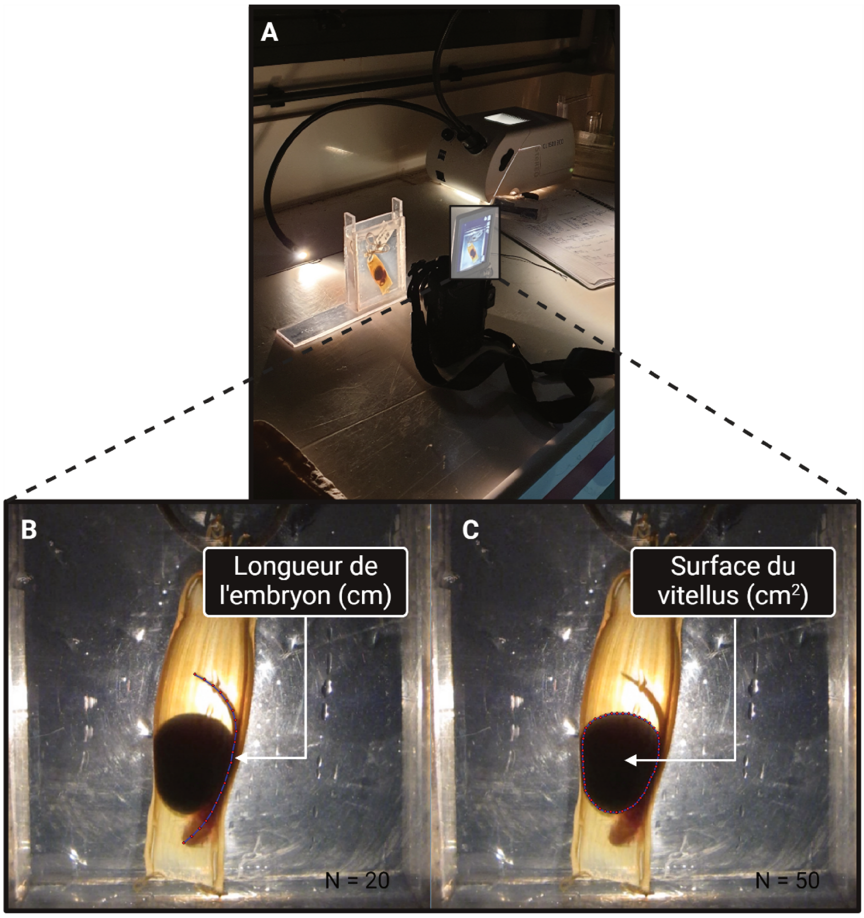

Figure 17 : Photographie hebdomadaire des embryons. A. Dispositif de prise de vue. Mesure de B. la longueur et C. la surface du vitellus d'un embryon à l'aide du logiciel TPSDig (Rohlf, 2015). Créée avec Biorender.com

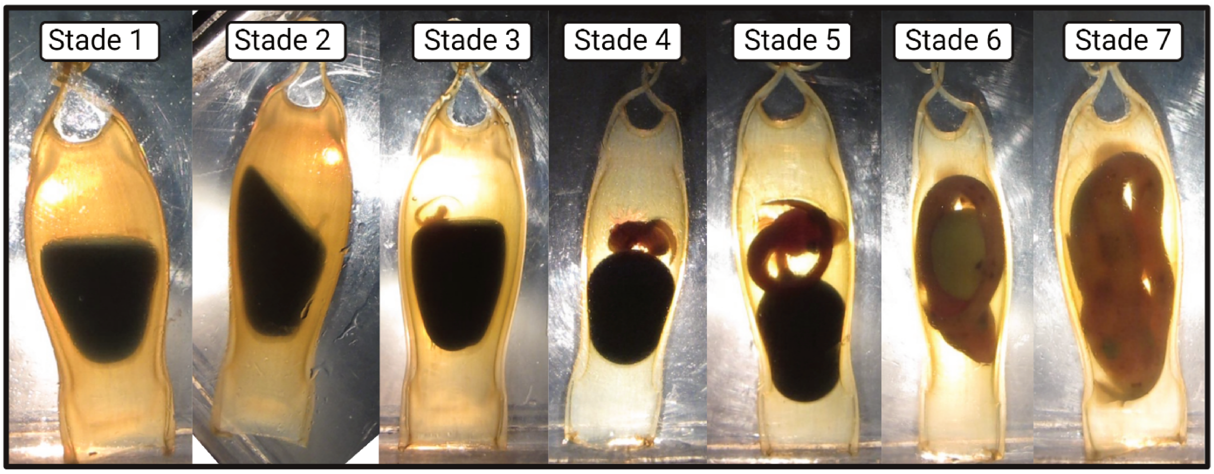

Figure 18 : Photographies des sept stades embryonnaires chez la petite roussette. Voir Tableau 3 pour la description des stades identifiés par Musa et al. (2018) à 16°C. Créée avec Biorender.com

Tableau 3 : Synthèse des 7 stades de développement embryonnaire identifiés par Musa et al. (2018) à 16°C

Stade de développement	Caractéristique clef	Age (semaines)	Longueur du corps (cm)	Taux de consommation du vitellus (%)
1	Pas d'embryon visible	0		0
2	Embryon précocement formé	3	0,62 ± 0,2	0
3	Développement d'une longue queue	4,25 ± 0.46	1,17 ± 0,16	0
4	Développement externe des filaments branchiaux	7 ± 0.53	2,47 ± 0,21	< 22,21 ± 5,42
5	Internalisation des filaments branchiaux	14,13 ± 0,64	6 ± 0,67	< 34,22 ± 7,23
6	Séparation des nageoires	16,25 ± 0,46	8,84 ± 0,91	< 98,35 ± 0,89
7	Vitellus entièrement consommé	21,38 ± 0,74	10,3 ± 0,42	100

En complément du suivi individuel de la croissance, nous avons mesuré la durée du comportement de *freezing* (immobilisation totale, y compris de la respiration), un mécanisme évitant que les embryons soient repérés par les prédateurs (Kempster et al., 2013 ; Ripley et al., 2021). Une fois les embryons parvenus au stade de développement 7, où les échanges d'eau entre la capsule et le milieu environnant sont mesurables, nous avons chronométré la durée du *freezing* depuis leur manipulation dans l'aquarium jusqu'à la reprise de l'activité respiratoire (Ripley et al., 2021). Chaque œuf a été placé dans une chambre de respirométrie en verre de 120 mL, remplie d'eau provenant de son aquarium d'origine. La saturation en oxygène a été mesurée à l'aide d'un mini capteur d'oxygène muni d'une sonde à immersion, connecté à un oxymètre Witrox 4 (LoligoSystems). Ce dispositif est également équipé d'une sonde de température, permettant d'ajuster automatiquement les mesures de saturation en fonction de la température de l'eau (Figure 19). Les embryons ont été maintenus dans la chambre de respirométrie jusqu'à ce que le taux de changement de saturation en oxygène puisse être calculé, tout en veillant à ce que la saturation reste toujours supérieure à 80%, soit pendant environ 15 à 20 minutes (Svendsen et al., 2016).

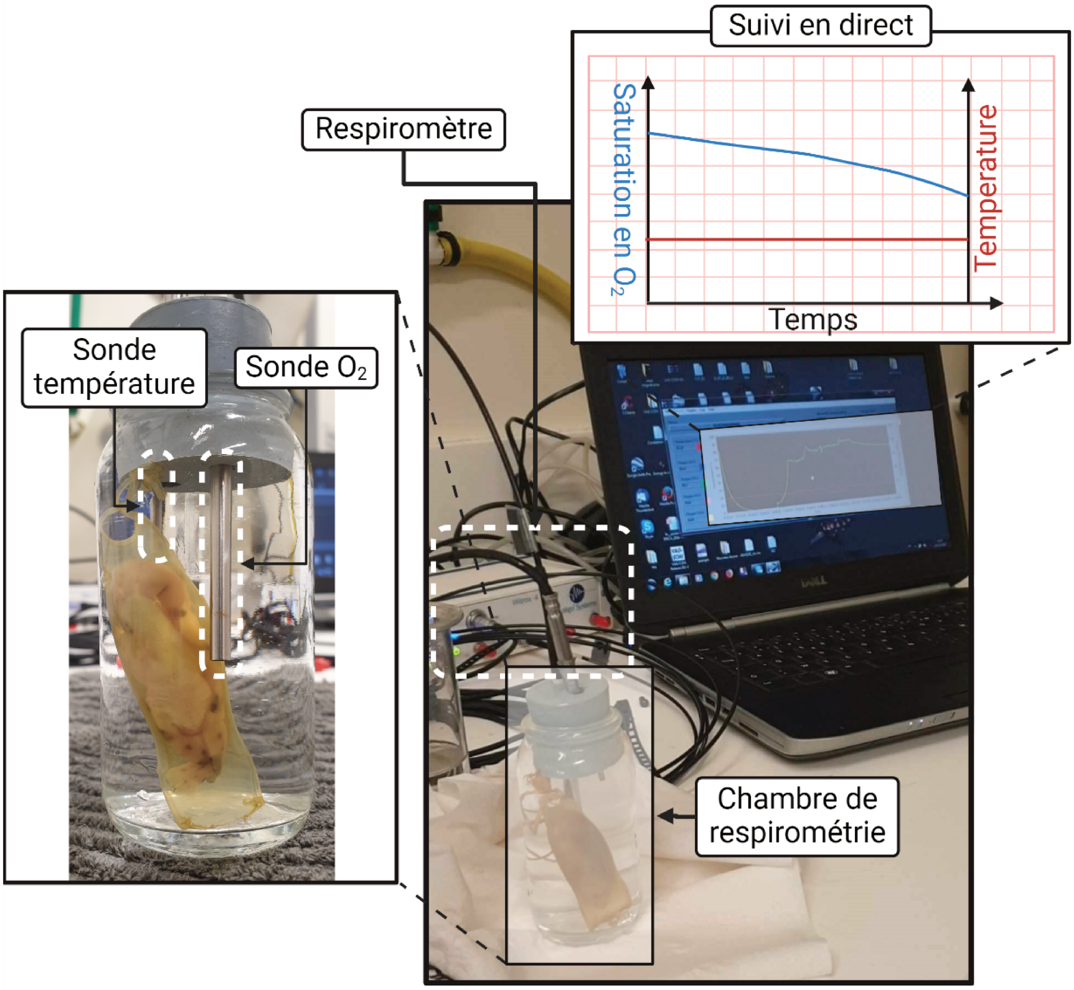

Figure 19 : Photographie de la mesure du taux de consommation d'O_2 chez un embryon de petite roussette par respirométrie statique. Créée avec Biorender.com

À l'éclosion, puis mensuellement par la suite, les individus ont été mesurés et pesés (Figure 20). Nous avons suivi individuellement le développement des embryons jusqu'à leur éclosion, car la variation interindividuelle à ce stade est généralement significative (par exemple, lors d'un échec du développement). Au stade juvénile, nous avons opté pour un suivi à l'échelle des groupes expérimentaux (les données des juvéniles étant regroupées par aquarium) en partant de l'hypothèse que la variation de croissance serait plus homogène au sein des juvéniles d'un même aquarium comparé à celle observée entre différents aquariums. Cette approche a également été dictée par des considérations éthiques, notamment la réticence à marquer individuellement les juvéniles ou à recourir à un suivi photographique hebdomadaire nécessitant une anesthésie répétée. En effet, les juvéniles sont particulièrement fragiles et le risque de mortalité lié à la manipulation a été jugé plus élevé que celui associé aux conditions expérimentales.

Figure 20 : Photographie de la biométrie de la petite roussette. A. Mesure de la longueur totale d’un nouveau-né. B. Mesure de la masse d’un individu de 2 mois. C. Mesure de la longueur totale d'un individu de 2 mois.

L’ensemble de ces mesures est utilisé pour explorer l'impact du réchauffement et de l'acidification des océans sur le développement embryonnaire et les juvéniles de la petite roussette.

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II- Shark critical life stage vulnerability to monthly temperature variations under climate change

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Résumé : Dans une étude expérimentale de 10 mois, nous avons évalué l'impact combiné du réchauffement et de l'acidification sur les stades critiques du développement de la petite roussette (*Scyliorhinus canicula*). En utilisant des approches statistiques récemment développées, nous avons démêlé les réponses des individus et des groupes expérimentaux à deux scénarios climatiques projetés pour 2100 (SSP2-4.5 : Middle of the road et SSP5-8.5 : Fossil-fuelled Development). Les simulations des fluctuations saisonnières de la température ont révélé la vulnérabilité aiguë des embryons aux températures estivales, avec un succès d'éclosion allant de 82 % pour le contrôle et les traitements SSP2-4.5 à seulement 11 % pour le traitement SSP5-8.5. La mort des embryons a été précédée de trajectoires de croissance individuelles distinctes entre les traitements, et a également révélé des variations interindividuelles au sein des traitements. Les embryons ayant le plus faible taux d'éclosion avaient des taux de consommation de vitellus plus faibles, et des taux de croissance associés à une assimilation d'énergie plus faible, et presque tous n'ont pas réussi à internaliser leurs branchies. Dans les 6 mois suivant l'éclosion, aucune mortalité supplémentaire n'a été observée, probablement en raison des températures plus fraîches.

Mots clés : acidification ; élasmobranches ; embryons ; réchauffement global ; scénarios du GIEC ; succès d'éclosion ; traits bio-écologiques

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Shark critical life stage vulnerability to monthly temperature variations under climate change

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ABSTRACT

In a 10-month experimental study, we assessed the combined impact of warming and acidification on critical life stages of small-spotted catshark (*Scyliorhinus canicula*). Using recently developed frameworks, we disentangled individual and group responses to two climate scenarios projected for 2100 (SSP2-4.5: Middle of the road and SSP5-8.5: Fossil-fueled Development). Seasonal temperature fluctuations revealed the acute vulnerability of embryos to summer temperatures, with hatching success ranging from 82% for the control and SSP2-4.5 treatments to only 11% for the SSP5-8.5 treatment. The death of embryos was preceded by distinct individual growth trajectories between the treatments, and also revealed inter-individual variations within treatments. Embryos with the lowest hatching success had lower yolk consumption rates, and growth rates associated with a lower energy assimilation, and almost all of them failed to transition to internal gills. Within 6 months after hatching, no additional mortality was observed due to cooler temperatures.

1. Introduction

Climate change is predicted to have unprecedented impacts at all levels of marine fish biological organisation (Pörtner and Peck, 2010). These impacts starts with the alteration of gene expression, such as protons pumps (Bunse et al., 2016) or heat shock proteins, and catalysts for lipid synthesis (Bernal et al., 2020). Additionally, whole-organism responses, including growth and fecundity are also affected (Neuheimer et al., 2011; Crozier and Hutchings, 2014; Butzin and Pörtner, 2016; Foo and Byrne, 2017; Huang et al., 2021), ultimately impacting population (Neer et al., 2007) and ecosystem (Morell et al., 2023) dynamics. While temperature has a direct thermodynamic effect on biochemical reaction rates (Alfonso et al., 2021; Little et al., 2020), ocean acidification can lead to acid-base disturbance affecting multiple physiological systems including mineralization process and neurological functions (Munday et al., 2009; Heuer and Grosell, 2014; Cattano et al., 2018) with possible combining effects with temperature (Domenici et al., 2014; Laubenstein et al., 2018).

Since the 2010's, studies have revealed mixed effects of ocean warming and acidification on biochemical, physiological and behavioural aspects of oviparous elasmobranchs, ranging from no response to lethal ones (Wheeler et al., 2021; Santos et al., 2021). These studies revealed intra- and interspecific variations on survival, development, metabolism (Rosa et al., 2014; Musa et al., 2020), physiology (Di Santo, 2015, 2016, 2019; Rummer et al., 2022), and behaviours (Green and Jutfelt, 2014; Pistevos et al., 2015, 2017). The variability in response could potentially stem from differences in exposure times, which need to be standardised according to the pressures experienced throughout the different life stages. For example, adults of the small-spotted catshark (*Scyliorhinus canicula)* increased their lateralization when exposed to acidified water for 4 weeks (Green and Jutfelt 2014), while neonates of the blacktip reef shark (*Carcharhinus melanopterus*) did not exhibit

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similar changes within seven days (Bouyoucos et al., 2020). Rearing large species under different climate change scenarios can also be particularly difficult (Smith et al., 2017), generally involving reduced numbers of experimental subjects and an increased overall variance caused by the predominance of inter-individual variations (Araujo and Frøyland, 2005). Rather than a limitation, this constraint calls for new experimental approaches that combine experimental groups and individuals responses to climate change. By considering the inter-individual variation in recruits, we can better assess the future ecological success of species in the face of climate change (Forsman and Wennersten, 2016).

In the Northeast Atlantic, elasmobranch studies carried out so far focused on the impacts of temperature on the small-eyed skate (*Raja microocellata*; Hume, 2019) and the small-spotted catshark embryos (Brüggemann, 2013; Ripley et al., 2021) either alone or combined with deoxygenation (Musa et al., 2020). In these studies, average annual temperatures ranging from 12.5 °C to 22 °C were used to assess temperature impacts on embryonic development from 4 to 7 months. However, to our knowledge, climate change studies on elasmobranchs have yet to consider the monthly temperature variations. These variations, marked by extremes, can significantly impact teleost fish embryos (e.g. reduction of body size, Spinks et al., 2019; developmental anomalies, Murray and Klinger, 2022). This is due to small differences between their maximum and minimum critical temperatures (i.e., a narrow temperature range) and because their optimal temperature for development differs from the average habitat temperature (Dahlke et al., 2020; Slein et al., 2023). Temporal variations of environmental parameters represent a particularly acute threat to embryos of oviparous elasmobranchs with anchored eggs, directly facing potential unfavourable environmental conditions. In particular, the impact of temperature variations on the developmental sequence is a critical factor requiring assessment. Furthermore, studies of the effects of acidification on oviparous elasmobranchs are scarce (but see Claiborne and Evans, 1992; Green and Jutfelt, 2014, Pegado et al., 2020a) although pH could explain a significant part of the variation in these species distribution (Coulon et al., 2024). The acidification has generally been studied independently of temperature rise, despite evidence demonstrating exacerbation of effects of elevated CO_2 with warming on the embryos of the little skate, *Leucoraja erinacea* (Di Santo, 2015) and the brown-banded bamboo shark, *Chiloscyllium punctatum* (Rosa et al., 2014). Moreover, elevated temperature and acidification had detrimental effects on sharks, increasing their energetic demands while decreasing metabolic efficiency and their ability to locate food through olfaction (Pistevos et al., 2015).

The small-spotted catshark is an abundant, widespread oviparous elasmobranch across a wide range of latitudes (OBIS, 2021). In the Northeast Atlantic, it spawns from shallow waters to depths greater than 200 m (Ellis et al., 2004). It is also a species with relatively short generation time compared to other oviparous elasmobranchs of the Northeast Atlantic (Coulon et al., 2023). Furthermore, *S. canicula* females produce eggs year round with a peak in early summer around the British Isles (Ellis and Shackley, 1997), anchoring their eggs to macroalgae and other solid structures (Wheeler, 1978). Adults of these species also present limited dispersal abilities and high site fidelity (Rodríguez-Cabello et al., 2004; Kousteni et al., 2015). The inability of embryo to disperse once fixed to a substrate and adult limited dispersal abilities make this species a good model for studying the effects of summer temperatures on embryos.

We analysed the effects of ocean warming (+2 and + 4 °C), within monthly temperature variations, combined with water acidification ($\Delta pH = -0.2$ and -0.4) over the first ten months of early life (from July to April) of *S. canicula*. Temperatures and pH values used in this study followed three predicted climate change scenarios ranging from actual conditions to extreme ones. Using a broad-scale approach at the individual and group levels, we evaluated (i) embryo growth pattern, freezing behaviour and associated metabolism (ii) hatching success and (iii) juvenile growth. One of the originalities of our study is to combine two recently developed frameworks, originally designed for ecological assessment and species extinction risk, to highlight inter-individual differences across developmental sequences according to the climate scenarios tested.

2. Materials and methods

2.1. Experimental design

We chose the Shared Socioeconomic Pathways (SSP) scenarios ‘SSP2: Middle of the road’ where CO_2 emissions stay around current levels until 2050, then falling but not reaching net-zero by 2100 (Fricko et al., 2017) and ‘SSP5: Fossil-fueled Development (Taking the Highway)’ where CO_2 emissions triple by 2075 (Kriegler et al., 2017). The two experimental treatments (SSP2-4.5 and SSP5-8.5) were compared to the control treatment corresponding to median water temperature and pH measured from 1995 to 2014 (AR6 1995–2014). The pH and temperature data were obtained from forecasts for Western and Central Europe and downloaded from http://interactive-atlas.ipcc.ch (Gutiérrez et al., 2021; Iturbide et al., 2021, Table 1). We subjected embryos to monthly median values for temperature, but we were unable to do so for monthly variation of pH, for which only annual averages were available (Gutiérrez et al., 2021; Iturbide et al., 2021, Table 1). Seawater tank supply was pumped from the Dinard coast (English Channel, France). Since the coastal context of the study implies more acidic water than the raw pH values predicted in the global ocean (Hönisch et al., 2012), we applied predicted annual pH differences between the scenarios and the control ($\Delta pH_{\text{AR6 1995-2014-SSP2-4.5}}$: -0.2, and $\Delta pH_{\text{AR6 1995-2014-SSP5-8.5}}$: -0.4).

Eggs used in this study originated from 65 mated females of *S. canicula* fished in the Tregastel Bay and in the Morlaix Bay (35 km apart). Females can store sperm from different males for several months (up to 214 days for *S. canicula*, Ellis and Shackley, 1997), and no population structure was shown for this species in the English Channel (Manuzzi et al., 2019). After their capture, all females were reared at 16 °C. Eggs were laid in captivity at the Aquarium Marin de Trégastel (n = 55) and the Station Biologique de Roscoff (n = 70) from June to July 2022 due to the biological constraints of the species (~2 eggs laid per week per female). Dinard, the location of the experiments performed in this study, and the Tregastel Bay and Morlaix Bay are all located within a radius of less than 200 km on the English Channel coast (Fig. S1). We thus postulated that the water chemistry of these three sites are similar.

The 125 eggs were individually identified (laying date known to within a day) before being introduced four weeks after in the nine 112-L biosphere tanks (three replicates per treatment; Table S1). From the fourth week, the embryo has a long tail that can be observed non-invasively (stage 3; Musa et al. (2018)); making it easy to differentiate between alive from unfertilized and dead embryos. Tanks were fully aerated to create a normoxic (>95% air saturation) environment with independent cascade filtration systems (Eheim Pro4+ 250; 950 L h^{-1}). Salinity (34 ppt), nitrite (<0.05 mg.L^{-1}) and nitrate (<40 mg.L^{-1}) were monitored weekly and 1/3 of the volume of tanks were renewed weekly to ensure good water quality. Additional water changes were also carried out in case of embryo death. Temperatures (Table 1) were individually maintained with a heater connected to a temperature control unit with a reliability of ± 0.2 °C (Greisinger GIR 300). For each tank, the first monthly temperature applied was always that of June, whatever the spawning month (between June and July). Temperatures were also checked independently when measuring salinity, with the device providing both information (Greisinger GLF 100). Monthly changes in temperature were achieved by modifying the desired threshold values and allowing the water to change gradually over the following 48 h. The pH (Table 1) was controlled with an aquarium computer (IKS Aquastar) which allows measuring the pH and adjusting it independently in each tank by bubbling CO_2 with a reliability of ± 0.01. The natural

Table 1
Temperatures (± 0.2 °C) and pH (day-night) applied on embryos and juveniles.

		~ embryos (n = 125)				~ juveniles (n = 63)					
Scenario	Variable	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
AR6 (1995–2014)	Temperature (°C)	18.4	19.4	18.4	16.3	14.0	12.1	10.8	10.0	9.9	10.7
	pH	7.90–7.80									
SSP2-4,5 (CMIP6)	Temperature (°C)	20.3	21.4	20.4	18.2	15.6	13.5	12.1	11.3	11.2	12.1
	pH	7.90–7.80		7.70–7.60							
SSP5-8,5 (CMIP6)	Temperature (°C)	21.9	23.1	22.1	19.6	16.9	14.8	13.3	12.5	12.3	13.2
	pH	7.90–7.80		7.50–7.40							

oscillations in pH between day and night were allowed for by applying a variation of 0.1. The pH probes were recalibrated every month after temperature changes, and independent measurements were taken before and after recalibration with a pH-metre (Orion 3-Star). The pH variations, following the pH expected under the SPP2-4.5 and SSP5-8.5, was modified from September, when 90% of all the embryos were at stage 6 and had developed fully developed gills, to the end of the experiment (i.e., six months after hatching). The egg is pre-open from the 4th stage (Jeffree et al., 2007) but the 6th stage was chosen because of the presence of functional gills and active water pumping (Leonard et al., 1999), which indicates a significant exchange of water and ions between the embryo and its environment (i.e., the pH inside the egg should be the same as outside).

2.2. *Experimental procedure and follow-up of embryos and juveniles*

Embryos were recorded and photographed weekly until hatching (Canon PowerShot G12) by candling, a method that involves shining a light through the eggs to observe their internal development non-invasively. Developmental stage timings were quantified weekly following Musa et al. (2018) description. If the observed stage was more than one step ahead of the last observation, it was assumed that the intermediate step lasted for less than one week. Total length and yolk surface were measured twice by two people from the randomly sorted photographs using tpsDIG (Rohlf, 2015) to minimise observer bias and keep constant the number of points used to make the measurements. This ensures that each measurement was made with the same accuracy regardless of the embryo positioning (see Supplementary Appendix S2 for details). The growth rate (cm.week^{-1}) of each individual was then calculated using a generalised linear model (GLM) using the *'glm'* function from the *'stats'* R package. As yolk sac consumption was negligible in the first weeks of survey, we identified the point at which it significantly began using the Pettitt test implemented in the *'trend'* R package (Pettitt, 1979; Verstraeten et al., 2006) to calculate the yolk sac consumption rate (cm^2.week^{-1}; Wheeler et al., 2021) over the remaining portion of the curve using a GLM. Embryos were checked daily to accurately determine the timing of their death, if any.

After hatching, total incubation time was quantified (± 1 day), and each individual was weighed and measured (see Supplementary Appendix S2 for details). Individuals were fed *ad libitum* with thawed shrimp and squid every day until they were four months old, then every two days. Substrate, enrichment, and hiding places were offered. Juveniles (n = 63) were sexed at the age of 1 month (Table S2), weighed and measured monthly (see Supplementary Appendix S2 for details). Over the juvenile follow up, external stress was kept at minimum, so that juveniles were not individually-identified, avoiding tagging or repeated photographic identification.

In this study, we individually followed the development of embryos until their hatching as juveniles, as inter-individual variation in development is expected to be important at this stage (e.g., developmental failure due to chromosomal defects, gene interactions; VanRaden and Miller, 2006). At the juvenile stage, we carried out replicate-scale tracking (i.e., juvenile data is pooled from each treatment), as we hypothesised that inter-individual variation in growth would be smaller between juveniles of the same tank than between tanks.

2.3. *Freezing capacity and embryo recovering*

Embryos are subjected to intense predation pressure (Powter and Gladstone, 2008) to which they respond by stopping ventilatory behaviour and ceasing to move, a so-called freezing response (Kempster et al., 2013). When the embryo holds its breath, it accumulates a 'metabolic debt' with respect to aerobic metabolism which it will have to recover (Leonard et al., 1999; Kempster et al., 2013). The rate of oxygen consumption measured after the expression of the freezing behaviour is a proxy of the cost involved. We assessed embryos freezing capacity and recovering throughout oxygen uptake measures with a static respirometry method. We focused on the pre-hatching stage (~October). Each egg was handled underwater to mimic the physical disturbances caused by a potential predator investigating the egg (Ripley et al., 2021) and placed in a 120 mL glass respirometry chamber directly capped into experimental tank (n = 55). We quantified the duration of the freezing response from handling in the tank to resumption of buccal pumping or uncoiling of the tail using a chronometer (Ripley et al., 2021) (n = 42). The oxygen saturation was measured using a mini oxygen sensor with a dip probe connected to a Witrox 4 oxygen metre (LoligoSystems) coupled with a temperature probe to automatically adjust oxygen saturation values to water temperature. Embryos were left in the respirometry chamber until we could calculate a rate of oxygen consumption (~15–20 min) taking care to have an oxygen saturation always above 80% in the chamber (Svendsen et al., 2016). The rate of oxygen consumption (mg.O$_2$.embryo^{-1}.h^{-1}) was calculated by multiplying the rate of decrease in oxygen saturation by the volume of the tank (Wheeler et al., 2021). We validated the measurements by following the recommendations of Chabot et al. (2021), with a R^2 threshold of 0.85. Respirometry measurements with a fresh empty egg, from an embryo not involved in the experiment, were carried out before and after the respirometry measurements on the embryos and did not reveal any significant microbial respiration rates (<1%).

2.4. *Embryos and juveniles growth patterns*

We anticipated a higher mortality under the two scenarios. Hence, our objective was to delve into the causes of embryo death, particularly emphasizing individual growth divergences over time. Embryos growth was analysed individually in two ways: (i) each week, we quantified the difference between the growth state of an embryo from an experimental treatment and each of the control embryos, (ii) at the end of embryonic development, we compared the whole growth trajectory of an embryo from an experimental treatment with the set of growth trajectories of the control embryos.

We used the ecological quality assessment (EQA) framework developed by Sturbois et al. (2023), to summarise the inter-individual differences in each growth state belonging to individuals trajectory between embryos under control condition compared to the two treatments. EQA is a statistical method based on a dissimilarity matrix projected on a multivariate space, and measures deviations from a set of reference conditions contained in a state-based or trajectory-based reference envelope. EQA was originally used for assessing and reporting the quality of ecosystems, but it can be applied to any traits based matrix. In our experiment, the space was defined with a distance matrix calculated from embryos length, yolk surface and developmental stage using the R package *'gawdis'* (de Bello et al., 2021) and was used to assess the quality of embryos growth trajectories. A state-based EQA was first performed to quantify the impact of the two treatments at each growth state (i.e. weeks) compared to each growth state belonging to the control conditions (squared distance). It was followed by a trajectory-based EQA to compare the whole growth trajectories of individuals which have experienced the two treatments with the control trajectory reference envelope ($Q \geq 0.5$: inside the trajectory reference convex hull; $Q < 0.5$: outside the trajectory reference convex hull). EQA was performed using the *'ecotraj'* R package (De Cáceres et al., 2019; Sturbois et al., 2023).

For juveniles, for which we did not have individual trajectories we calculated average growth rates for all the juveniles in a tank and differences in growth rates (length and weight) between experimental treatments were computed using Dunn's tests.

2.5. *Hatching success and developmental traits*

The impact of treatments on the hatching success was analysed with a GLM with a binomial distribution and a logit link function, with the hatching success (0: no hatching; 1: hatching) as a response and experimental treatments as predictors. Conversely, the treatment impacts on mortality were assessed through weekly survival outcomes, implemented in a Cox's proportional hazards model, with tanks as a random effect, using the *'survival'* R package (Therneau and Grambsch, 2000). The analysis included a total of 1183 observations, with 49 events (i.e., occurrences of mortality) observed (see Supplementary Appendix S2 for details). A Wald Test was used to assess whether treatments contributed significantly to the model, and a Score (Logrank) Test was used to assess global differences between treatments (Agresti, 2007). We also performed a Pearson's Chi-squared test for count data to test whether embryo mortality is evenly distributed between the different embryonic stages.

Then, we aimed to identify the key characteristics contributing to the success of the embryonic development. We studied the embryos' developmental trait combinations involved in the different probability of hatching. Adapting the method used in Carmona et al. (2021) and Coulon et al. (2023) that links the extinction risk of species to their traits, we chose nine developmental traits: growth rate, yolk consumption start, yolk consumption rate, stages duration (from 4 to 7), freezing, and O_2 consumption rate (Table S3; see Supplementary Appendix S2 for details) for studying the probability of embryo hatching. A distance matrix was calculated from these developmental traits using the '*gawdis*' R package (de Bello et al., 2021). Then, a principal coordinate analysis (PCoA) was performed on the dissimilarity matrix to summarise the inter-individual dissimilarities in a biplot called 'development space'. In parallel, differences of each developmental trait between experimental treatments were computed using Dunn's tests.

We calculated the functional dissimilarity between individuals in a treatment (e.g. control) and all other individuals (for this example: SSP2-4.5 and SSP5-8.5) to test the difference between experimental treatments (based on developmental traits dissimilarities), using the *'dissim'* R function of the *'TPD'* R package (Carmona et al., 2019). It reflects the degree of functional dissimilarity between the probabilistic distributions of individuals in the development space between the two treatments, and ranges from 0 (complete overlap) to 1 (no overlap). We then tested whether this functional dissimilarity was lower or higher than expected by chance given the number of individuals in each treatment.

We estimated the occurrence probability of developmental trait combinations within the developmental space using kernel density estimation with unconstrained bandwidth using the *'funspace'* R package (Carmona et al., 2024; Duong, 2007). We then compared the observed functional dissimilarity to a null model where the experimental treatments were randomly assigned to individuals, keeping the number of individuals in each treatment constant using the *'TPD'* R package. We drew 999 simulated assemblages and compared simulated and observed functional dissimilarities. Standardised effect sizes (SES) were calculated as the difference between the observed values and the mean of the simulated values after standardisation by their standard deviations: P-values higher (lower) than 0.975 (0.025) indicate that the observed functional dissimilarity is significantly lower (higher) than expected by chance (using a 5% threshold).

Hatching probabilities were then mapped in the developmental space, and tested with a generalised additive model (GAM), using the individual hatching success (0: no hatching; 1: hatching) as a response, and the dimensional position in the developmental space (i.e. PCoA axes) as predictors using the *'funspace'* R package (Carmona et al., 2019; Duong, 2007).

The flowchart of the methodology developed for our analyses is presented in Fig. S2.

3. Results

3.1. *Embryo hatching success*

The GLM and Cox's proportional hazards models showed that the hatching success and, conversely, risk of mortality (Table S4) were highly dependent on the experimental treatments (Wald test: $\chi^2 = 66.1$, df = 2, $p < 0.001$; Score (logrank) test: $\chi^2 = 111.2$, df = 2, $p < 0.001$). Values ranged from 81% (26 out of 32) and 83% (34 out of 41) of hatching for the control and SSP2-4.5 treatments respectively (GLM, p = 0.85), to 11 % for the SSP5-8.5 treatment (5 out of 45; GLM, $p < 0.001$) (Fig. 1; Fig. S3a).

The survival probability dropped in the SSP5-8.5 treatment between the last week of August and the first week of September, at the end of the developmental stage 5 (Fig. 1; Fig. S4). This mortality was preceded by embryos departing growth trajectories highlighted by increasing squared distance from the state reference growth envelope (i.e., from control individuals; Fig. 2). SSP2-4.5 embryos also deviated from the

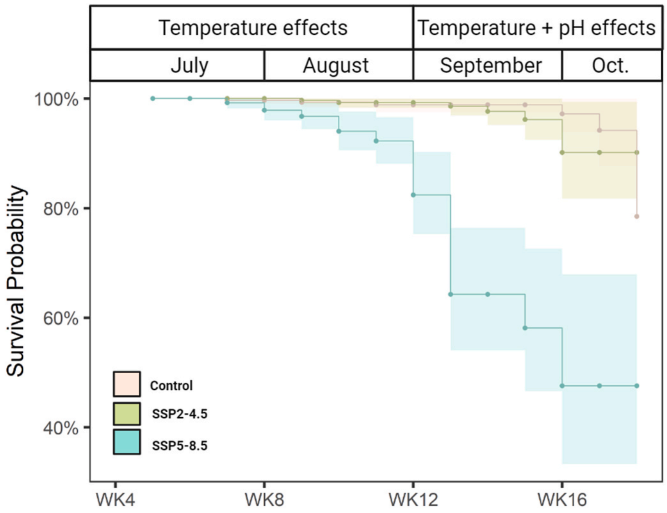

Fig. 1. Embryos survival analysis. Kaplan-Meier survival plot illustrating the survival probabilities of control (beige; n = 35), SSP2-4.5 (green; n = 44) and SSP5-8.5 (blue; n = 45) embryos based on a Cox proportional hazards regression analysis. The x-axis and y-axis represent the time in weeks and the estimated survival probability, respectively. The shaded regions indicate the 95% confidence intervals. The log-rank test yielded a significant difference in survival between the groups ($p < 0.001$). Censored observations are denoted by tick marks on the survival curves. Created with BioRender.com.

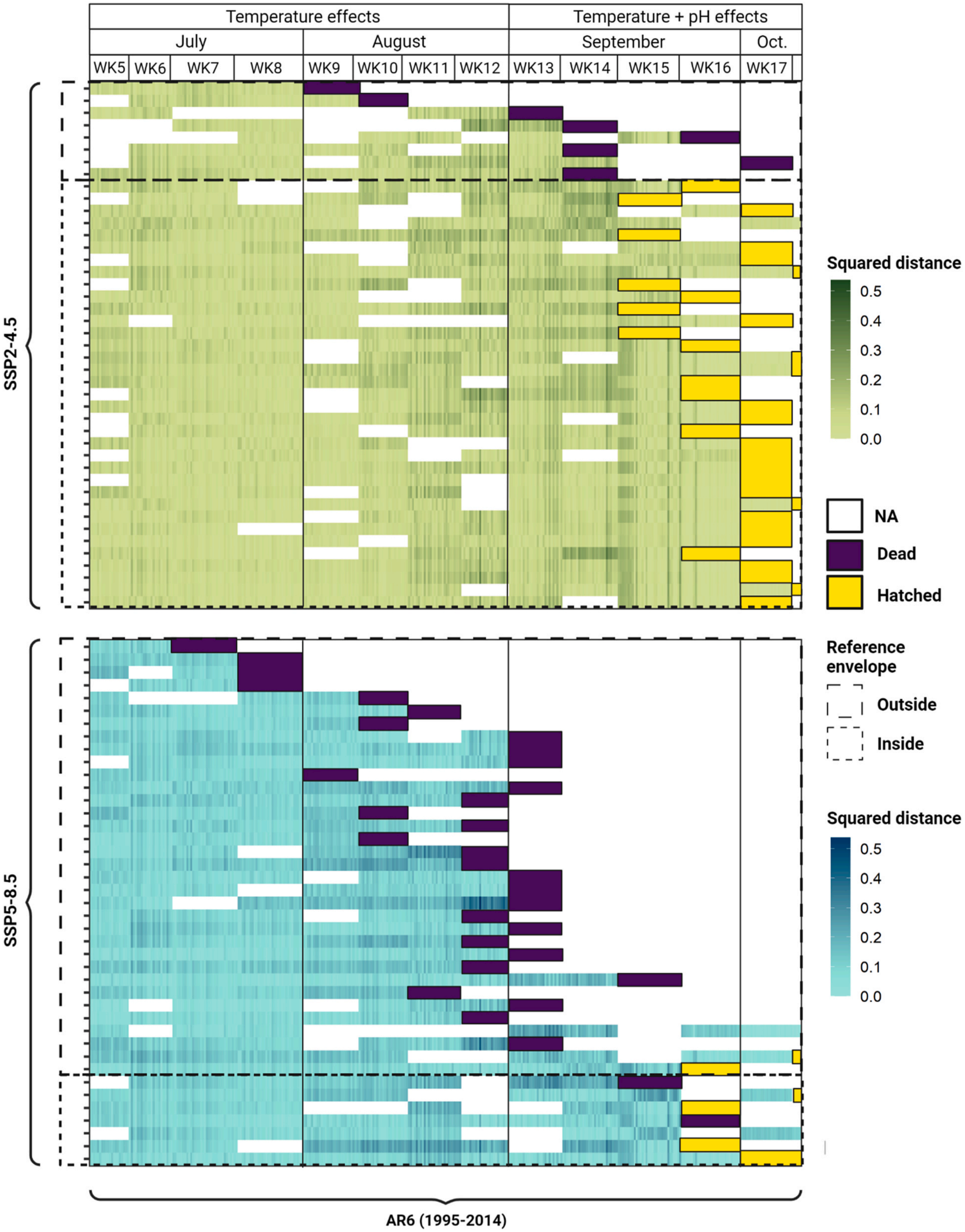

Fig. 2. Embryo growth pattern. Heatmaps showing inter-individual differences at each state (i.e., weeks) belonging to the growth trajectory of SSP2-4.5 (n = 41) and SSP5-8.5 embryos (n = 39) (y-axis; one raw for each embryo) when compared to AR6 (1995–2014) control embryos (x-axis; on column for each embryo for each week) (i.e. the state reference of the growth envelope). Light colours indicate a low distance to the state reference of the growth envelope, while dark colours indicate a high distance. Embryos inside or outside the trajectory reference growth envelope are framed by dotted boxes. Photos did not always make it possible to determine the embryo total length, yolk area and developmental stage, and certain inter-individual differences at each stage (i.e., weeks) could not be assessed (i.e. NA values). Embryo death or hatching are represented by dark purple and yellow boxes, respectively, but are not involved in the calculations. Created with BioRender.com.

state reference growth envelope in August and were able to recover towards the state reference growth envelope in September (stage 6; Fig. S4; Fig. 2). Trajectory based-EQA performed at the scale of the whole individual trajectories pointed out that 81 % (35 out of 43) of SSP2-4.5 embryos trajectories were included in the trajectory reference envelope, against only 17 % (7 out of 41) for SSP5-8.5 embryos (Fig. S5). This analysis also highlights inter-individual differences in growth trajectories within the same treatment. In the SSP5-8.5 treatment, two individuals were outside the trajectory reference envelope but still managed to hatch and, conversely, although inside the trajectory reference envelope, two embryos did not hatch and died at the 7th stage of development (Fig. 2). They weighed 0.8 g and 0.9 g and measured 6.9 cm and 5.9 cm respectively.

3.2. Developmental traits and probability of hatching

The first two axes of the PCoA (80% of total variance; Fig. 4A) showed that embryos with the lowest probability of hatching (Fig. 4B) were also the most dissimilar ones in the developmental space (SES = 0.48), namely SSP5-8.5 embryos, a dissimilarity greater than random expectation (SES = 5.62, p = 1) (Fig. 4B; Table S5). This means that SSP5-8.5 embryos had the lowest probability of hatching and the most different combination of developmental traits.

Axes summarising the inter-individual differences between embryos (i.e., PCoA axes) and testing for the relationship between each developmental trait and the treatments (Fig. 5), show that embryos with the lowest probability of hatching (i.e., SSP5-8.5 embryos; Fig. 3) had a lower yolk consumption rate, with a lower growth rate than SSP2-4.5 and control individuals, and yolk consumption started earlier than control individuals. Stage 4 was shorter for SSP5-8.5 embryos than for control and SSP2-4.5 embryos (Fig. 4). The stage 5 was particularly critical for SSP5-8.5 embryos, with 52% mortality (17 out of 33, Fig. S3b; Pearson's Chi-squared test for Count Data, $p < 0.01$) coinciding with the mortality peak observed in August and the first week of September (Fig. 1). Stage 7 was halved for SSP2-4.5 and SSP5-8.5 embryos compared with control embryos (Fig. 4). The duration of the freezing behaviour of SSP5-8.5 embryos in pre-hatching stage (stage 7) was reduced by more than half compared with that of control and SSP2-4.5 embryos (Fig. 4). The oxygen consumption rates after freezing behaviour was 1.5 times higher in SSP5-8.5 embryos (Fig. 4).

3.3. Neonates condition and juveniles growth

Incubation time was about 10 days shorter for SSP2-4.5 (n = 36) than for control individuals (n = 30). Moreover, inter-individual variability in incubation time was significantly higher in SSP5-8.5 treatment so that individuals had an intermediate incubation time (n = 5; Fig. 5).

Hatchlings had similar total length whatever the treatment, but SSP5-8.5 and SSP2-4.5 individuals had a lower weight than control ones (Fig. 5). The SSP5-8.5 juveniles (n = 5) were characterised by a higher growth rate than those from the control treatment (n = 26), however the high variability in their weights did not translate in a significant increased weight gain (Fig. 5).

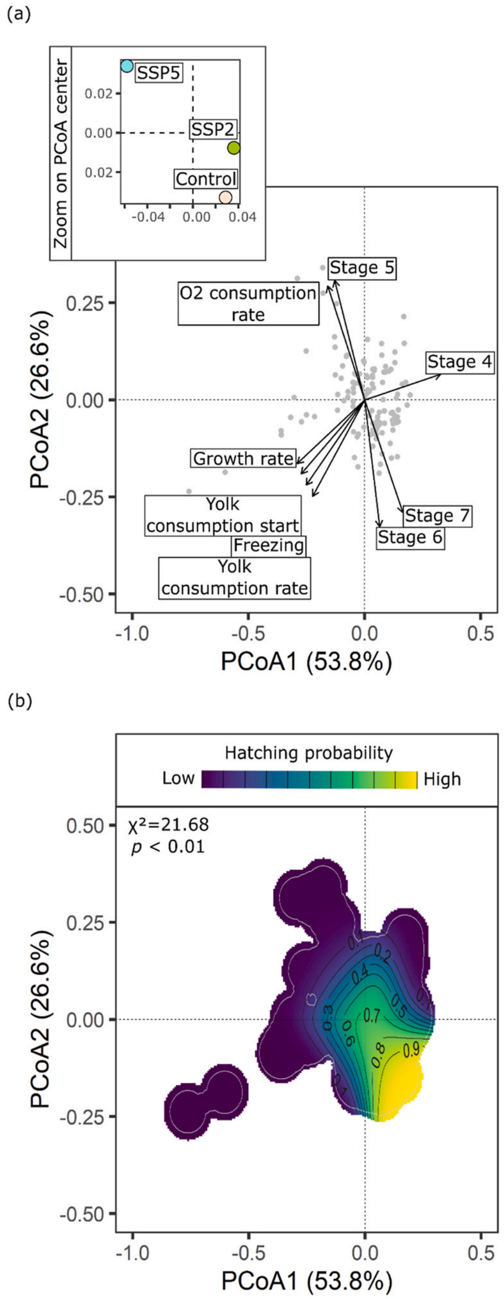

Fig. 3. Hatching success and developmental traits. (a) Projection of embryo developmental traits on the two principal axes of the principal coordinate analysis (PCoA). Annotations in the zoom on PCoA centre refer to the centroid of each experimental treatment, SSP2 stands for SSP2-4.5 and SSP5 for SSP5-8.5. **(b) Probability of embryos hatching according to the generalised additive model (GAM) with binomial distribution, using the position of embryos in the developmental space as predictors.** Yellow to purple gradient tones indicate a high to low probability of hatching, respectively. The grey line indicates the 0.99 quantile of the spectra of each group.

4. Discussion

The purpose of this study was to investigate, at the individual and group levels, responses of early life stages of a temperate oviparous elasmobranch model species (*S. canicula*) to two conditions of ocean warming and acidification expected for the late 21st century. We showed that effects of increased temperature combined with decreased pH are highly dependent on the climatic scenario applied. The use of the EQA and TPDs frameworks made it possible to determine, from the comparison of individual development trajectories, which embryos did not hatch, and at what time they diverged from the others. Through our weekly follow-up and integrative study, we can also infer hypotheses on the causes of mortality. While embryos of the 'SSP2: Middle of the road' scenario were weakly impacted in terms of hatching success and growth, almost all embryos (i.e. 89%) exposed to the 'SSP5: Fossil-fueled Development (Taking the Highway)' scenario never hatched. Mortality peak was recorded in August, when the 5th developmental stage of embryos (Musa et al., 2018) experienced the highest temperatures. At hatching, SPP5-8.5 and SPP2-4.5 neonates were slimmer than control ones, but SPP5-8.5 juveniles subsequently had a higher growth rate than

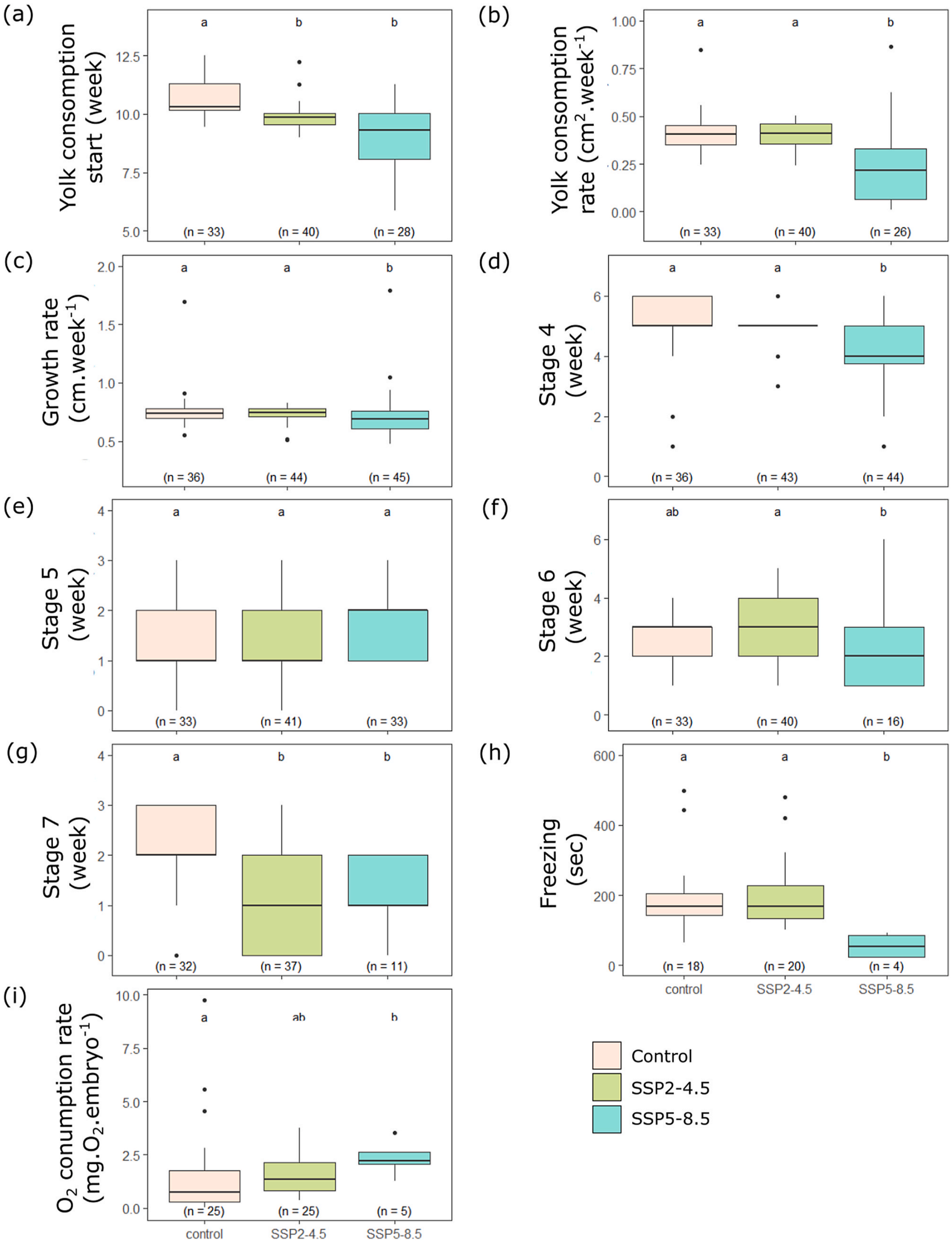

Fig. 4. Embryos developmental traits. (a) Yolk consumption start (week); (b) Yolk consumption rate (cm.week^{-1}); (c) Growth rate (cm^{-1}); (d) Stage 4 duration (week); (e) Stage 5 duration (week); (f) Stage 6 duration (week); (g) Stage 7 duration (week); (h) Freezing duration (sec); (i) O2 consumption rate (mg.O$_2$.embryo^{-1}.h^{-1}). Boxplots are filled according to treatments (beige = Control; green = SSP2-4.5; blue = SSP5-8.5). Letters above boxplots denote significant differences between developmental traits attributes (Dunn's test).

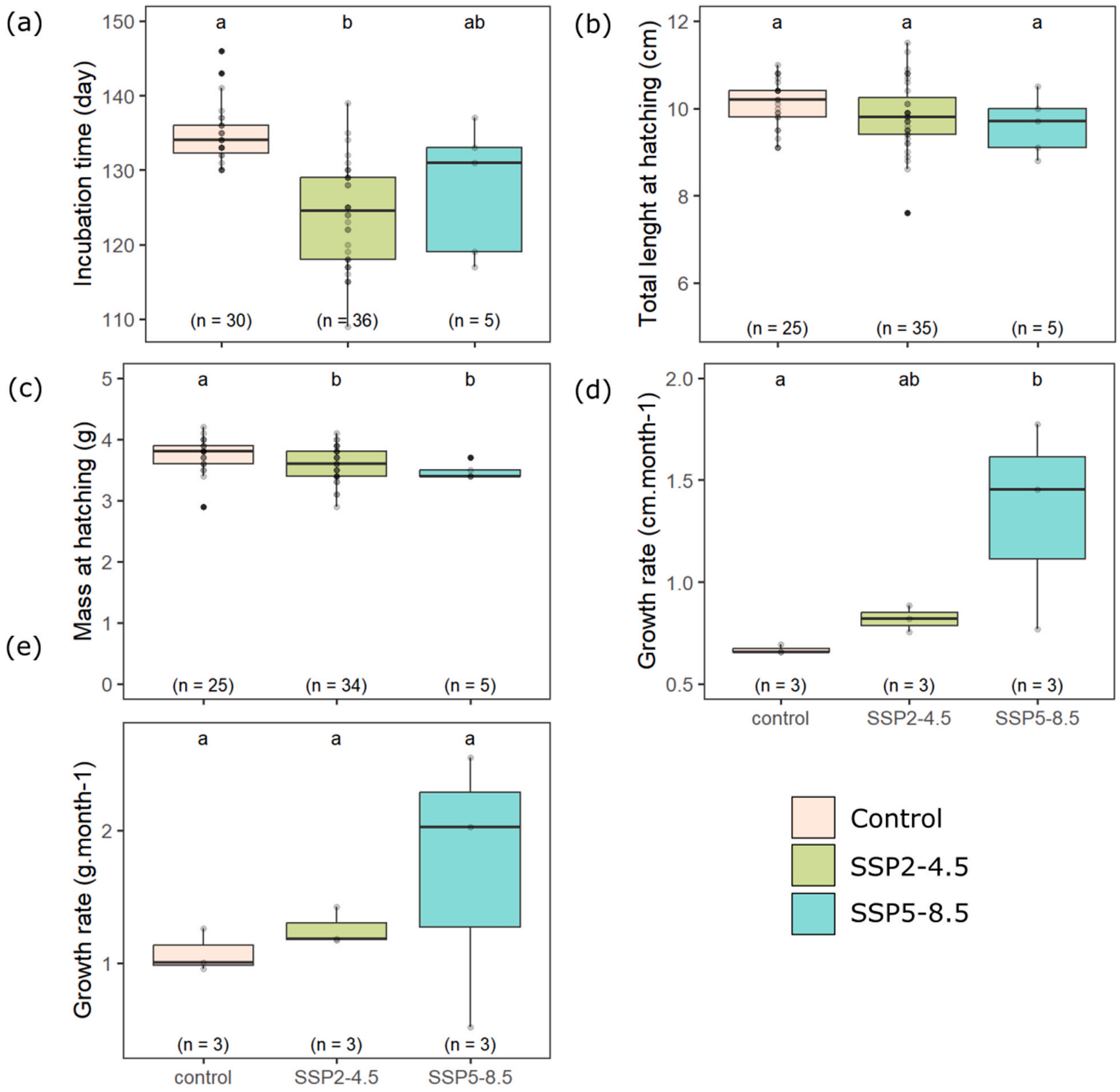

Fig. 5. Neonates condition and growth. (a) Incubation time (day); (b) Size at hatching (cm); (c) Mass at hatching (g); (d) Growth rate (cm.month^{-1}); (e) Growth rate (g.month^{-1}). Boxplots are filled according to treatments (beige = Control; green = SSP2-4.5; blue = SSP5-8.5). Letters above boxplots denote significant differences between attributes (Dunn's test).

control and SSP2-4.5 juveniles.

In this study, we demonstrated that monthly temperature variations can have significant effects on early life stages of the small-spotted catshark. Between July and September (stage 4–6), embryos from treatments SSP2-4.5 and SSP5-8.5 were incubated at an average temperature of 20.0 °C and 21.6 °C respectively (Table 1), but with gradual increase or decrease of 1–3 °C depending on months. This temperature regime led to the survival of 83% (34 out of 41) and 11% (5 out of 45) of embryos for SSP2-4.5 and SSP5-8.5 respectively. In a similar study, but with constant temperature regimes of 19 °C and 22 °C, 63% (12 out of 19) and 56% (9 out of 16) of embryos survived respectively (Brüggemann, 2013). In our study, we obtained a higher survival rate of embryos exposed to a moderate increase of temperature. Therefore, we can hypothesize that gradual increase and small variations around the mean temperature of 20.0 °C could be less detrimental to the survival of embryos of the small spotted catshark than a long exposure to constantly high temperature. However, this does not hold for a higher increase of temperature. This can be explained by the temperature of 23.1 °C experienced by SSP5-8.5 embryos in August (Table 1) that appears to be critical for the embryonic development of *S. canicula*. The temperature causing embryo death is consistent with threshold temperatures for embryonic development ranging from 3 °C to 5 °C above the current temperature documented in *C. punctatum* (Rosa et al., 2014), the epaulette shark (*Hemiscyllium ocellatum*; Gervais et al., 2018), *L. erinacea* (Di Santo, 2015) and the Port Jackson shark (*Heterodontus portusjacksoni;* Vila Pouca et al., 2019). Our study highlights the importance of monthly temperature variations for the development of the small-spotted catshark embryos as compared to constant temperatures (Brüggemann, 2013), which comforts that these variations should be taken into account in experiments assessing the effects of global warming (Slein et al., 2023). Additionally, our study points to the risks of additional or synergetic effects of marine heat waves on the survival of early life stages in the Northeast Atlantic (Pegado et al., 2020b; Simon et al., 2023), related to a poor embryo tolerance to extreme high temperature. This emphasises the need for new experimental approaches closely aligned with the environmental pressures experienced by marine organisms, particularly in coastal nurseries.

In parallel, we showed an increased risk of mortality at the 5th embryonic stage of the small-spotted catshark under the SSP5-8.5 scenario when they experienced high temperature in summer. This developmental stage is characterised by the shrinking of gill filaments (Musa et al., 2018) and the transition to internal gills (Pelster and Bemis, 1992). In our experimental set-up, we ensured a stable oxygen saturation, whatever the temperatures, to avoid a significant increase in embryonic mortality (Musa et al., 2020). Hence, the observed increased mortality could be due to the inability of embryos to consume enough oxygen while their gills are modifying. We also showed a lower but earlier yolk consumption rate, associated with a reduced growth rate. This may indicate that embryos exposed to the SSP5-8.5 scenario had earlier energy demands associated with a poor yolk to body conversion, resulting in starvation. Therefore, lipid metabolic pathways (Wen et al., 2013; Bernal et al., 2020), as well as gill development (Takata et al., 2018), particularly involved at the 5th embryonic stage (e.g., membrane biogenesis), would require further study. Weeks during which the growth trajectories of SSP5-8.5 embryos deviated from the state reference growth envelope should be particularly targeted. In addition, the individual approach showed that some embryos whose growth trajectories deviate from the state reference growth could still hatch. The origin of such phenotypic change is unknown, but it could be genetically based or the result of phenotypic plasticity (Crozier and Hutchings, 2014; Merilä and Hendry, 2014). Conversely, embryos with growth trajectories similar to those of control embryos do not necessarily hatch. This could be explained by the proportionality between size and weight, which remains similar to that of hatched embryos, but whose very low values do not allow the embryos to free themselves from their egg.

Surviving embryos also suffered from limited ability to express freezing behaviour in the pre-hatching stage occurring in October (respectively at 16.3 °C; 18.2 °C; 19.6 °C). The duration of freezing behaviour was reduced by more than half for SSP5-8.5 embryos ($n = 4$) compared to that of control ($n = 18$) and SSP2-4.5 embryos ($n = 20$), which may translate in reducing their potential ability to hide from predators (Kempster et al., 2013). Additionally, their oxygen consumption rates after freezing behaviour were 1.5 times higher ($n = 5$) compared to the control. This result may imply that freezing was limited by a higher oxygen need to fulfil enhanced metabolic rate in these embryos (Leonard et al., 1999; Kempster et al., 2013). In a similar study conducted on embryos at stage 6 (with the vitellus not fully consumed), the freezing reaction duration was 7 times shorter for embryos reared and tested at 20 °C compared to 15 °C (Ripley et al., 2021). These differences may indicate a threshold effect at 20 °C or a greater effect of temperature on freezing behaviour at the sixth stage of development compared with the pre-hatching stage.

In our study, we deliberately confounded warming and acidification from the 6th embryonic stage of development of *S. canicula* (September), when a significant exchange of water and ions took place between the embryo within its pre-opened egg and the external environment due to embryo active water pumping. However, earlier in their development, in August when the tanks were not yet acidified, the growth trajectory of SSP5-8.5 embryos deviated from that of control ones. Consequently, the deaths observed in August were solely due to the warming. By contrast, mortality observed in September may have been triggered by acidification (Santos et al., 2021) on top of warming temperatures experienced in August; the August surviving embryos may have indeed reached their physiological thermal limits. This is consistent with previous analyses showing that the combined effects of acidification and warming are similar to those observed with warming alone (Santos et al., 2021), with acidification exacerbating global warming impacts, as described for *L. erinacea* embryos (Di Santo, 2015). It is worth adding that earlier exposure to acidification could have triggered these effects earlier in the development of *S. canicula* embryos.

At hatching, we showed as expected (Di Santo, 2015; Hume, 2019; Rosa et al., 2014; Wheeler et al., 2021) that SSP5-8.5 and SSP2-4.5 neonates had lower body weights than control ones. Additionally, all SSP5-8.5 juveniles ($n = 5$) survived over the six-month period after hatching, contrasting with previous studies where mortality was observed within 30 days after hatching (Rosa et al., 2014; Di Santo, 2015; Gervais et al., 2018). We also detected a lower but positive growth rate gradient as a function of increased temperatures and acidification, while Gervais et al. (2018) found the opposite. These contrasting results can be explained by the monthly temperatures applied during the juvenile stage, which were lower than the annual average temperatures chosen in these related studies. In addition, in our experimental set-up, juveniles were fed *ad libitum* to fulfil any potential increase in energy demand and prevent growth restriction (Cominassi et al., 2020).

Females of the small-spotted catshark produce and anchor eggs to a substrate (Wheeler, 1978) from shallow waters to depths greater than 200 m (Ellis and Shackley, 1997), rendering their embryos unable to move or escape the laying site. The loss of coastal habitats suitable for spawning due to global change is expected to slow down population turnover and may be linked to population size reduction (Lyon et al., 2011; Levy et al., 2015), if females cannot shift towards more suitable laying sites (Crear et al., 2020). Therefore, identifying and subsequently protecting deep spawning sites (e.g., from trawling) become critical (Kinney and Simpfendorfer, 2009; Sguotti et al., 2016; Wheeler et al., 2020). It should also be noted that we focused on the effects of climate change on summer spawning, as it is the period of the year the most intensely impacted in terms of temperature rise (Ellis and Shackley, 1997; ICES, 2022), but winter or spring spawnings could be positively impacted by a moderate increase in temperature (Salinas-de-León et al., 2018; Wheeler et al., 2020). In the SSP2-4.5 scenario, we observed a reduction of around 10 days in incubation time, demonstrating that the low temperature increase did not lead to significant effects, which might support this assumption. Time shift in spawning periods could also be possible, particularly through the selection of early-spawning individuals (McQueen and Marshall, 2017; Olmos et al., 2023). Northeast Atlantic populations suffering from increased temperature and acidification are expected to migrate towards higher latitudes and deeper depths in search of more suitable habitat, as observed recently for the small-spotted catshark (Coulon et al., 2024), and be replaced in their unsuitable habitat by more tolerant ones (i.e., from warmer latitudes) (Di Santo, 2016; Gervais et al., 2021). These hypotheses should be explored through spatial models of population dynamics incorporating data on species thermal tolerance (Neer et al., 2007; Levy et al., 2015).

Finally, a ‘middle-of-the-road’ scenario for the 21st century will not entail a decrease of embryo survival of the small-spotted catshark, but a ‘fossil-fueled development’ scenario could lead to population dynamic imbalances through very high embryo mortality. Our study attests the importance of analysing both individual and group responses in assessing the vulnerability of elasmobranch critical life stages to temporal variations in temperature. This new insight will provide responses closer to what species experienced *in situ*. This study highlights the detrimental effects of climate change on the fitness of embryos of a widely distributed and non-threatened species of oviparous elasmobranch. These results raise concerns about the future of species with higher distribution constraints and/or endangered ones.

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Ethics

The experiments complied with the ARRIVE guidelines and have been carried out in accordance with the EU Directive 2010/63/EU for animal experiments.

CRediT authorship contribution statement

Noémie Coulon: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Stanislas Pilet:** Software, Investigation, Formal analysis. **Anne Lizé:** Writing – review & editing, Writing – original draft, Validation, Methodology, Conceptualization. **Thomas Lacoue-Labarthe:** Writing – review & editing, Validation, Resources, Methodology. **Anthony Sturbois:** Writing – review & editing, Software, Methodology. **Aurèle Toussaint:** Writing – review & editing, Software, Methodology. **Eric Feunteun:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Alexandre Carpentier:** Writing – review & editing, Validation, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are shared in Appendices

Acknowledgement

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106531.

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III- Conclusion

L'objectif de ce chapitre était d'examiner les réponses des premiers stades de vie de la petite roussette, face à deux scénarios de réchauffement et d'acidification des océans prévus d'ici la fin du 21ème siècle. Notre étude a démontré que les effets combinés d'une augmentation de la température et d'une diminution du pH varient de manière significative en fonction du scénario climatique considéré. En effet, alors que les embryons exposés au scénario « SSP2 : Middle of the road » semblent avoir subi un impact limité en termes de succès d'éclosion et de croissance, près de 89 % des embryons soumis au scénario « SSP5 : Fossil-fuelled Development (Taking the Highway) » n'ont pas éclos. En comparant les trajectoires individuelles de développement, nous avons pu déterminer à quel moment du développement des embryons qui n'ont pas éclos a divergé de celui des autres. Le pic de mortalité a été enregistré en août, période correspondant au 5ème stade de développement des embryons (Musa et al., 2018), et aux températures les plus élevées.

Ce chapitre ouvre des perspectives importantes pour explorer les réponses physiologiques et moléculaires décrites dans l'introduction de cette thèse, et qui auraient pu être observées chez les embryons soumis aux conditions expérimentales. Il amène également à une réflexion sur la dynamique des populations de la petite roussette, qui pourraient être fortement compromises dans le scénario SSP5. Étant donné que l'espèce présente une fécondité relativement élevée par rapport à d'autres espèces de raies et de requins, ainsi qu'une large répartition dans l'Atlantique Nord-Est, la question nous est apparue particulièrement pertinente et fait l'objet du troisième chapitre de cette thèse. Nous comparons également les réponses de la petite roussette à celles d'une espèce phylogénétiquement proche, la grande roussette, qui partage un mode de vie similaire, mais se distingue par une fécondité plus faible et une aire de répartition plus restreinte.

Musa, S. M., Czachur, M. V., & Shiels, H. A. (2018). Oviparous elasmobranch development inside the egg case in 7 key stages. *PLOS ONE*, *13*(11), e0206984. https://doi.org/10.1371/journal.pone.0206984

CHAPITRE 3 : Contraintes physiologiques et dynamique des populations de petite et grande roussettes face au changement climatique

I- Introduction à la modélisation bioénergétique

1. Histoire et applications

Historiquement, la bioénergétique a joué un rôle clé dans le développement de modèles visant à optimiser les conditions de croissance des poissons en aquaculture et mariculture (Chary et al., 2022). Ces modèles se sont concentrés non seulement sur la quantité et la qualité de la nourriture, mais aussi sur les conditions d'alimentation et les profils nutritionnels spécifiques (Cuenco et al., 1985a ; 1985b ; Jobling, 2011). En plus d'optimiser la croissance, la bioénergétique permet d'estimer l'efficacité alimentaire, ainsi que la quantité d'aliments non consommés et de fèces rejetées dans des systèmes d'élevage tels que les cages à poissons (Brigolin et al., 2010 ; Chowdhury et al., 2013). Dans le cas des élasmobranches, la bioénergétique a d'abord été développée pour déterminer le régime alimentaire le plus approprié selon l'âge et l'espèce. Par exemple, les petites et grandes roussettes maintenues en captivité durant cette thèse et sur lesquelles se base ce chapitre ont été nourries avec du calmar et du merlu, apportant respectivement 85 kcal pour 100 g et 92 kcal pour 100 g. Ces aliments contiennent entre 13 et 18 g de protéines pour 100 g, avec des teneurs en lipides variant de 0,2 à 1 g pour le calmar et de 0,4 à 3 g pour le merlu (Janse et al., 2004).

La bioénergétique joue également un rôle crucial dans l'établissement de liens entre les conditions environnementales et la dynamique des populations de poissons, ce qui permet une gestion plus efficace des pêcheries (Chipps et Wahl, 2008 ; Hansen et al., 1993 ; Hartman et Kitchell, 2008 ; Kitchell et al., 1977). Par exemple, la modélisation bioénergétique a été utilisée pour examiner l'impact de la densité sur les caractéristiques physiologiques des poissons (Taylor et al., 2019), pour analyser la dynamique spatiale du flux d'énergie dans les écosystèmes aquatiques (Hartman et Kitchell, 2008), et pour étudier les interactions prédateur-proie, influençant ainsi les pratiques d'empoissonnement (Jones et al., 1993).

En parallèle, la bioénergétique est essentielle pour comprendre comment les facteurs environnementaux interagissent avec le métabolisme des poissons, influençant leur comportement, leur utilisation de l'espace et leur répartition géographique (Brownscombe et al., 2017a ; Payne et al., 2015). Par exemple, l'utilisation de la bioénergétique a permis d'évaluer les contraintes énergétiques liées à l'investissement reproducteur chez les femelles de la raie *Mobula eregoodootenkee* (Lawson et al., 2020) et à la dispersion des jeunes requins Hâ (*Galeorhinus galeus*) depuis les habitats de mise bas (McMillan et al., 2021). Depuis plus récemment, elle a été utilisée pour évaluer les coûts énergétiques associés aux facteurs de stress anthropiques et climatiques (Watson et al., 2020). Par exemple, la bioénergétique peut être utilisée pour analyser comment la variabilité environnementale, telle que les fluctuations de température et la disponibilité alimentaire, impacte le timing et la durée de la période de reproduction chez des espèces de poissons à reproduction multiple, comme l'anchois (*Engraulis encrasicolus*) (Pecquerie et al., 2009 ; Pethybridge et al., 2013). Chez les élasmobranches, la bioénergétique a également été utilisée pour évaluer les impacts de l'écotourisme, en particulier le nourrissage des requins-baleines (Barry et al., 2023) et des grands requins-marteaux (*Sphyrna mokarran*) (Heim et al., 2021).

2. Bilan de masse bioénergétique

La bioénergétique repose en grande partie sur une équation généralisée du bilan énergétique, qui peut être exprimée comme suit : l'énergie consommée est répartie entre le métabolisme, les déchets et la croissance (Brett, 1979 ; Winberg, 1956). Chez la plupart des poissons, poïkilothermes, l'allocation de cette énergie peut varier considérablement en fonction de plusieurs facteurs, notamment les conditions environnementales telles que la température et le régime alimentaire, les caractéristiques physiologiques comme la taille du corps et le statut reproductif, les aspects ontogéniques tels que l'âge de maturité et l'allocation des ressources à la reproduction, ainsi que les facteurs comportementaux comme le niveau d'activité (Clarke et Johnston, 1999 ; Jerde et al., 2019 ; Killen et al., 2010).

L'énergie est consommée sous forme d'aliments, dont une partie est éliminée sous forme de déchets (par exemple, par égestion et excrétion), et une autre partie est dépensée dans les processus digestifs. L'énergie assimilée est premièrement allouée au maintien du métabolisme, et une quantité variable est allouée à l'activité locomotrice. Lorsque l'énergie consommée excède les besoins métaboliques, l'excédent peut être stocké ou alloué à la croissance, ce qui implique sa répartition entre divers tissus somatiques et, au stade de maturation, à la reproduction (Brownscombe et al., 2022 ; Tytler et Calow, 1985 ; Figure 21). Par conséquent, les combinaisons de facteurs qui influencent la consommation et le métabolisme déterminent en fin de compte la quantité d'énergie disponible pour la croissance.

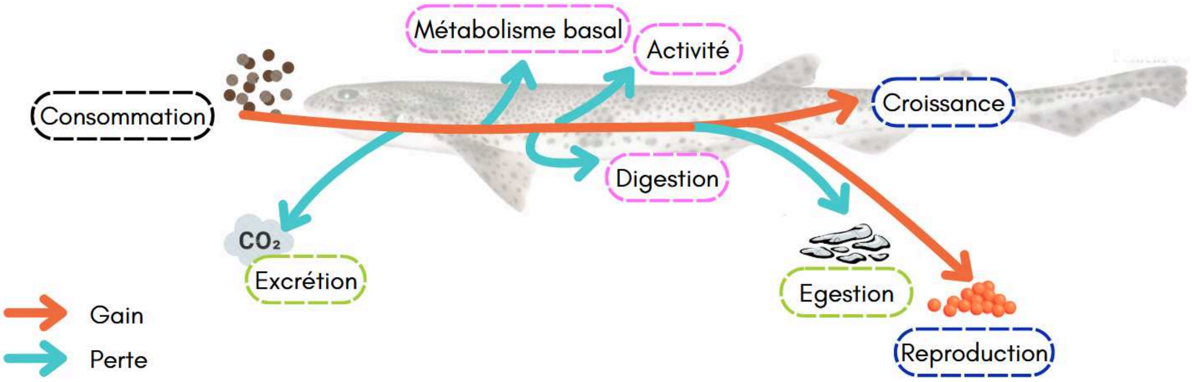

Figure 21 : Composantes générales de l'équation du bilan énergétique illustrées chez une petite roussette L'énergie est consommée sous forme d'aliments, dont une partie est rejetée sous forme de déchets (ingestion et excrétion), tandis qu'une certaine quantité est utilisée pour les processus digestifs. L'énergie assimilée est d'abord allouée au métabolisme de base, puis une part variable est dédiée à l'activité (locomotion). L'énergie nette restante est investie dans la croissance somatique et/ou la reproduction. Les lignes turquoises représentent les gains énergétiques, tandis que les lignes oranges indiquent les coûts énergétiques et les pertes sous forme de déchets. D'après Brownscombe et al. (2022).

3. Différentes approches

Les modèles bioénergétiques, bien qu'ils décrivent généralement les mêmes processus, diffèrent par leurs hypothèses, leurs données d'entrée et de sortie. La plupart se répartissent en deux grandes approches. D'une part, les modèles basés sur les réponses écophysiologiques de l'organisme, qui estiment la capacité de croissance (SGF, Scope For Growth) en se fondant sur un budget énergétique intégrant l'énergie ingérée et les coûts métaboliques observés (Fry, 1971 ; Winberg, 1956). D'autre part, les modèles fondés sur les principes de la chimie, de la physique, de la thermodynamique et de l'évolution, avec une approche mécaniste de la bioénergétique (Jusup et al., 2017 ; Sousa et al., 2010). Le modèle « Wisconsin Energy Budget » (WEB) illustre l'approche SFG (Kitchell et al., 1974 ; 1977), tandis que le modèle « Dynamic Energy Budget » (DEB) (Kooijman, 2010) suit une approche mécaniste. Le modèle « Physiological Energy Budget » (PEB), également mécaniste, se distingue du DEB par l'utilisation de paramètres biologiquement mesurables (Sibly et al., 2012) :

- Un modèle **WEB (Wisconsin Energy Budget)** estime les taux spécifiques de croissance en soustrayant les coûts énergétiques liés à l'évacuation des déchets (fèces et excrétion) et à la respiration (métabolisme standard, actif et post prandial ou SDA) du taux de consommation de nourriture. Les sous-modèles de respiration et de consommation dépendent de la taille de l'individu et de la température. La SDA, l'éjection des fèces et l'excrétion sont généralement modélisées comme une perte proportionnelle à l'énergie apportée par la nourriture ingérée. Le modèle intègre une « p-value », qui correspond à la proportion de la consommation maximale théorique de nourriture (C_{max}), pour équilibrer le budget énergétique. Cette valeur varie entre 0 et 1, et est souvent utilisée comme indicateur de la qualité de l'habitat, les valeurs les plus élevées étant associées à une plus grande disponibilité de nourriture (Figure 22).

- Un modèle **DEB (Dynamic Energy Budget)** décrit comment les organismes absorbent et utilisent l'énergie provenant de leur environnement pour des fonctions essentielles telles que l'entretien, la croissance, le développement et la reproduction tout au long de leur cycle de vie. Il s'appuie sur trois variables d'état principales : les réserves d'énergie, la structure corporelle, et le tampon de maturité ou de reproduction, selon le stade de développement. L'énergie assimilée est d'abord stockée dans les réserves, qui contiennent alors les composés prêts à être utilisés sans nécessiter d'entretien. La mobilisation de cette énergie se fait selon la « règle du kappa », qui divise l'énergie disponible en deux flux : une fraction (κ) est dédiée à la croissance somatique et à l'entretien métabolique, tandis que le reste (1-κ) est alloué à la maturité et à la reproduction. En plus de la température, le modèle intègre la disponibilité alimentaire, qui peut être représentée par une échelle allant de 0 (jeûne) à 1 (alimentation à volonté) ou par une série temporelle, selon les données disponibles (Figure 22).
- Le modèle **PEB (Physiological Energy Budget)** décrit l'acquisition et l'allocation de l'énergie provenant des aliments présents dans l'environnement, répartie entre les processus vitaux tels que l'entretien, la croissance, la reproduction et le stockage. Si les apports alimentaires sont suffisants, l'énergie est d'abord allouée à l'entretien, puis à la croissance et/ou à la reproduction, et enfin au stockage. En cas de déficit, la croissance et la reproduction sont réduites en priorité, et lorsque les réserves atteignent un seuil critique, toute l'énergie est allouée à l'entretien. Si l'énergie disponible devient insuffisante pour couvrir les coûts d'entretien (période de jeûne ou de pénurie alimentaire), l'organisme puise dans ses réserves jusqu'à épuisement, entraînant la mort. Le modèle prend en compte les variations des taux d'acquisition et d'allocation en fonction de la masse corporelle et de la température, selon des relations théoriques bien établies. Tous les paramètres utilisés sont des mesures biologiquement significatives, ce qui facilite leur estimation par ajustement aux données expérimentales. Le PEB se distingue du DEB en relâchant certaines

contraintes, notamment la « règle du kappa » qui impose une proportion fixe d'énergie allouée à la reproduction tout au long de la vie (Figure 22).

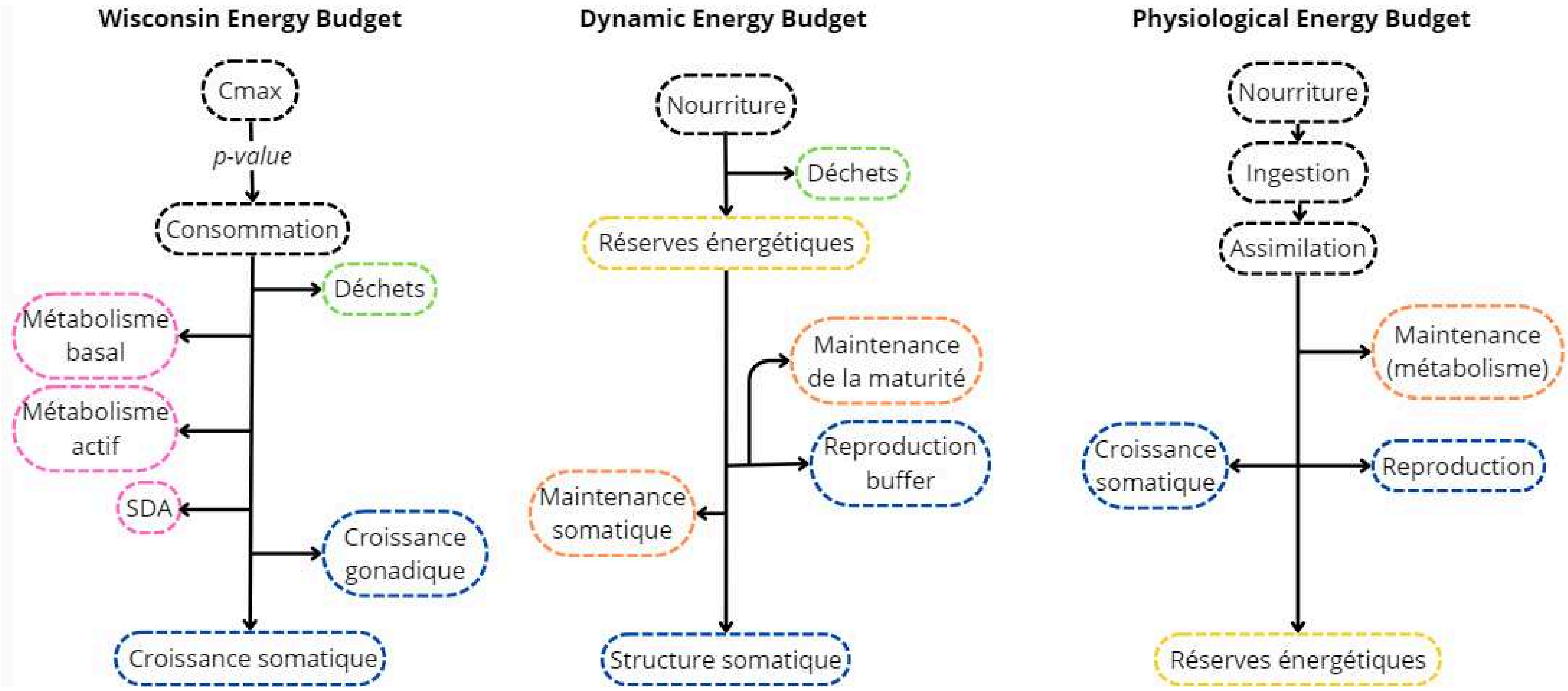

Figure 22 : Diagrammes conceptuels illustrant la structure de trois approches courantes de modélisation bioénergétique. Les nœuds d'apport énergétique sont représentés en noir, les pertes en gris, les coûts énergétiques en orange, l'allocation à la production en bleu, et les réserves énergétiques en jaune. D'après Brownscombe et al. (2022).

Dans ce chapitre, le modèle WEB a été choisi pour évaluer les effets du réchauffement des océans sur la survie, la croissance somatique et la production d'œufs de la petite et de la grande roussette car il repose sur des données relativement accessibles, telles que la consommation alimentaire et la respiration. En comparaison, les modèles DEB et PEB nécessitent des paramètres plus complexes, comme des estimations précises de l'énergie stockée et allouée aux processus de reproduction, qui sont plus difficiles à mesurer directement chez les requins. De plus, ces modèles utilisent une variable d'état de stockage qui ne reflète pas la physiologie des élasmobranches. Bien que ces derniers soient connus pour accumuler des lipides, principalement dans leur foie, la nature de ces lipides varie. Les triacylglycérides et les éthers de diacylglycérol sont considérés comme des molécules de stockage énergétique, tandis que le squalène, un intermédiaire de la synthèse du cholestérol, ne peut être converti en une forme oxydable pour produire de l'énergie, aucune voie métabolique connue chez les animaux ne permettant cette transformation (Ballantyne, 1997).

4. De l'individu à la population

Les modèles bioénergétiques illustrent comment les organismes réagissent à leur environnement. Une approche courante pour étendre ces réponses à l'échelle de la population consiste à utiliser des modèles individu-centrés (IBM, Individual-Based Models) (DeAngelis et Grimm, 2014 ; Grimm et Railsback, 2013). Dans ces modèles, une population est représentée par ses individus, chacun étant défini par un ensemble de variables telles que sa taille corporelle ou ses réserves d'énergie. Les IBM ont été développés et appliqués dans divers contextes. Par exemple, ils permettent de prédire la dynamique des populations en fonction de la disponibilité de la nourriture et de la température (Politikos et al., 2015), des effets combinés de la disponibilité alimentaire et de l'exposition aux produits chimiques sur la dynamique des populations (Mintram et al., 2020), ou encore d'analyser les impacts potentiels des changements climatiques et des scénarios de gestion sur les stocks halieutiques et les pêcheries associées (Boyd et al., 2020).

Similairement, des IBM ont été utilisés dans ce chapitre afin d'analyser les variations de la croissance, de la maturation sexuelle, de la production de descendants, ainsi que la dynamique des populations de la petite et de la grande roussette, dans le cadre de deux scénarios climatiques futurs projetés pour 2100. Pour chaque scénario, nous avons calculé les taux de croissance finis (λ) et instantanés (r) de la population, le taux de reproduction net et le temps de génération.

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II- Illustration du dispositif expérimental

1. Infrastructure et conditions expérimentales

La calibration du modèle bioénergétique (WEB) a nécessité de maintenir en captivité des petites roussettes de tailles variées afin de mesurer leurs taux de consommation de dioxygène en fonction de leur poids. En plus d'une salle thermo-photorégulée, la plateforme d'expérimentation animale sur les poissons de la Station marine du Muséum national d'Histoire naturelle à Dinard dispose de plusieurs bassins permettant d'accueillir des juvéniles, subadultes et adultes de petites roussettes. Chaque bassin est équipé d'un système de filtration et de thermorégulation indépendant, bien que le pH ne puisse être régulé (Figure 23).

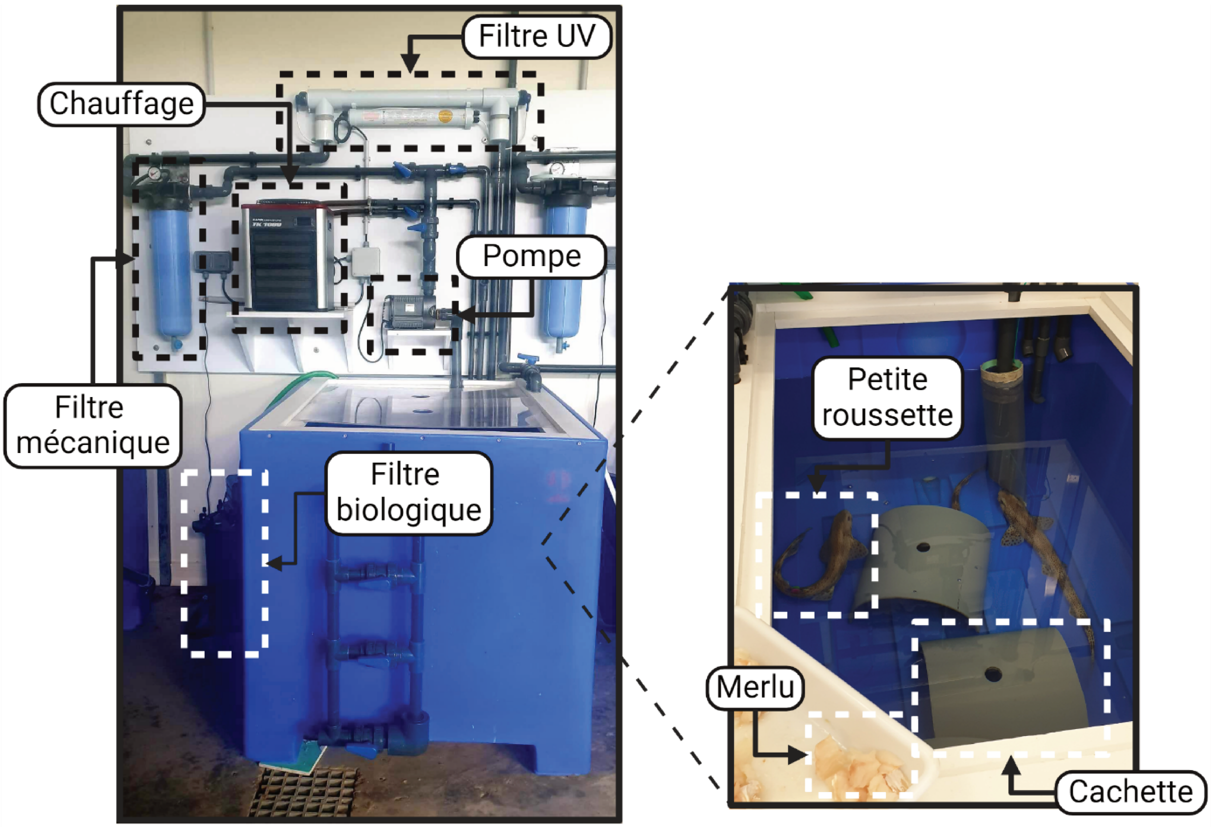

Figure 23 : Photographie d'un bassin expérimental et de ses différents équipements. Créée avec Biorender.com

Les petites roussettes ont été exposées pendant un mois à trois conditions expérimentales distinctes : les conditions climatiques observées historiquement en juin entre 1995 et 2014 pour l'Europe occidentale et centrale, ainsi que les conditions potentielles pour 2100 selon les scénarios SSP2 (Fricko et al., 2017) et SSP5 (Kriegler et al., 2017), tels que définis dans le sixième rapport d'évaluation du GIEC et téléchargés à partir de http://interactive-atlas.ipcc.ch (Gutiérrez et al., 2021 ; Iturbide et al., 2021).

Chaque individu a ensuite été placé dans une chambre de respirométrie adaptée à sa taille, ce qui a posé des défis méthodologiques, notamment pour les petites roussettes de grande taille et la conception de chambres de respirométrie sur mesure. Le test de respirométrie statique à flux intermittent alternait entre des périodes de mesure de la consommation d'oxygène de 15 à 60 minutes, en fonction de la température, et des périodes de renouvellement de l'oxygène de 60 minutes (Figure 24). Les requins ont été maintenus dans les chambres de respirométrie pendant 16 heures. L'intervalle entre les renouvellements d'oxygène était suffisamment long pour permettre une détection précise de la baisse d'O_2, tout en étant assez court pour éviter que les niveaux d'O_2 ne descendent en dessous de 80 % de saturation à la fin de la période de mesure, afin de minimiser le stress des individus (Svendsen et al., 2016). La saturation en oxygène a été mesurée à l'aide d'un capteur avec une sonde à immersion connectée à un oxygénomètre Witrox 4 (LoligoSystems). Une biométrie a été effectuée après chaque test afin d’estimer les taux métaboliques en fonction de la masse de chaque individu. Les individus ont été retirés individuellement des chambres de respirométrie, anesthésiés avec de la benzocaïne (40 mg.L^{-1} tamponnée au bicarbonate ; Figure 25a), et mesurés pour leur longueur totale et leur masse (Figure 25b).

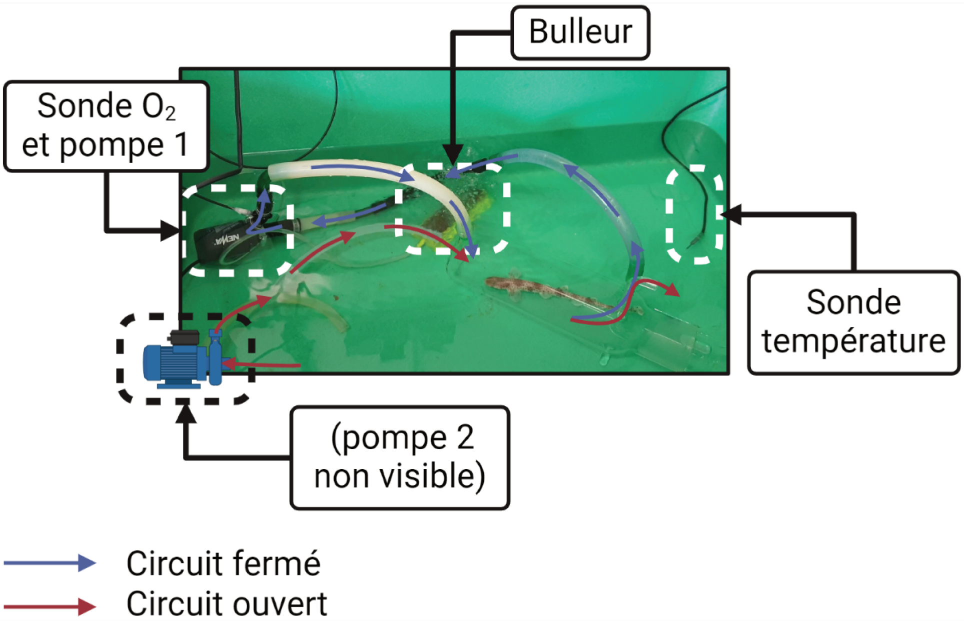

Figure 24 : Photographie de la mesure du taux de consommation d'O_2 chez un juvénile de petite roussette par respirométrie statique à flux intermittent. Créée avec Biorender.com

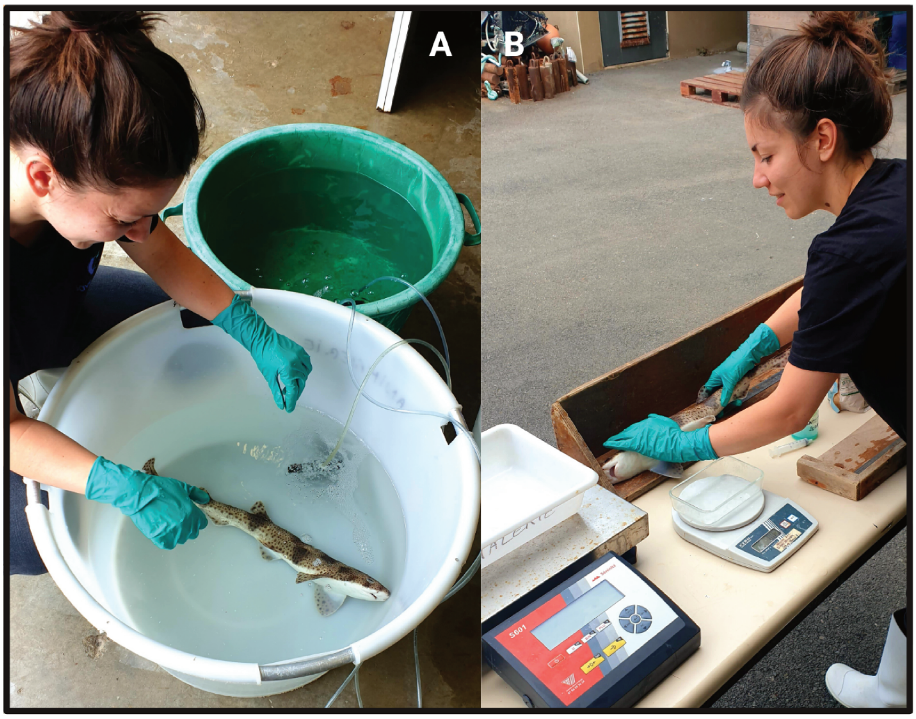

Figure 25 : Photographies illustrant la biométrie effectuée sur une petite roussette après un test de respirométrie statique à flux intermittent. A. Anesthésie de l'individu à l'aide de benzocaïne (40 mg.L^-1) tamponnée au bicarbonate. B. Mesure de la longueur totale.

Au moment de la mise en place de l'expérimentation, l'idée de comparer les réponses physiologiques entre petites et grandes roussettes n'avait pas encore été pleinement explorée. En conséquence, seules quelques données sur le suivi embryonnaire ainsi que sur la taille et le poids à la naissance de quatre grandes roussettes ont été collectées (Figure 26) et leurs taux de consommation de dioxygène en fonction de la température n’ont pas été mesurés.

Figure 26 : Photographies de la grande roussette. A. Embryon de grande roussette au stade embryonnaire 6. B. Mesure de la longueur totale d’un nouveau-né.

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III- Elasmobranch vulnerability to global warming: insights from bioenergetic modelling of catsharks under climate scenarios

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Résumé : Les ectothermes sont supposés être très vulnérables au réchauffement global en raison de leur sensibilité aux fluctuations de température, qui affectent directement leurs processus métaboliques, leurs taux de survie et leur succès reproducteur. Les élasmobranches, qui se caractérisent par un cycle de vie lent et un faible taux de reproduction, pourraient être confrontés à des risques encore accrus. Dans cette étude, nous avons examiné les réponses de deux espèces ayant des cycles biologiques et des aires de répartition distinctes : la petite roussette (*Scyliorhinus canicula*) et la grande roussette (*S. stellaris*). Dans l'Atlantique Nord-Est, les femelles de *S. canicula* atteignent leur maturité sexuelle plus tôt et produisent trois à six fois plus d'œufs que *S. stellaris*, qui est principalement distribuée le long des côtes britanniques. Nous avons utilisé des modèles bioénergétiques pour analyser les variations de la croissance, de la maturité sexuelle, de la production de descendants et de la dynamique de la population pour deux scénarios climatiques futurs projetés pour 2100 par le modèle CMIP6 : « SSP2 : Middle of the road », et « SSP5 : Fossil-fuelled Development (Taking the Highway) ». Ces scénarios ont été comparés aux données historiques de températures entre 1995 et 2014. Alors que le scénario SSP2 a eu un impact modéré sur le taux de survie des deux espèces, le scénario SSP5 aggrave considérablement les conditions, en particulier pour les premiers stades de la vie. Si les taux de survie sont restés à peu près équivalents et élevés pour les températures historiques (80 %) et le scénario SSP2 (83 %) pour les deux espèces, ils ont chuté de manière spectaculaire à 33 % pour *S. canicula* et à 23 % pour *S. stellaris* dans le cadre du scénario SSP5. Les taux de croissance de *S. canicula* restent similaires aux niveaux historiques sous SSP2, tandis que *S. stellaris* présente de légères diminutions. *S. canicula* présente un léger retard de maturation à la fois sous SSP2 et SSP5 par rapport aux températures historiques, mais la proportion d'individus matures finit par dépasser les niveaux historiques sous SSP2. Inversement, *S. stellaris* connaît des retards de maturation croissants avec l'augmentation des températures. Dans le cadre du SSP5, la réduction des taux de croissance et l'altération des taux de reproduction et de survie entraînent une diminution de la croissance de la population et une prolongation des temps de génération, provoquant l'effondrement de la population de *S. stellaris*. Ces résultats mettent en évidence les effets contrastés du réchauffement global sur des espèces pourtant étroitement apparentées, allant jusqu’à des prévisions d'extinction des populations *S. stellaris* dans la zone géographique concernée.

Mots clés : bioénergétique ; dynamique des populations ; modèles individu-centrés ; réchauffement global ; requin ; traits d'histoire de vie

Elasmobranch vulnerability to global warming: insights from bioenergetic modelling of catsharks under climate scenarios

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Conflict of Interest

The authors have no conflicts of interest to declare.

Author Contributions

Noémie Coulon: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - Original Draft, Visualization, Funding acquisition; **Sophie Elliott**: Conceptualization, Validation, Writing - Original Draft, Supervision; **Thomas Barreau**: Validation, Investigation, Resources, Writing - Review & Editing; **Julie Lucas**: Methodology, Investigation, Resources, Writing - Review & Editing; **Emma Gousset**: Formal analysis, Investigation; **Eric Feunteun**: Writing - Review & Editing, Supervision, Project administration; **Alexandre Carpentier**: Conceptualization, Validation, Writing - Review & Editing, Supervision, Project administration

Data availability statement

The length and weight data used for this study are freely available at https://doi.org/10.1017/S0025315416001752 (Mahé et al., 2018); https://doi.org/10.1016/j.marenvres.2024.106531 (Coulon et al., 2024a) or in the supplementary data.

Elasmobranch vulnerability to global warming: insights from bioenergetic modelling of catsharks under climate scenarios

Abstract

Ectotherms are supposed to be highly vulnerable to global warming due to their sensitivity to temperature fluctuations, which directly affect their metabolic processes, survival rates, and reproductive success. Elasmobranchs, characterised by slow life histories and low reproductive rates, may face heightened risks. In this study, we investigated two catshark species with distinct life history traits and distribution ranges: Small-spotted Catshark (*Scyliorhinus canicula*) and Nursehound (*S. stellaris*). In the Northeast Atlantic, *S. canicula* females mature earlier and produce three to six times more eggs than *S. stellaris*, which is mainly distributed along the British coast. We used bioenergetic models to analyse variations in growth, sexual maturity, offspring production, and population dynamics under two future climate scenarios projected for 2100 by the CMIP6 model: SSP2-4.5, a 'Middle of the Road' pathway, and SSP5-8.5, a 'Fossil-fueled Development' pathway. These were compared to historical temperature data from 1994-2015. While the SSP2 scenario showed moderate impacts on the survival rate of both species, SSP5-8.5 significantly worsens conditions, particularly for early life stages. If survival rates remained roughly equivalent and high under historical temperatures (80%) and SSP2 (83%) for both species, it declined dramatically to 33% for *S. canicula* and 23% for *S. stellaris* under SSP5. Growth rates for *S. canicula* remain similar to historical levels under SSP2, whereas *S. stellaris* shows slight differences*. S. canicula* exhibits a slight delay in maturation under both SSP2 and SSP5 compared to historical temperatures, but the proportion of mature individuals eventually surpasses historical levels in SSP2. Conversely, *S. stellaris* experiences increasing delays in maturation with rising temperatures. Under SSP5, reduced growth rates and altered reproduction and survival rates lead to decreased population growth and extended generation times resulting in *S. stellaris's* population crashing.These results highlight the contrasting effects of climate change on closely related species, potentially leading to the extinction of the species with late maturity, low fecundity, and restricted distribution. This underlines the crucial need for conservation strategies that address their vulnerability to global warming.

Keywords

Individual-Based Models; IPCC; life history traits; population dynamics; shark; temperature

1. INTRODUCTION

Global warming is causing rapid and widespread disruptions across all levels of biological organisation, from physiological processes (Little et al., 2020) and life history traits (Holt & Jørgensen, 2015; Huss et al., 2019) to population dynamics (Lindmark et al., 2022; Munday et al., 2008). Most teleost fish, being ectothermic, have metabolisms intrinsically tied to temperature variations (Lefevre et al., 2021; Schulte, 2015). Consequently, changes in survival rates due to metabolic constraints (Madeira et al., 2016) are among the first responses expected to directly and significantly impact population size. Additionally, surviving fish may experience altered growth and/or maturation due to the combined effects of thermal stress (Niu et al., 2023) and increased unpredictability in resource availability (Brodersen et al., 2011; Lindmark et al., 2022). Population dynamics could either accelerate or slow down according to the temperatures experienced by individuals, the species' activity and reproductive strategies (Otero et al., 2012; Shapiro Goldberg et al., 2019). Lastly, considering that the physical condition of fish and ambient temperatures significantly impact the quantity and quality of their eggs and sperm (Baudron et al., 2014; Bobe & Labbé, 2010; Donelson et al., 2010; Pankhurst et al., 1996), variations in temperature could potentially influence the size of initial cohorts.

This is particularly concerning for elasmobranchs, which are late-maturing species with very low fecundity compared to teleost fish (Coulon et al., 2023). Given their slow rate of population renewal, the effects of climate change on elasmobranch population dynamics may not be fully realised until populations have already collapsed (i.e., time-lag effect). For example, bioenergetic model-based predictions by Lear et al. (2020) suggest that future increases in temperature regimes could severely affect the survival, growth and body condition of endangered Bull Shark (*Carcharhinus leucas*) and Largetooth Sawfish (*Pristis pristis*). Similarly, Neer et al. (2007) found that a 2°C average temperature increase could delay the age at maturity of the American Cownose Ray (*Rhinoptera bonasus*) by 1-2 years, depending on its ability to meet increased energy requirements. Rising temperatures are expected to have a major impact on the embryos of oviparous species. Rising temperatures could significantly reduce their hatching success (Musa et al., 2020; Rosa et al., 2014), potentially dropping to only 11% in a scenario where greenhouse gas emissions triple by 2075 (Coulon et al., 2024a). In the Northeast Atlantic, skates and sharks are particularly vulnerable due to the rapid warming of the North Sea and English Channel (Dulvy et al., 2008; Coulon et al., 2024b; Sgotti et al., 2016; Simon et al., 2023), to which is added substantial modern fishing efforts (Rousseau et al., 2019) and non-selective fishing techniques (Smith & Garcia, 2014; Walls & Dulvy, 2021).

The small-spotted catshark (*Scyliorhinus canicul*a) is a demersal shark widely distributed across the Northeast Atlantic, ranging from the North Sea to the Bay of Biscay, and inhabits various depths from coastal waters to the deeper regions of the Celtic Sea. In contrast, Nursehound (*S. stellaris*), a shark with a similar lifestyle, is more commonly found in shallow waters around the British Isles (Bisch et al., 2024; Coulon et al., 2024b; Ellis et al., 2004). As a result, *S. canicula* experiences a broader temperature range compared to *S. stellaris.* These two catsharks also have markedly distinct life-history traits. *S. canicula* females mature before *S. stellaris* ones and produce three to six times more eggs (Ellis & Shackley, 1997; Ivory et al., 2004; Pecuchet et al., 2017). Conversely, *S. canicula* can reach a maximum size of up to 70 cm, which is half that of *S. stellaris* in this geographic region. Therefore, these disparities make *S. canicula* and *S. stellaris* prime candidates for evaluating the potential pressure of temperature rise on population dynamics driven by metabolic processes.

Bioenergetic models are powerful tools for assessing population dynamics (Boyd et al., 2020; Politikos et al., 2015a; 2015b) and species range (Duncan et al., 2020; Payne et al., 2016) by incorporating physiological constraints. By simulating temperature changes, these models provide insights into species' responses to climate change, highlighting potential impacts and adaptive plasticity (Christianson & Johnson, 2020; Holsman et al., 2019). Most bioenergetic models follow one of two approaches (see Brownscombe et al., 2022 for details). The first, exemplified by the Dynamic Energy Budget (DEB; Kooijman, 2010) and Physiological Energy Budget (PEB; Sibly et al., 2013) models are grounded in principles of chemistry, physics, and thermodynamics, aiming for a mechanistic description of bioenergetics (Boult et al., 2018; Boyd et al., 2020). The second approach relies on ecophysiological responses at the organism level to estimate the Scope For Growth (SFG) of individuals, based on a budget of ingested energy and metabolic costs derived from observed physiological responses like consumption and respiration rates (Winberg, 1956). The Wisconsin Energy Budget (WEB; Kitchell et al., 1974, 1977) is based on this SFG approach. WEB is particularly effective for assessing how environmental conditions affect individual growth and survival, providing precise predictions based on temperature or food availability variations (Cerino et al., 2013; Hartman & Jensen, 2017). The data required for this model is often more readily available or easier to measure than those needed for more complex models like DEB. This is especially relevant for elasmobranchs, where such information is limited. With a history of successful application and validation (Deslauriers et al., 2017), the Wisconsin Energy Budget (WEB) model offers a credible and robust method for studying catsharks' responses to environmental changes and population dynamics with limited data.

We developed a bioenergetic model under Wisconsin formulation in conjunction with a population dynamic matrix model, to assess the impact of end-of-century temperature projections on (i) individual growth, (ii) life history traits, and (iii) the population dynamics of *S. canicula* and *S. stellaris*. Our analysis encompassed three climate change scenarios, depicting future socio-economic trajectories and their potential implications for greenhouse gas emissions spanning from current to extreme conditions, as outlined by the Shared Socio-Economic Pathways (SSP) framework (IPCC, 2021). Beyond developing a bioenergetic model specific to *S. canicula* and adapting it to *S. stellaris*, this study aimed to test the hypothesis that species with slower life paces and narrower environmental tolerances exhibit greater sensitivity.

2. MATERIAL & METHODS

2.1. Temperature scenarios

The Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report assessed projected climate outcomes of a set of five scenarios that are based on the framework of the SSPs (IPCC, 2021). In this study, we used historical temperature data from 1994 to 2015 and future temperature projections for 2100 based on two scenarios from the CMIP6 climate model. We considered 'SSP2-4.5: Middle of the Road' and 'SSP5-8.5: Fossil-fuelled Development' climate scenarios. SSP2-4.5 represents a scenario where CO_2 emissions stabilise at current levels until 2050 and then gradually decline, though they do not reach net zero by 2100 (Fricko et al., 2017). In contrast, SSP5-8.5, characterised by a 'Fossil-fuelled Development' pathway, anticipates a dramatic increase in CO2 emissions, which are projected to triple by 2075 (Kriegler et al., 2017). The monthly temperatures were obtained from forecasts for Western and Central Europe and downloaded from http://interactive-atlas.ipcc.ch (Gutiérrez et al., 2021; Iturbide et al., 2021; Figure 1).

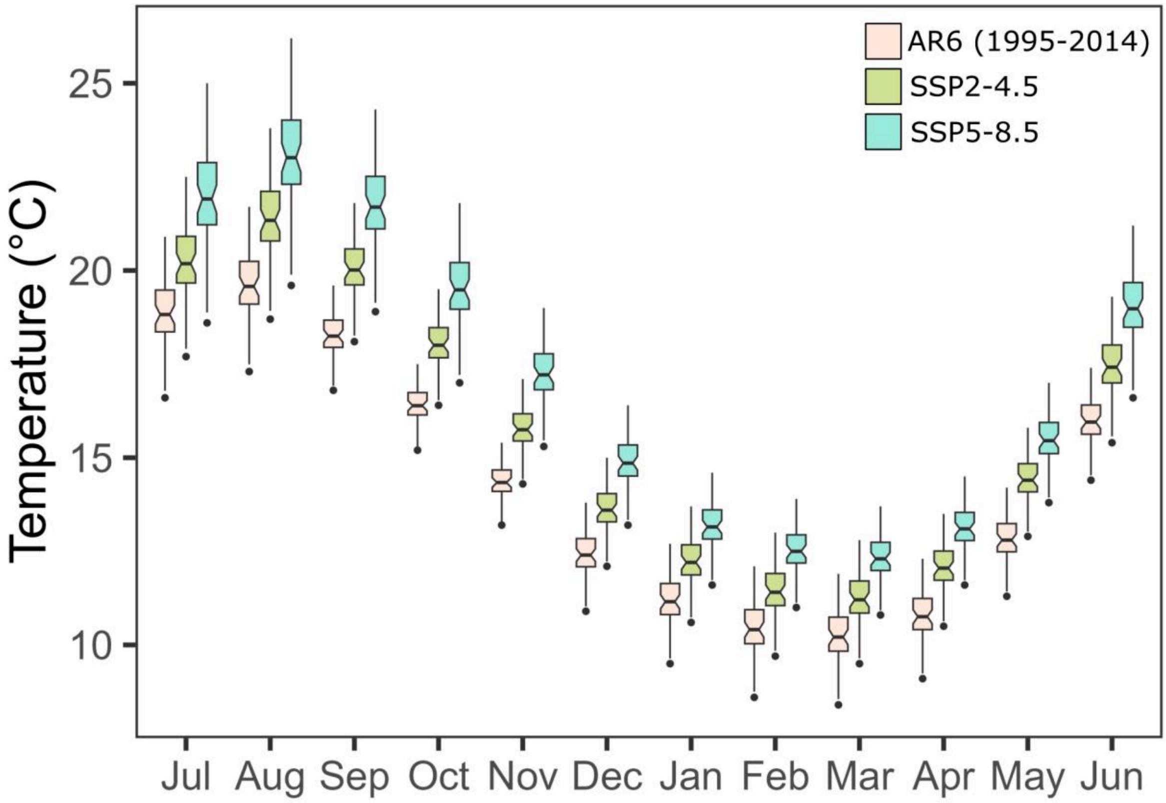


FIGURE 1. Monthly temperature applied to each individual. The temperatures were obtained from forecasts for Western and Central Europe and downloaded from http://interactive-atlas.ipcc.ch (Gutiérrez et al., 2021; Iturbide et al., 2021). Historical

temperatures from 1994 to 2015 (AR6 1994-2015) are shown in beige. Temperatures predicted for 2100 under the climate scenarios "SSP2: Middle of the road" and "SSP5: Fossil-fuelled Development (Taking the Highway)" are respectively shown in light green and light blue. The order of the months indicates the order of the temperatures experienced by the individuals during a simulation.

2.2. Bioenergetic model parameters

Bioenergetic models under Wisconsin formulation (Hanson et al., 1997) use an energy balance equation in which each of the physiological processes (metabolism, wastes, and growth) is described by a set of functions that are regulated primarily by water temperature and body weight (Winberg, 1956). They can be used to estimate growth, linking fish physiology to environmental conditions and quantifying the relative importance of various environmental factors on individual growth (Hanson et al., 1997). Consumed energy is first allocated to metabolism, some is lost as waste and that left over can be allocated to growth.

The parameters for the bioenergetics models developed for *S. canicula* and *S. stellaris* follow the naming and parameter convention used in the Fish Bioenergetics 4.0 software (Deslauriers et al., 2017; Table 1). Maximum daily consumption (Cmax) is expressed as a specific rate (g of prey consumed per g body mass per day) and is estimated as an allometric function of mass from *ad libitum* feeding experiments ranging from 0.07 of the weight of the smallest individuals to 0.03 of the weight of the largest (Neer et al., 2007), where CA and CB are the intercept and slope respectively.

$$C_{max} = CA \times W^{CB}$$

Maximum daily consumption was then modified by a temperature dependence function (F(T)) and a proportionality constant (p) that accounts for ecological constraints on the maximum feeding rate (Cmax). The p value theoretically ranges from 0 to 1, with 0 representing no feeding, and 1 indicating the fish is feeding at its maximum rate based on its size and water temperature.

$$C \ = C_{max} \times p \ \times F(T)$$

The Thornton & Lessem (1978) model (consumption equation 3; Deslauriers et al., 2017) was used to describe the temperature dependence of C_{max} for each species (F(T)). This model provides a better fit for some cool- and coldwater species and is essentially the product of two sigmoid curves, one fit to the increasing portion of the temperature dependence function and the other to the decreasing portion. Records from the Ocean Biodiversity Information System (OBIS, 2023) openly available on https://obis.org/, were used to parametrize it (Figure S1, Table 1). Egestion (faecal waste, F) and excretion (nitrogenous waste, U) were computed as a constant proportion of consumed energy (Kitchell et al., 1977) (waste loss equation 1; Deslauriers et al., 2017). Specific rate of respiration (R) is dependent on individual mass (W), water temperature (G(T)) and an activity multiplier (ACT):

$$R = RA \times W^{RB} \times G(T) \times ACT$$

where RA and RB are the intercept and slope for the allometric mass function. RA and RB parameters for *S. canicula* were determined by Butler & Taylor (1985) but not using intermittent flow static respirometry method, commonly used method nowaday to measure standard metabolic rates (SMR)—the minimum oxygen consumption necessary for maintaining fundamental physiological functions such as respiration, blood circulation, and ion balance (Little et al., 2020). This method has been recognized as crucial and highly sensitive in bioenergetic models of fish (Bartell et al., 1986; Rice & Cochran, 1984). For this reason, we determined the relationship afresh by measuring standard metabolic rates and converting O_2 consumption rates (g O2. g fish^{-1}. day^{-1}; Figure S2) using the oxy-calorific coefficient of 13,560 J. g O2^{-1}. Limited data on *S. stellaris* is available in the literature (Figure S2; Piiper et al., 1977). The O_2 consumption rates were not obtained using current methods and units, and we were unable to conduct additional laboratory measurements for this species. Therefore, we combined these data with those obtained experimentally for *S. canicula*. We determined a single model for both species, which was found to be similar to that defined for *S. canicula* alone (Figure S2). Consequently, the parameters characterising the specific rate of respiration of *S. canicula* were imputed to *S. stellaris*. The Kitchell et al. (1977) model (respiration equation

2; Deslauriers et al., 2017) was used to describe the temperature-dependence of respiration (G(T)) adjusted by an activity multiplier (ACT).

TABLE 1. Models and parameters used in the bioenergetic models for *S. canicula* and *S. stellaris*. Parameter names follow the convention of the Fish Bioenergetics 4.0 software (Deaslauriers et al., 2017) under the Wisconsin Energy Budget formulation (Kitchell et al., 1974, 1977).

<table>
<tr><th>Model parameter</th><th>Explanation</th><th><i>S. canicula</i>
</th><th><i>S. stellaris</i>
</th></tr>
<tr><td colspan="2">Consumption model equation</td><td colspan="2">3</td></tr>
<tr><td>CA</td><td>Intercept of the allometric mass function</td><td colspan="2">0.0853</td></tr>
<tr><td>CB</td><td>Slope of the allometric mass function</td><td colspan="2">-0.15</td></tr>
<tr><td>CQ</td><td>Lower water temperature where the temperature dependence is a small proportion (CK1) of C_{max}</td><td>9.7</td><td>10</td></tr>
<tr><td>CTO</td><td>Water temperature corresponding to 0.98 of C_{max}</td><td>11.3</td><td>11.4</td></tr>
<tr><td>CTM</td><td>Water temperature still corresponding to 0.98 of C_{max}</td><td>12.8</td><td>12</td></tr>
<tr><td>CTL</td><td>Upper water temperature where the temperature dependence is a small proportion (CK4) of C_{max}</td><td colspan="2">18.5</td></tr>
<tr><td>CK1</td><td>Small proportion of C_{max}</td><td colspan="2">0.397</td></tr>
<tr><td>CK4</td><td>Small proportion of C_{max}</td><td colspan="2">0.655</td></tr>
<tr><td colspan="2">Respiration model equation</td><td colspan="2">2</td></tr>
<tr><td>RA</td><td>Intercept of the allometric mass function</td><td colspan="2">0.000933</td></tr>
<tr><td>RB</td><td>Slope of the allometric mass function</td><td colspan="2">-0.0501</td></tr>
<tr><td>RQ</td><td>Approximate the Q10 (the rate at which the function increases over relatively low water temperatures).</td><td colspan="2">1.32</td></tr>
</table>

RT0	Optimum temperature for respiration (where respiration is highest),	19	
RTM	Maximum (lethal) water temperature	21	
ACT	Activity multiplier	2.6 (Sims et al., 2006)	1.47 (Piiper et al., 1997)
SDA	Specific dynamic action	0.12 (Sims & Davies; 1994)	
Egestion model equation		1	
FA	Constant proportion of consumption	0.16	
Excretion model equation		1	
UA	Constant proportion of assimilated energy (consumption minus egestion)	0.1	

During calibration process, iterative simulations for 1000 females of *S. canicula* and *S. stellaris* were performed to adjust the p value for each age class (Deslauriers et al., 2017) until the daily growth simulated by the model resulted in a predicted weight at the end of each age that matched the observed weights at age determined from weight-length field data converted into weight-age data with the *'fishR'* R package (Appendix 1). Weight-length field data were from the western part of the English Channel, the Irish Sea, the Celtic Sea and the Bay of Biscay. They included juveniles hatched at the Dinard marine station (Coulon et al., 2024a), females collected during the scientific bottom trawl surveys CAMANOC, EVHOE, and CGFS (Mahé et al., 2018), and females gathered from a survey at French fish auctions, Elasmobranch-on-Shore (EOS), as part of the European Data Collection Framework, which aims to collect, analyse, and share data on elasmobranch fishing. Given that Von Bertalanffy growth parameters are highly dependent on the location of individuals, we used the parameters determined by Ivory & Nolan (2004) for females of *S. canicula* in the Irish Sea and the Celtic Sea ($Lm_{S.\ canicula} = 57$ cm; $Linf_{S.\ canicula} = 75.14$ cm; $K_{S.\ canicula} = 0.150$, $t0_{S.\ canicula} = -0.96$). Since the available growth parameters for *S. stellaris* are derived exclusively from Mediterranean specimens (Capapé et al., 2006), we used the growth parameters calculated by Greenstreet et al. (2012) for the North Sea. However, the size at maturity reported in this study is questionable, as it is smaller than that observed in the Mediterranean (Finucci et al., 2021) although the size structure of *S. stellaris* in the North East Atlantic tends to present larger individuals (Bisch et al., 2024). Therefore, we considered as a proxy for the size at maturity, the smallest size female with an egg emerging from the cloaca observed opportunistically at fish auctions during EOS (Table S1) ($Lm_{\textit{S. stellaris}} = 90$ cm; $Linf_{\textit{S. stellaris}} = 140$ cm; $K_{\textit{S. stellaris}} = 0.094$, $t0_{\text{S. stellaris}} = -4.35$).

2.3. Standard Metabolic Rate (SMR)

The care and use of experimental animals complied with French animal welfare laws, guidelines and policies as approved by the Ministry of Higher Education and Research in accordance with the provisions of the French Rural and Maritime Fishing Code, in particular articles R.214-87 to R.214-126 [approval number A3509547]

Twelve eggs were laid in captivity at the marine aquarium of Tregastel from wild females fished in the Bay of Saint Anne (English Channel, France), incubated (~5 months) and bred at the marine station of Dinard until the experiment (~8 months) at 16 ± 1°C. The juveniles were six males and six females. We included the 12 juveniles in the study to make use of all the hatched individuals, regardless of their sex, considering there was no reproductive investment (i.e., reproductive energy allocation) in the first year. We also captured 12 females using bottom trawl along the Bay of Saint Brieuc (English Channel, France) at the end of May 2023. The 24 individuals were placed in three 700-L biosphere tanks with four juveniles and four captured females per tank. Juveniles were separated from larger individuals to avoid any risk of cannibalism and to ensure optimal feeding, using a crate suspended in the tanks. Sharks were fed *ad libitum* twice a week with thawed hake and squid. Tanks were fully aerated to create a normoxic (>95% air saturation) environment under each condition with independent filtration systems. Nitrite (< 0.05 mg.L^{-1}) was monitored daily and

1/3 of the tanks' volume was renewed to ensure good water quality, while salinity (34 ppm) and nitrate (< 40 mg.L^{-1}) were monitored weekly.

We chose June temperatures to study standard metabolic rate responses to warm conditions, while ensuring that the temperatures tested were within *S. canicula* current temperature range. As the sea surface temperature at the end of May was around 15°C at the time of capture, water temperature was progressively increased by 2°C per week until the desired temperatures were reached ($T_{control}$ = 15.5°C; $T_{SSP2-4.5}$ = 17.4°C; $T_{SSP5-8.5}$ = 19.5°C) and maintained with a heater connected to a temperature control unit. This acclimatisation time also ensured that the individuals caught were in a healthy state before starting the experiment. Individuals were then maintained at the experimental temperatures for a month.

SMRs were determined using intermittent flow static respirometry method, commonly used in elasmobranch species that are capable of buccal pumping (Chen et al., 2008; Molina et al., 2020; Rummer et al., 2022; Sims, 1996). Two homemade transparent respirometers with enrichments were used: 1.5 L for individuals under 28 g and 75 L for individuals over 190 g, and immersed by two in larger mesocosms (reducing individual isolation), with filtered, oxygenated seawater at the same temperature as the stabulation tanks for the duration of the test, all set in a photo-thermoregulated room with no walk-through. Individuals were fasted for 5 days before oxygen consumption measurements were taken to reach a postabsorptive state for this species (Hopkins & Cech, 1994; Neer et al., 2006; Chen et al., 2008). Individuals were placed in respirometry chambers adapted to their weight, and the first hour was devoted to acclimatisation to the respirometry chamber with a continuous water flow (Tullis & Baillie 2005; Lear et al. 2018). Then the test alternated between 15 to 60 minutes of oxygen consumption measurements (depending on the temperature treatment) and 60 minutes of oxygen renewal. The sharks were then left in the respirometry chambers for 16 hours. The time interval between oxygen renewal was long enough for O_2 decline to be detected, but short enough that O_2 levels in the chambers did not fall below 80% saturation at the end of the measurement period, to avoid stressing individuals (Svendsen et al., 2016). The oxygen saturation was measured using a mini oxygen sensor with a dip probe connected to a Witrox 4 oxygen metre

(LoligoSystems). We validated the measurements by following the recommendations of Chabot et al. (2020) and defining a threshold R^2 of 0.85. Oxygen saturation with empty chambers were measured before and after the respirometry measurements on the sharks and did not reveal any significant microbial respiration rates. As metabolic rates were estimated in relation to the weight of each individual, biometry was carried out after each test. The sharks were individually removed from the respirometry chambers and anaesthetised (benzocaine, 40 $mg.L^{-1}$ buffered with bicarbonate) for biometry (total length, mass).

The rate of oxygen consumption ($mg.O_2.individual^{-1}.h^{-1}$) was calculated by multiplying the rate of decrease in oxygen saturation by the volume of the tank (Wheeler et al., 2021). Rates were used to calculate a RQ parameter (approximates the Q10) and converted into $g.O2.g\ fish^{-1}.day^{-1}$ to determine RA and RB parameters (Deslauriers et al., 2017; Figure S2).

2.4. Reproduction

The proportion of mature individuals based on size was converted into the proportion of mature individuals based on weight (Figure S3). The probability of an individual reproducing was determined based on a logistic function that related the fraction of mature individuals at that age to body weight (Ellis & Shackley, 1997 ; Figure S3). During catsharks peak egg-laying period (1st -30th June) (Ellis & Shackley, 1997), if the random number drawn from a uniform distribution was less than the mature fraction based on an individual's weight each day, then the individual would lay that day (Neer et al., 2007). The number of eggs laid per individual during this period was calculated by multiplying the number of laying events (in days) with a daily egg production rate. The June daily egg production rate of *S. canicula* was determined from Ellis & Schackley (1997) ($egg.rate_{S.canicula}$ = 0.28 $egg.day^{-1}.female^{-1}$) while that of *S. stellaris* was determined from Capapé et al. (2006) and observations from the Tregastel Aquarium, located in the western part of the English Channel, from 2012 to 2013 ($egg.rate_{S.stellaris}$ = 0.03 $egg.day^{-1}.female^{-1}$). Reproductive investment was calculated by multiplying the number of eggs laid by the average weight of an egg ($egg.weight_{S.canicula}$ = 4g;

Mellinger, 1983: egg.weight$_{S.stellaris}$ = 17g; Musa et al., 2018), and subtracting this from the female's weight on June 30th.

2.5. Mortality

The probability of dying was assigned to natural mortality of catsharks (n = 0.15) according to the ecopath model of Sánchez et al. (2005) calibrated in the Cantabrian Sea. Mortality was determined by fitting a decreasing curve between annual mortality rate and body weight (Roff 1993, Cortés 2004; Figure S4). The Instantaneous annual natural Mortality Rate (IMR) for the smallest individuals of both species was determined for each scenario from the first-year mortality rates determined by Coulon et al. (2024a). These rates were obtained from experiments exposing *S. canicula* embryos and juveniles to historical temperatures spanning from 1994 to 2015 (AR6 1994-2015), as well as temperatures predicted for the year 2100 under the climate scenarios SSP2-4.5 and SSP5-8.5 ($IMR_{Age\ 0,\ control} = 0.19$; $IMR_{Age\ 0,\ SSP2\text{-}4.5} = 0.17$; $IMR_{Age\ 0,\ SSP5\text{-}8.5} = 0.89$). The IMR decreases exponentially with weight, approaching 0.15 for the heaviest (oldest) individuals (Sanchez et al., 2005; Figure S4). The life expectancy of each species was determined from its growth parameters (i.e., 13 years for *S. canicula* and 16 years for *S. stellaris*). Annual mortality rates were converted to daily rates and if the randomly generated number from a uniform distribution was less than the daily probability of dying, then the individual died and was removed from the simulation.

2.6. Simulation process

The three temperature scenarios (AR6 1994-2015; SSP2-4.5: Middle of the road and SSP5-8.5: Fossil-fuelled Development; Figure 1) were simulated using the bioenergetic and matrix projection models. All simulations of the bioenergetic model started with 1000 females on the 1st of July. Initial weights for each scenario were generated from a normal distribution based on observed weight-at-birth information of *S. canicula* and *S. stellaris* (Appendix 1). As the *S. stellaris* individuals were not exposed to the experimental conditions, their initial weights for the SSP2-4.5 and SSP5-8.5 scenarios were estimated based on the weight differences observed in *S. canicula* under the same scenarios (Coulon et al., 2024a). Body weight of each individual was updated daily. Weight-dependent maturity was used to determine reproduction (Figure S3). Weight loss associated with laying events was based on the observed average weight of eggs. Numbers of individuals in the cohort were decreased daily on a specified weight-dependent mortality rate (Figure S4). The model predicted the number of individuals alive, average weight of an individual, and number of pups produced by year. These predictions were used to estimate the parameters of age structured matrix projection models.

Weight-age data were transformed into weight-length data using the 'fishR' R package. The predicted length-at-age curves for each scenario were fitted using the 'nls' R function to estimate their parameters (Linf, K, t0). Subsequently, these growth models were compared using an ANOVA test. The size at maturity (Lm) for each species determined the maturity status of individuals (binomial variable; 0: immature, 1: mature). For each age class, a chi-squared test was conducted to compare the number of mature individuals across scenarios, using maturity as the response variable and scenarios as predictors. The impact of scenarios on offspring production was analysed using a Generalised Linear Model with a Gaussian distribution for *S. canicula* (continuous number of offspring between 0 and 8) and a quasi-binomial distribution with a logit link for *S. stellaris* (continuous number of offspring between 0 and 1).

2.7. Individual-level variability

Two sources of individual variability in the growth of catsharks were simulated. First, individual temperature variability was incorporated to account for the fact that not all individuals are in the same location and therefore experience similar, but not identical, daily temperatures. For each day of the simulation, each individual was assigned a daily water temperature drawn from a normal distribution with the mean equal to the temperature predicted by the temperature function and a standard deviation of the simulated data's variability around the predicted temperatures (Figure 1). Variability in p values was incorporated to reflect the variability of prey encountered and ingested by individuals depending on their location, as well as variability in prey capture capacity (Neer et al., 2007). Individuals were assigned values of p from a normal distribution having a mean of the age-specific p-value determined through the calibration process, and a coefficient of variation of 1% (Neer et al., 2007; Table S2).

2.8. Matrix projection models

We used Leslie age-structured matrix projection models to analyse the population-level impacts of warmer water temperature scenarios (Eq. 1).

$$\begin{pmatrix} 0 & P_0 \cdot m_0 & 0 & \cdots & 0 & 0 \\ P_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & P_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & P_{n-1} & 0 \\ 0 & 0 & 0 & \cdots & 0 & P_n \end{pmatrix} \qquad \text{Eq. 1}$$

The matrix projection models followed females using a birth-pulse structure with a post-breeding census (Caswell 2001). Annual survival rates (sub-diagonal elements, Table S3) and fertility values, (top row; defined as fi = Pi · mi where fi = fertility at age i, Pi = age-specific survival probability and mi = age-specific reproductive output, Table S4) of each matrix were estimated from the numbers surviving and pup production (number of pups per female) predicted by the bioenergetics model under the AR6 1994-2015; SSP2-4.5 and SSP5-8.5 scenarios. The age-specific fecundity estimates predicted by the bioenergetics model were divided by 2 to reflect a 1:1 male:female sex ratio.

For each scenario, we calculated the finite (λ) and instantaneous (r) population growth rates, net reproductive rate, and generation time using the *'pop.bio'* R package. The finite population growth rate (λ) indicates whether a population is growing (λ > 1) or declining (λ < 1) from one period to the next. The instantaneous growth rate (r) is derived from the natural logarithm of λ and reflects the continuous growth rate of the population (r > 0 indicates growth;

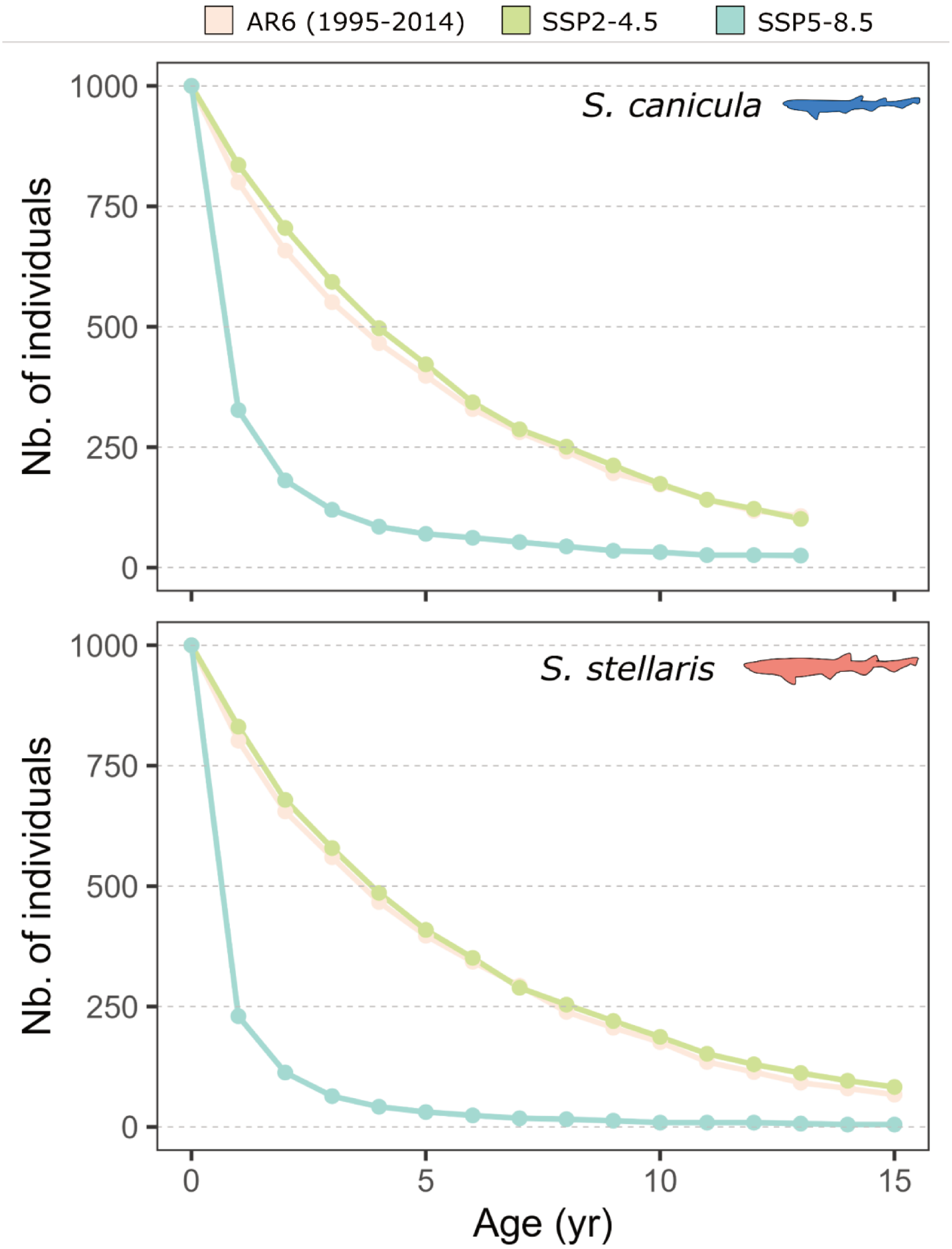
$r < 0$ indicates decline). The net reproductive rate (R_0) represents the average number of offspring produced by each individual over its lifetime, determining whether the population can replace itself. Generation time refers to the average age of parents producing the offspring at stable age distribution.

3. RESULTS

3.1. Bioenergetics model

Model-predicted weights-at-age under the AR6 1994-2015 scenario closely matched the mean weights from a Von Bertalanffy growth curve and individual measurements derived from observed size-at-age data for both species (ANOVA, $p = 1$; Figure S5, Table S5), indicating that the model predictions are robust.

The bioenergetics model predicts that the number of individuals from the cohort ($N = 1000$) surviving to the first age is markedly lower under the SSP5-8.5 scenario compared to the AR6 1994-2015 and SSP2-4.5 for both species (Figure 2, Table S3). Survival rates decreased from 80% and 83% (Figure 2) under the AR6 1994-2015 and SSP2-4.5 scenarios to 33% for *S. canicula* and 23% for *S. stellaris* under the SSP5-8.5 scenario (Figure 2; Table S3). Mortality peaks between July and October of age 0 (Figure S6), the first few months of the simulation, when temperatures are the warmest (Figure 1).



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391 **FIGURE 2. Predicted survival curves on June 30 of each year.** Predicted survival curve under the historical temperatures from 1994 to 2015 (AR6 1994-2015) is shown in beige. Predicted survival curves under the temperatures predicted for 2100 under the climate scenarios "SSP2: Middle of the road" and "SSP5: Fossil-fuelled Development (Taking the Highway)" are respectively shown in light green and light blue. The top panel describes the responses of *S. canicula* (blue shape) and the bottom panel those of *S. stellaris* (light red shape).

The growth curve of *S. canicula* individuals under the SSP5-8.5 scenario differs significantly from those under the SSP2-4.5 and AR6 (1994-2015) scenarios (F(3372, 1083) = 7.2593, $p < 0.001$). Similarly, the growth curve of *S. stellaris* individuals under the SSP5-8.5 scenario differs significantly from that under the AR6 (1994-2015) scenario F(4623, 592) = 3.20; $p < 0.001$; Figure 3) and shows marginal differences compared to the SSP2-4.5 scenario (F(4855, 592) = 1.08 ; $p = 0.10$; Figure 3). Under the SSP5-8.5 scenario, the average weight of *S. canicula* individuals ranged from 72% (W = 18.5 ± 2.9 g; $N_{SSP5\text{-}8.5;\ \mathit{S.canicula;\ Age\ 1}}$ = 328) to 94% (W = 814.8 ± 150.1 g; $N_{SSP5\text{-}8.5;\ \mathit{S.canicula;\ Age\ 10}}$ = 26) compared to that under the AR6 1994-2015 scenario at similar ages (W = 25.7 ± 4.1 g; $N_{AR6\ (1994\text{-}2015);\ \mathit{S.canicula;\ Age\ 1}}$ = 801 and W = 861.9 ± 265.7 g; $N_{AR6\ (1994\text{-}2015);\ \mathit{S.canicula;\ Age\ 10}}$ = 141; Table S6). While the difference in weight diminished as *S. canicula* individuals aged, it did not appear for *S. stellaris* individuals (Figure 3). Under the SSP2-4.5 scenario, the average weight of *S. stellaris* individuals ranged from 98% (W = 53.2 ± 1.6 g; $N_{SSP2\text{-}4.5;\ \mathit{S.stellaris;\ Age\ 1}}$ = 679) to 89% (W = 5518.9 ± 892.9 g; $N_{SSP2\text{-}4.5;\ \mathit{S.stellaris;\ Age\ 14}}$ = 83) compared to that under the AR6 1994-2015 scenario between age 1 (W = 54.2 ± 3.9 g; $N_{AR6\ (1994\text{-}2015);\ \mathit{S.stellaris\ Age\ 1}}$ = 655) and age 14 (W = 6199.9 ± 1565.6 g; $N_{AR6\ (1994\text{-}2015);\ \mathit{S.stellaris;\ Age\ 15}}$ = 141; Table S6). Under the SSP5-8.5 scenario, the average weight of *S. stellaris* individuals ranged from 74% (W = 39.2 ± 3.3g; $N_{SSP5\text{-}8.5;\ \mathit{S.stellarisa;\ Age\ 1}}$ = 113) to 70% (W = 3879.3 ± 619.3g; $N_{SSP5\text{-}8.5;\ \mathit{S.stellaris;\ Age\ 14}}$ = 67) compared to that under the AR6 1994-2015 scenario between ages 1 and 14.

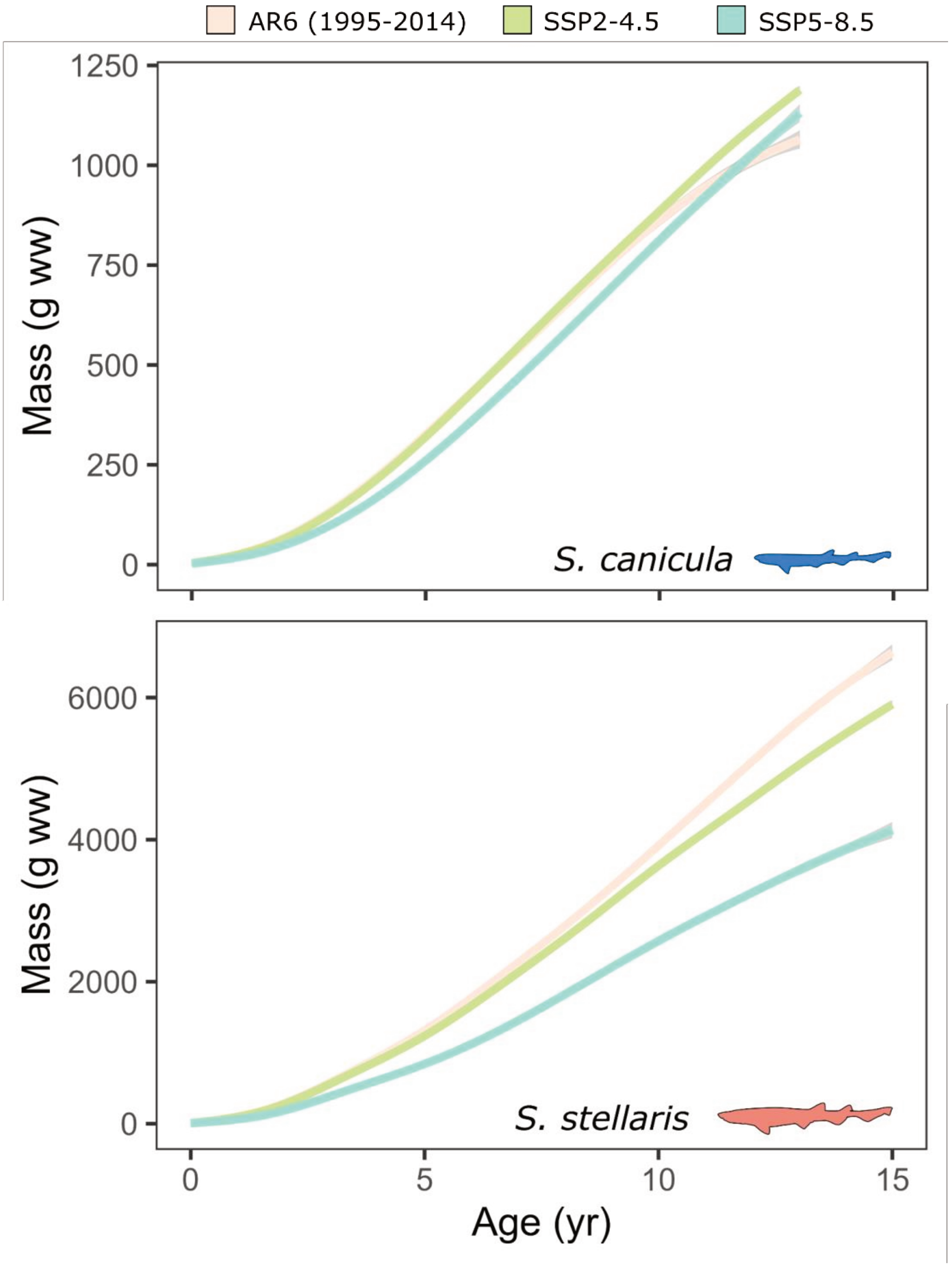

FIGURE 3. Predicted average weights of all individuals live on June 30 of each year. Predicted average weights curve under the historical temperatures from 1994 to 2015 (AR6 1994-2015) is shown in beige. Predicted average weights under the temperatures predicted for 2100 under the climate scenarios "SSP2: Middle of the road" and "SSP5: Fossil-fuelled Development (Taking the Highway)" are respectively shown in light green and light blue. The

top panel describes the responses of *S. canicula* (blue shape) and the bottom panel those of *S. stellaris* (light red shape).

At 7 years old, only 5% (13 out of 281) of *S. canicula* individuals in scenario AR6 (19942015) were mature ($\chi^2(2) = 16.06$, $p < 0.001$). By age 8, scenario AR6 (1994-2015) had a higher proportion of females mature compared to SSP2-4.5 and SSP5-8.5 ($\chi^2(2) = 32.46$, $p < 0.001$). Between ages 9 and 10, the proportion of mature *S. canicula* was higher in scenarios AR6 (1994-2015) and SSP2-4.5 than in SSP5-8.5 ($\chi^2(2) = 12.16$, $p < 0.01$). This is also the age at which more than half of the *S. canicula* populations under the AR6 (1994-2015) and SSP2-4.5 scenarios are mature. At age 10, SSP2-4.5 had more mature individuals than AR6 (1994-2015) and SSP5-8.5 ($\chi^2(2) = 26.28$, $p < 0.001$). From age 11 onwards, SSP2-4.5 and SSP2-8.5 had more mature *S. canicula* individuals compared to AR6 (1994-2015; $\chi^2(2) = 17.17$, $p < 0.001$; $\chi^2(2) = 21.52$, $p < 0.001$; $\chi^2(2) = 20.23$, $p < 0.001$). At 8 years old, only 17% (41 out of 239) of *S. stellaris* individuals in scenario AR6 (19942015) were mature ($\chi^2(2) = 50.38$, $p < 0.001$). The first maturity occurred at 9 years under scenario SSP2-4.5 (76 out of 220 individuals), and at 11 years under scenario SSP5.8.5 (1 out of 8 individuals; Figure 4). In the AR6 scenario (1994-2015), more than 50% of the population reached maturity by age 9, in the SSP2-4.5 scenario by age 10, and in the SSP5-8.5 scenario by age 13. Between ages 9 to 13, the proportion of mature *S. stellaris* was higher under scenarios AR6 (1994-2015) and SSP2-4.5 compared to scenario SSP5-.5 ($\chi^2(2) = 44.19$, $p < 0.001$; $\chi^2(2) = 23.55$, $p < 0.001$; $\chi^2(2) = 31.83$, $p < 0.001$; $\chi^2(2) = 34.57$, $p < 0.001$; $\chi^2(2) = 20.32$, $p < 0.001$; $\chi^2(2) = 11.69$, $p < 0.01$; $\chi^2(2) = 9.63$, $p < 0.01$).

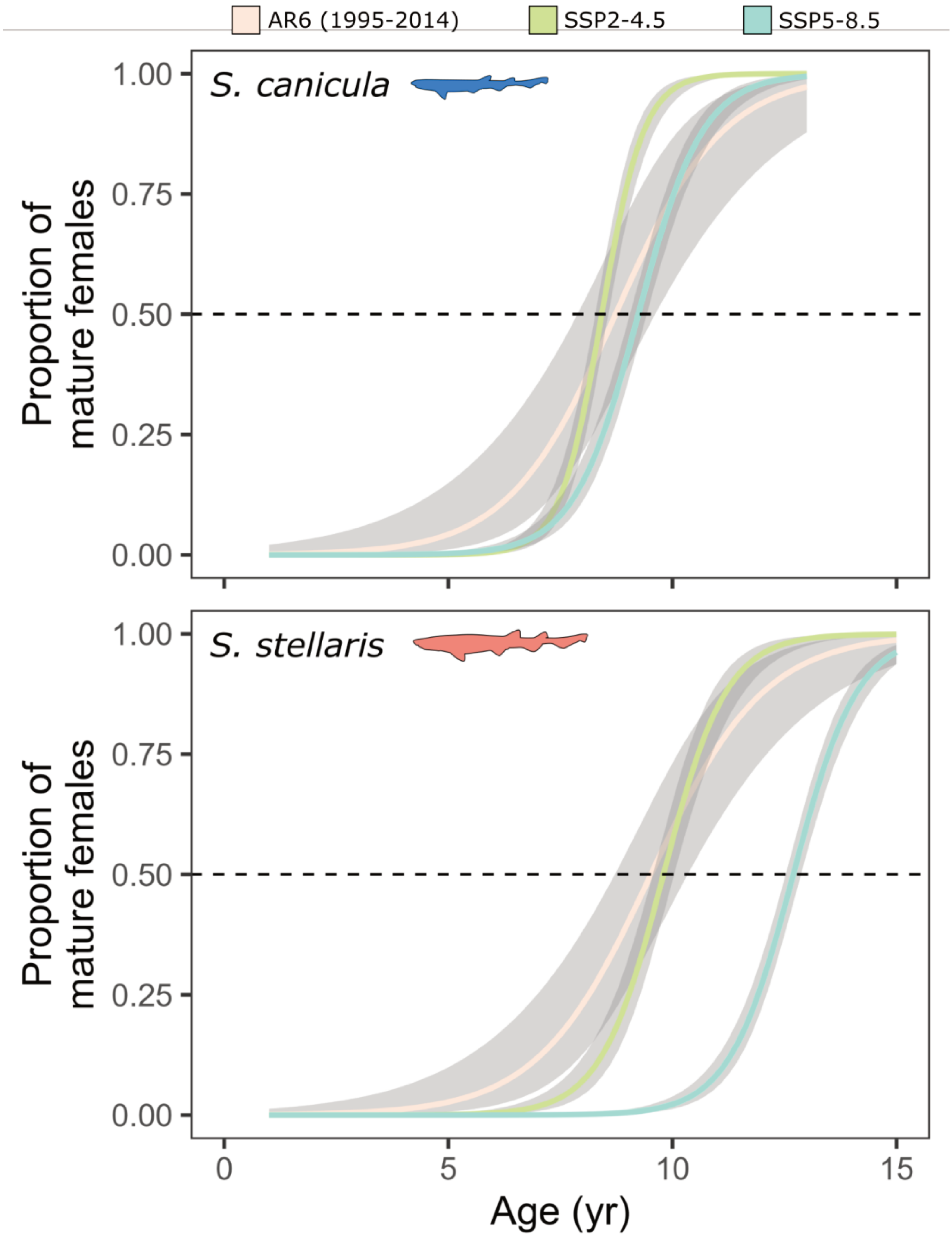

FIGURE 4. Predicted percent maturity by age on June 30 of each year. Predicted percent maturity by age under the historical temperatures from 1994 to 2015 (AR6 1994-2015) is shown in beige. Predicted percent maturity by age under the temperatures predicted for 2100 under the climate scenarios "SSP2: Middle of the road" and "SSP5: Fossil-fuelled Development (Taking the Highway)" are respectively shown in light green and light blue. The

top panel describes the responses of *S. canicula* (blue shape) and the bottom panel those of *S. stellaris* (light red shape).

The number of eggs laid per female *S. canicula* in the SSP5-8.5 scenario was significantly lower at ages 1 (log likelihood = 556.51, RDf = 1541, p = 0.03), 2 (log likelihood = -157.99, RDf = 1261, p = 0.02), 3 (log likelihood = -585.12, RDf = 1045, p < 0.001), 4 (log likelihood = -884.87, RDf = 887; p < 0.001), 5 (log likelihood = -960.87, RDf = 731; p < 0.001) and 6 (log likelihood = -963.03, RDf = 618, p < 0.001) compared to females in the AR6 (1994-2015) scenario (Figure 5). In the SSP2-4.5 scenario, egg laying was marginally lower at age 2 (log likelihood = -157.99, RDf = 1261; p = 0.08), much lower at ages 3 (log likelihood = -585.12, RDf = 1045; p < 0.01), 4 (log likelihood = -884.87, RDf = 887; p = 0.05), 5 (log likelihood = -960.87, RDf = 731; p < 0.01). Conversely, egg laying was marginally higher at age 7 (log likelihood = -934.62, RDf = 533; p = 0.06) and higher at ages 9 (log likelihood = -709.67, RDf = 375; p = 0.05), 10 (log likelihood = -590.91, RDf = 305; p = 0.01), 11 (log likelihood = -504.40, RDf = 263; p < 0.01) and 12 (log likelihood = -446.54, RDf = 230; p < 0.001) compared to the AR6 (1994-2015) scenario (Figure 5). For *S. stellaris*, the number of eggs laid per female in the SSP5-8.5 scenario was significantly lower at age 1 (coefficient = -0.66, RDf = 1445; p < 0.01), marginally lower at age 2 (coefficient = -0.34; RDf = 1200; p = 0.05), lower at age 4 (coefficient = -0.75; RDf = 834; p < 0.001), and ages 11 to 14 (coefficient = -1.08, RDf = 250; coefficient = -1.10, RDf = 208; coefficient = -1.25, Rdf = 178; coefficient = -1.27, RDf = 152; p < 0.001) compared to the AR6 (1994-2015) scenario (Figure 5). Similarly, in both the SSP2-4.5 and SSP5-8.5 scenarios, the number of eggs laid per female was lower at age 3 (RDf = 992, coefficient = -0.15, p < 0.01 and coefficient = -0.72, p < 0.001), age 5 (RDf = 715; coefficient = -0.10, p = 0.03 and coefficient = -0.82, p < 0.001), and from ages 6 to 10 (RDf = 597, coefficient = -0.15, p < 0.01; coefficient = -0.96, p < 0.001; RDf = 506, coefficient = -0.21, coefficient = -1.14, p < 0.001; RDf = 436, coefficient = -1.15, p = 0.15, coefficient = -0.99, p < 0.001; RDf = 369, coefficient = -0.17, p = 0.02, coefficient = -1.18, p < 0.001; RDf = 293, coefficient = -0.23, p < 0.01, coefficient = -1.00, p < 0.001) compared to the AR6 (1994-2015) scenario (Figure 5)

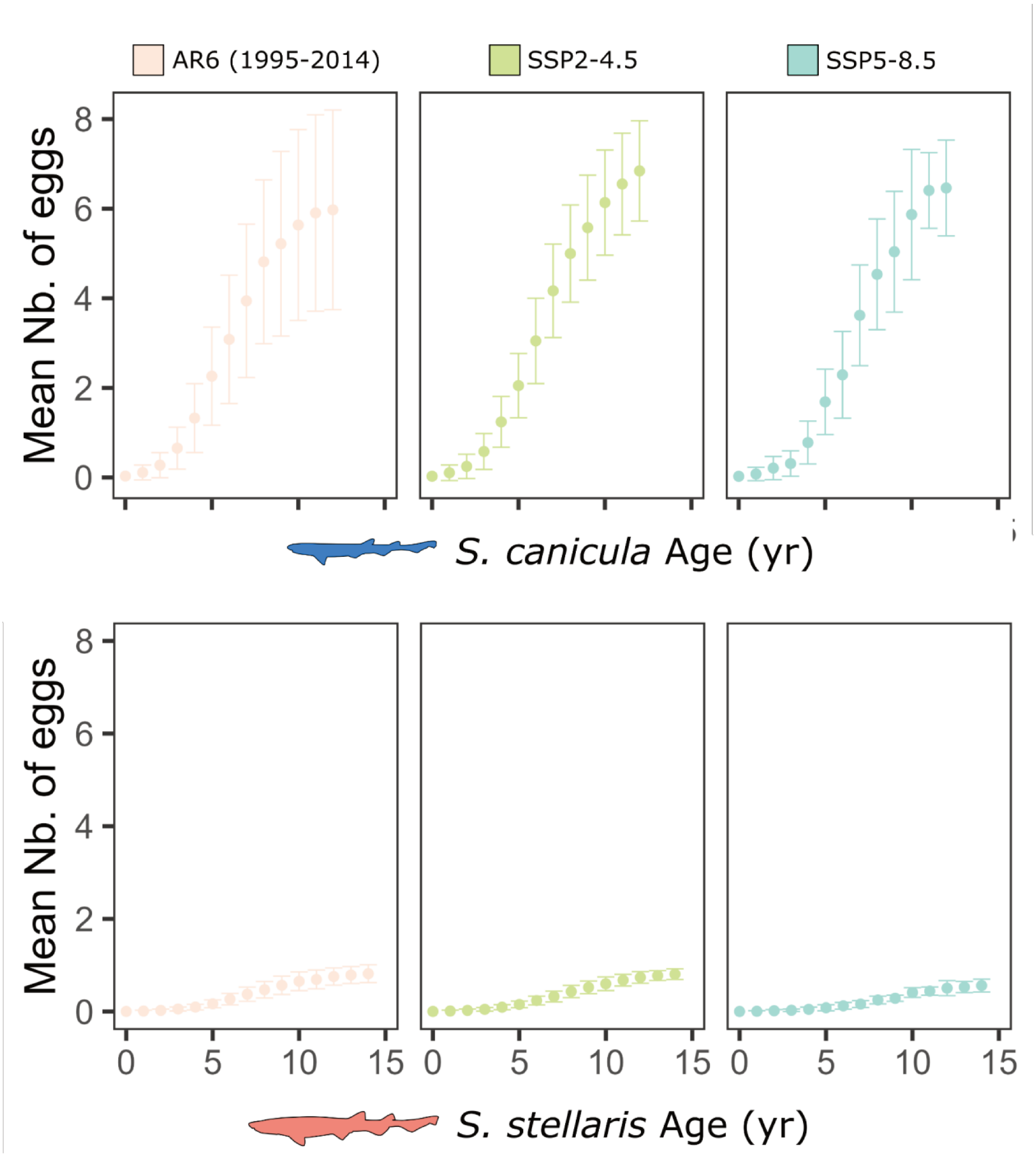

FIGURE 5. Predicted June reproductive output by age on June 30 of each year. Predicted reproductive output by age under the historical temperatures from 1994 to 2015 (AR6 1994-2015) is shown in beige. Predicted reproductive output by age under the temperatures predicted for 2100 under the climate scenarios "SSP2: Middle of the road" and "SSP5: Fossil-fuelled Development (Taking the Highway)" are respectively shown in light green and light

blue. The top panel describes the responses of *S. canicula* (blue shape) and the bottom panel those of *S. stellaris* (light red shape).

3.2. Matrix projection model

The population of *S. canicula* is growing steadily ($\lambda = 1.18$; $r = 0.17$), while that of *S. stellaris* remains stable ($\lambda = 0.98 \sim 1$; $r = -0.02 \sim 0$) under the AR6 (1994-2015). Moderately faster individual growth under the SSP2-4.5 scenario resulted in population growth rates, net reproductive rates, and generation times similar to those observed under the AR6 (1994-2015) scenario (Table 3). Conversely, the slower growth of individuals under the SSP5-8.5 scenario, accompanied by changes in reproduction and survival rates, led to a reduced population growth rate, lower reproductive rates, and longer generation times for both species (Table 3). Although there was a sharp decline in egg production in *S. canicula* under the SSP5-8.5 scenario ($R_0 = 1.61$), the finite population rate and instantaneous population growth rate remained positive ($\lambda = 1.09$; $r = 0.09$), indicating a steady population. For *S. stellaris*, the population underwent a marked decline ($\lambda = 0.75$; $r = -0.29$) accompanied by an increase in generation time of 1.22 years.

TABLE 3. **Finite and instantaneous population growth rates (yr^{-1}), net reproductive rate, and generation time (yr) calculated from the matrix projection models.**

Species	**Scenario**	**Finite population growth rate (λ)**	**Instantaneous population growth rate (r)**	**Net reproductive rate (R_0)**	**Generation time**
S. canicula 	AR6 (1994-2015)	1.18	0.17	6.79	8.01
	SSP2-4.5	1.19	0.17	7.00	8.13

	SSP5-8.5	1.09	0.09	1.61	9.39
S. stellaris 	AR6 (1994-2015)	0.98	-0.02	1.47	10.11
	SSP2-4.5	0.98	-0.02	1.48	10.37
	SSP5-8.5	0.75	-0.29	1.02	11.59

4. DISCUSSION

We assessed the projected effects of end-of-century temperatures on individual growth, life history traits, and population dynamics of *S. canicula* and *S. stellaris* across SSP2-4.5 and SSP5-8.5 scenarios. Our findings reveal that the moderate warming simulated in SSP2-4.5 exerted discernible impacts on both species at individual and population levels. In contrast, under the more severe warming scenario of SSP5-8.5, we observed pronounced negative effects on the populations of *S. canicula* and *S. stellaris*. Our integration of a bioenergetics model with a matrix projection model provided a robust framework to translate limited to moderate physiological information on environmental changes affecting individual growth into meaningful population-level responses for oviparous sharks.

We showed the survival rate of the first-year classes is a critical determinant of the population dynamics of catsharks, as highlighted for several other elasmobranchs previously (e.g., Undulate Ray, *Raja undulata*; Elliott et al., 2020). For the AR6 (1994-2015) and SSP2-4.5 scenarios, the survival rate was relatively high, ranging from 80% to 83% for both species. However, under the SSP5-8.5 scenario, the survival rate drastically decreased, dropping to 33% for *S. canicula* and only 23% for *S. stellaris*, supporting the vulnerability of oviparous elasmobranch embryos and juveniles to warming temperatures (Coulon et al., 2024a; Musa et al., 2020; Rosa et al., 2014). This finding is particularly concerning given that catsharks produce only a few dozen eggs annually, with *S. stellaris* laying 3 to 6 times fewer eggs than *S. canicula* (Ellis & Shackley, 1997; Pécuchet et al., 2017). Under the SSP5-8.5 scenario, these two species may respond by shifting their spawning areas to deeper waters or migrating to colder regions (Coulon et al., 2024b; Sundby & Nakken, 2008). Additionally, they might alter their peak spawning periods to months with milder temperatures, such as spring or late summer (Rogers & Dougherty, 2019; Pankhurst & Munday, 2011). Spatio-temporal monitoring of egg-laying sites could help detect shifts in the species' functional zones rather than focusing solely on suitable habitat, allowing for more effective conservation strategies that address the species dynamic needs. Implementing mobile protection measures could enhance species survival, given the critical role of juvenile survival in the recovery of elasmobranch populations (Ward-Paige et al., 2012). In addition, the lower survival rate of *S. stellaris* compared to *S. canicula* suggests that the early life stages of *S. stellaris* are more sensitive to temperature increases than those of *S. canicula*. While *S. stellaris* is primarily found around the British Isles and lays its eggs in colder waters, *S. canicula* has a broader geographic and environmental range, depositing its eggs across various latitudes and depths (Ellis et al., 2004). This wider distribution is likely to contribute to the observed increased tolerance in the early life stages of *S. canicula.*

The growth rates of surviving *S. canicula* individuals under the AR6 (1994-2015) and SSP2-4.5 scenarios were similar, but they differ significantly from those under the SSP5-8.5 scenario. These differences tended to diminish over time, which may indicate that SSP5-8.5 individuals could compensate for their lower initial growth rates. In this case, it appears that once individuals survive the critical early years, their growth may no longer be threatened by rising temperatures, as is generally observed in fish (Pankhurst & Munday, 2011). In contrast, *S. stellaris* consistently showed lower growth rates at higher temperatures. This suggests that the temperatures encountered by these individuals were no longer optimal for their metabolic functioning. Their energy consumption may be insufficient, or their respiration rate may be excessively high (Scott et al., 2017). Increasing the proportion of ingested energy could compensate for higher metabolic demands (Neer et al., 2007); however, with rising temperatures, access to resources may become less predictable (Brodersen et al., 2011; Lindmark et al., 2022). Furthermore, reducing activity levels could help limit overall energy expenditure (Johansen et al., 2014). However, activity patterns are directly related to prey encounter rates, the ability to capture prey, and avoid predators. Any reductions in activity are likely to decrease overall foraging success and energy intake, thereby limiting the energy available for growth.

Catsharks' population growth rates are closely tied to the individuals' ability to mature. While *S. canicula* females mature first under the AR6 scenario (1994-2015), the proportion of mature individuals increases more rapidly under the SSP2-4.5 scenario. By age 9, more than half of the populations are mature under both scenarios, with the proportion of mature individuals under the SSP2-4.5 scenario surpassing the AR6 scenario by age 10. Despite a delay, the SSP2-4.5 scenario would favour the maturation of individuals, thereby maintaining a finite population growth rate and generation time comparable to those under the AR6 scenario. Concerning *S. stellaris*, while more than half of individuals reach maturity between the ages of 9 and 10 in the AR6 (19942015) and SSP2-4.5 scenarios, under the SSP5-8.5 scenario half of the population reach maturity only from the 13th year (4 out of 7 individuals). On the one hand, the number of individuals reaching maturity is exceedingly low; on the other hand, maturity occurs only two years before the species' life expectancy, posing critical risks to population renewal. Nevertheless, in this study, maturation is determined by a threshold of individual length and weight, which was defined as the minimum size observed at fishing markets with an egg emerging from the cloaca. Firstly, we emphasise the age at maturity determined by modelling only partially reflects the age that could be determined by biological observations. Given that *S. stellaris* is a larger species than *S. canicula*, we would expect it to reach maturity at a later age. This strongly supports the need to precisely define the size at maturity for *S. stellaris* and females of many elasmobranchs. This could be achieved through ultrasound scans (Whittamore et al., 2010) conducted during fishery-independent bottom trawl surveys in the Northeast Atlantic (ICES, 2022). Then, predicting maturation and subsequent reproduction based solely on growth may be insufficient. Individuals may have biological age increasing more rapidly in response to increased temperatures, resulting in earlier maturation at smaller sizes and potentially increasing the number of reproductive events in a lifetime (Angiletta, 2004). By comparison, catsharks' Mediterranean populations exhibit maturation at smaller sizes (Capapé et al., 2006; Finotto et al., 2015), suggesting that under the SSP5-8.5 scenario, Northeast Atlantic individuals may mature at lower sizes by the end of the century. Additionally, temperature can influence fish maturation independently of warming-induced changes in body growth (Kuparinen et al., 2011; Niu et al., 2023). For instance, experiments with Japanese Medaka (*Oryzias latipes*) have shown that temperature affects both the age and size at maturation, even when growth rates are similar due to varying food levels (Dhillon & Fox, 2004).

The model suggests that some individuals lay eggs before reaching sexual maturity, which is biologically implausible. Therefore, we focus solely on egg production post-maturity. While egg production rates for the oldest age groups of *S. canicula* in the AR6 (1994-2015) and SSP5-8.5 scenarios are similar, in the SSP2-4.5 scenario, higher egg laying was observed at ages 7-12. Daily egg production may increase in response to temperature and mass, as observed in other elasmobranch species such as Thornback Ray (*Raja clavata*), Blonde Ray (*Raja brachyura*), and Spotted Ray (*Raja montagui*), where the highest egg production rates were observed under warmer conditions (Holden et al., 1971). Conversely, increased frequency of egg laying may imply greater energy demand over a given period; thus, maternal investment could be reduced if individuals do not increase their food intake (e.g., by decreasing oocyte diameters; King et al., 2003; McCormick, 1998). For *S. stellaris* both individuals under the SSP2-4.5 and SSP5-8.5 scenarios exhibited lower egg laying rates at various ages (6-14) compared to AR6 (1994-2015). This may indicate that the available resources for individuals are inadequate to support both growth and egg production (Thunell et al., 2023). Furthermore, while the effects of global warming on the reproductive biology of many ectotherms, including teleost fish, are well documented (Alix et al., 2020; Walsh et al., 2019), the impacts on the reproductive biology of elasmobranchs—from gametogenesis to post-zygotic development or pup production, including mate search and gamete storage—are poorly understood. A better understanding of these effects would allow for more accurate population dynamic models that are constrained by species physiology (Horodysky et al., 2015). Furthermore, our bioenergetics models were based on females according to general assumptions; however, the potential effects of temperature on male reproductive biology should not be overlooked (Rankin & Kokko, 2007). For example, mismatches between the reproductive timing of the two sexes (Pratt et al., 2022) or alterations in sperm quantity and quality (Alavi & Cosson, 2005; Wyffels et al., 2015) could cause populations to reach a bottleneck.

Finally, we would like to emphasise that our models were constrained solely by temperature, as the equations calibrating it were temperature-dependent. However, other parameters, such as ocean acidification or deoxygenation, could also significantly impact the survival, growth and reproductive biology of elasmobranchs (Rummer et al., 2022). Acidification may influence elasmobranch behaviour, especially foraging, by modifying the efficiency of energy intake. However, the exact effects of these changes remain unclear. For instance, Port Jackson Shark (*Heterodontus portusjacksoni*) has been observed to take more time to locate food under acidified conditions (Pistevos et al., 2015), whereas elevated pCO_2 levels do not seem to impact activity levels or foraging behaviour in Epaulette Shark (*Hemiscyllium ocellatum*) (Heinrich et al., 2014). Regarding deoxygenation, a significant concern is that under low oxygen conditions (50% air saturation), the survival rate of *S. canicula* embryos decreased markedly (Musa et al., 2020), which could further diminish the survival rate of the first age class determined in this study. Integrating these additional environmental factors into future models could provide a more comprehensive understanding of the challenges faced by these species (Koenigstein et al., 2016).

Through the study of *S. canicula* and *S. stellaris*, we demonstrate that populations of a species with later maturity, lower fecundity, and more restricted distribution are more vulnerable to global warming than those of a species with higher fecundity and fewer environmental constraints, highlighting the importance of considering life history traits in conservation strategies. Building on this, and recognizing the impracticality of calibrating a bioenergetics model for each species, we emphasise the urgent need to address the additional pressure of global warming on elasmobranch populations already impacted by human activities.

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Supplementary Figures

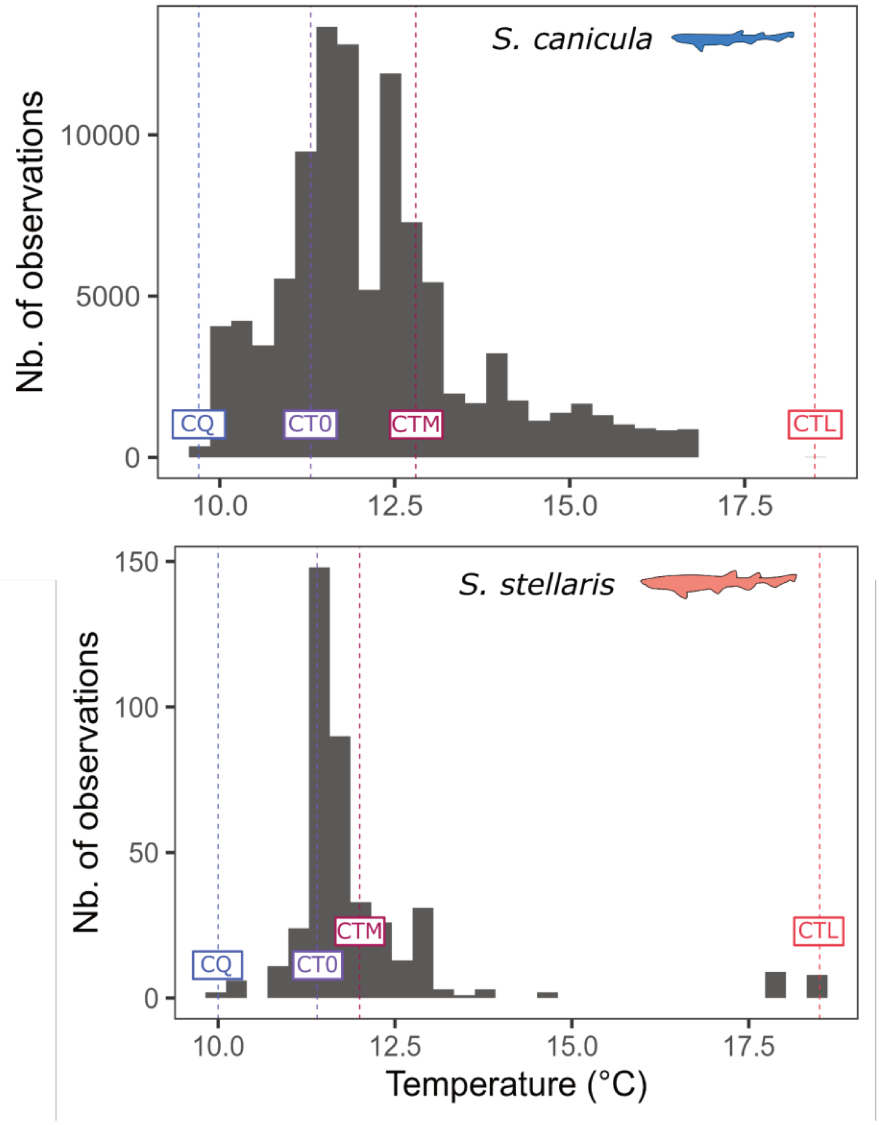


FIGURE S1. Determination of CQ, CTO, CTM and CTL parameters from OBIS data (2023) for *S. canicula* and *S. stellaris.* The top panel with the blue shape corresponds to the data for *S. canicula* while the bottom panel with the light red shape corresponds to *S. stellaris*. CQ is the lower water temperature where the temperature dependence is a small proportion of C_{max} ; CTO is the water temperature corresponding to 0.98 of C_{max} ; CTM is the water temperature still corresponding to 0.98 of C_{max} and CTL is the upper water temperature where the temperature dependence is a small proportion (CK4) of C_{max}

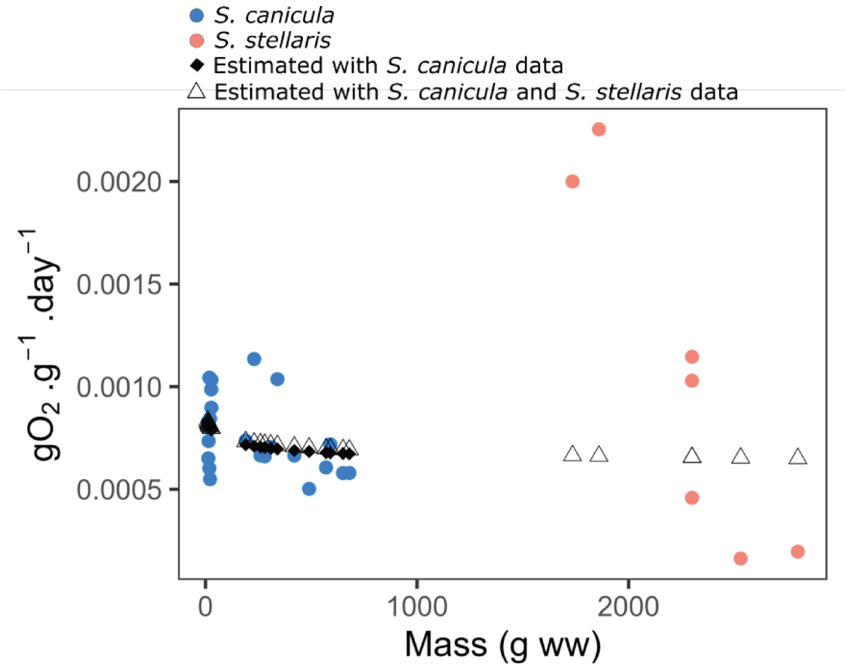
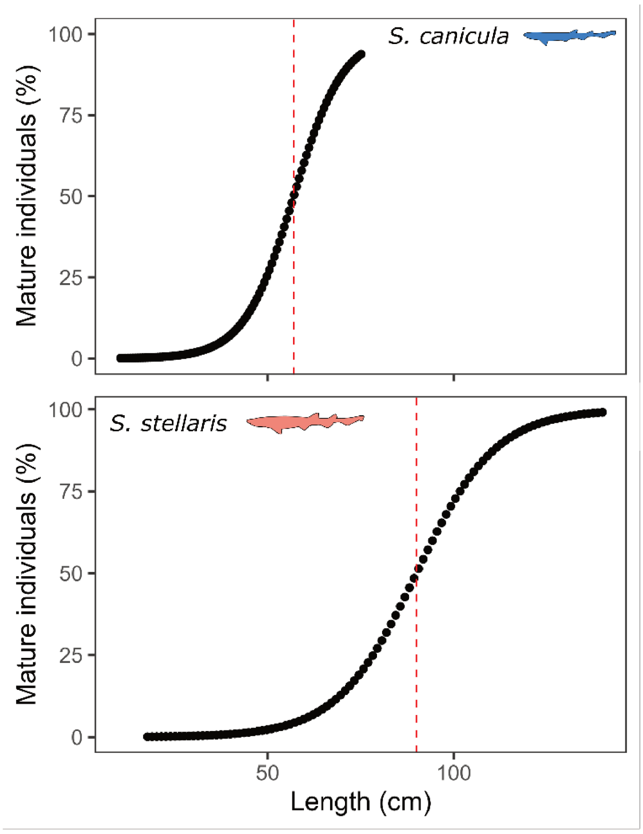
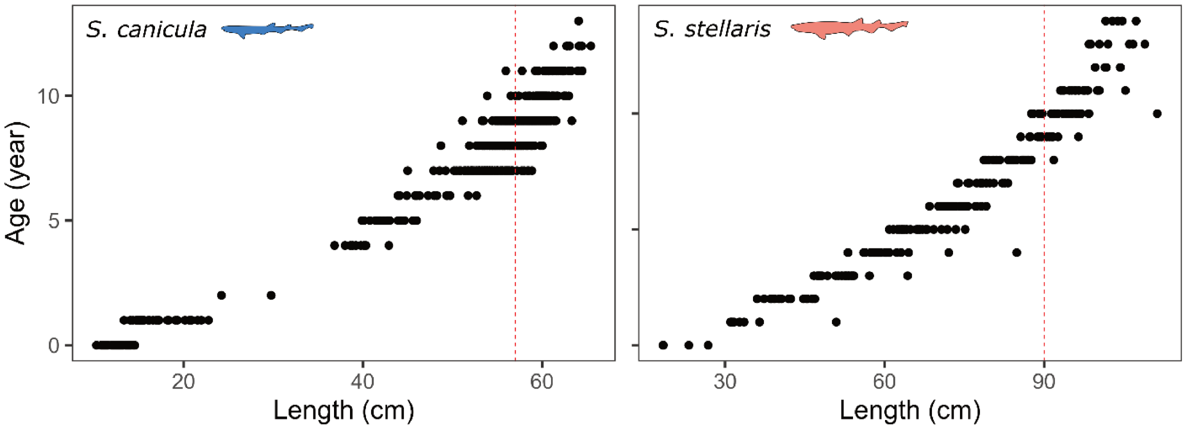


FIGURE S2. O_2 consumption rates (g O2. g fish^{-1}. day^{-1}). The blue circles correspond to data for *S. canicula* from this study while the light red circles correspond to data for *S. stellaris* from Piper et al. (1970; 1977). The solid diamonds correspond to data predicted from *S. canicula* data. The triangles correspond to data predicted from *S. canicula* and *S. stellaris* data.


S. canicula
S. stellaris
Mature individuals (%)
100
75
50
25
0
50
100
Length (cm)


S. canicula
S. stellaris
Age (year)
10
5
0
20
40
60
Length (cm)
30
60
90
Length (cm)

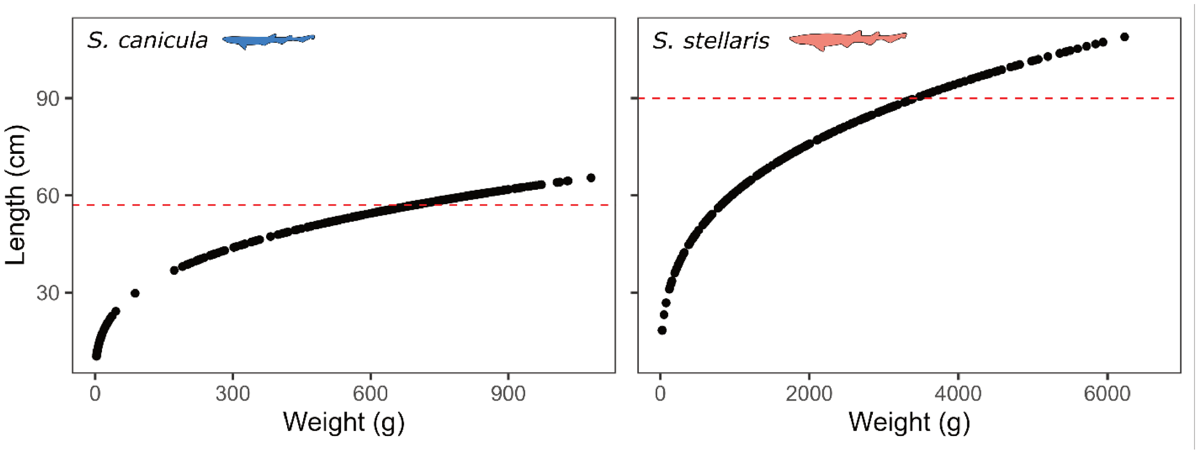

S. canicula
S. stellaris
Length (cm)
90
60
30
0
300
600
900
Weight (g)
0
2000
4000
6000
Weight (g)

FIGURE S3. Fraction of mature individuals at that age to body weight and length. The panels with the blue shape correspond to the data for *S. canicula* while the panels with the light red shape correspond to *S. stellaris*.

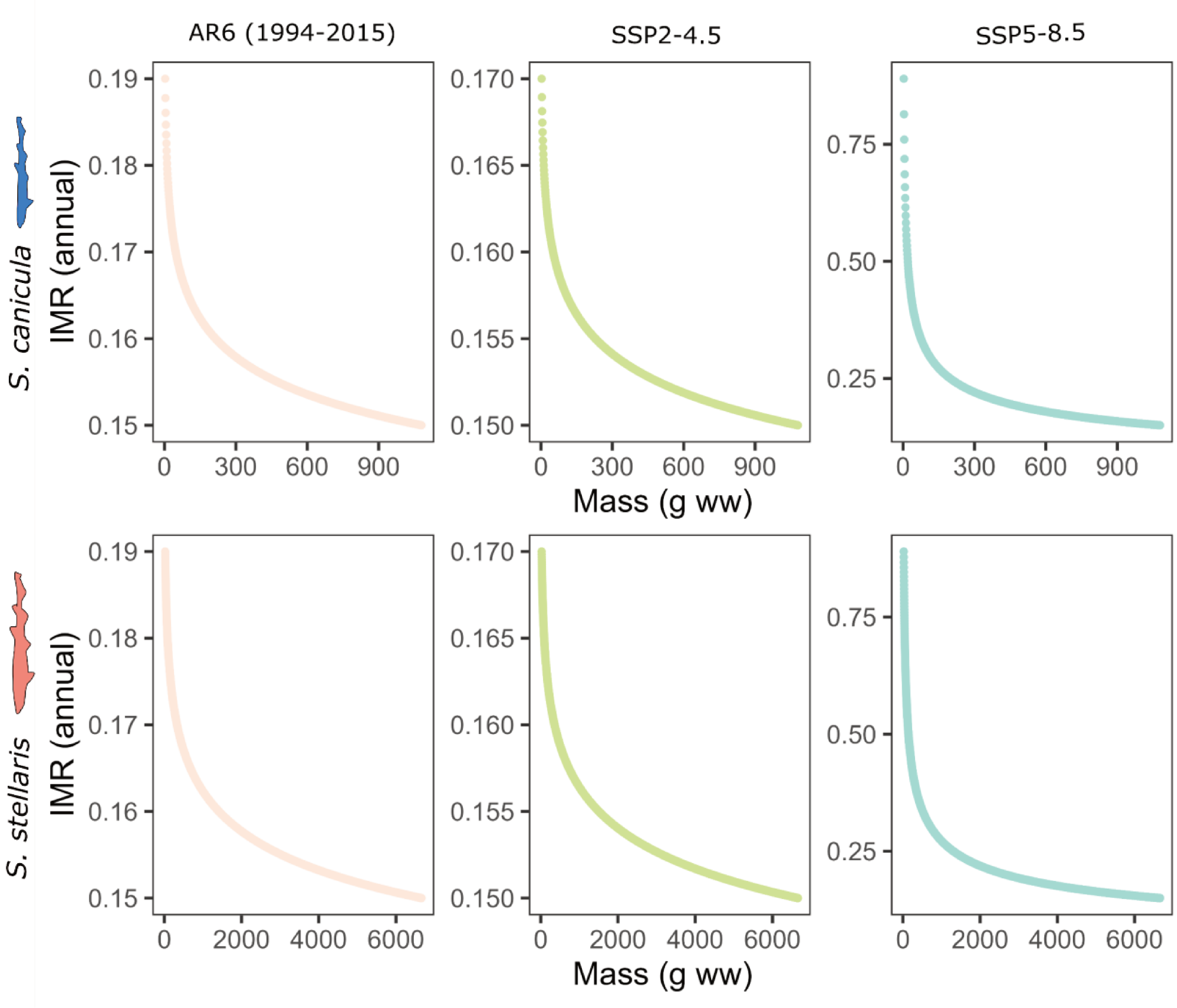


FIGURE S4. Weight dependent annual instantaneous mortality rate (IMR). The top panel with the blue shape corresponds to the rates for *S.canicula* and the right-hand side with the light red shape corresponds to the rates for *S. stellaris*. Natural mortality rates by scenario are shown in beige (AR6 1994-2015), light green (SSP2-4.5) and light blue (SSP5-8.5) respectively.

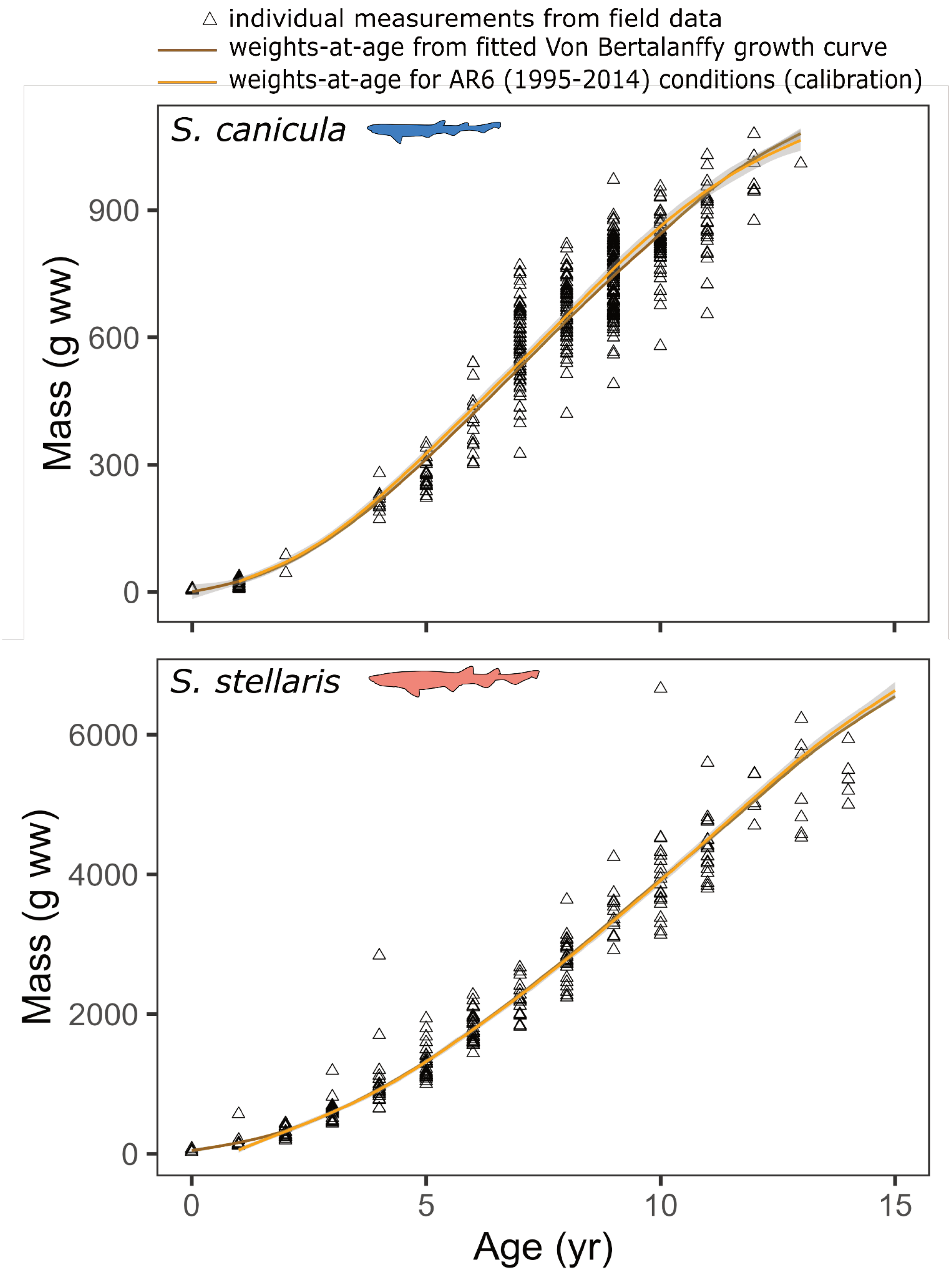


FIGURE S5. Bioenergetics model predictions of average and individual weights-at-age for AR6 (1995-2014) conditions (calibration), compared with weights-at-age from fitted Von Bertalanffy growth curve and individual measurements from field data. The top panel with the blue shape corresponds to the data for *S. canicula* while the bottom panel with the red light shape corresponds to *S. stellaris*. The blank triangles correspond to the individual measurements from field data, the brown line to the weights-at-age from fitted Von Bertalanffy growth curve and the orange line to the bioenergetics model predictions of average and individual weights-at-age for AR6 (1995-2014) conditions.

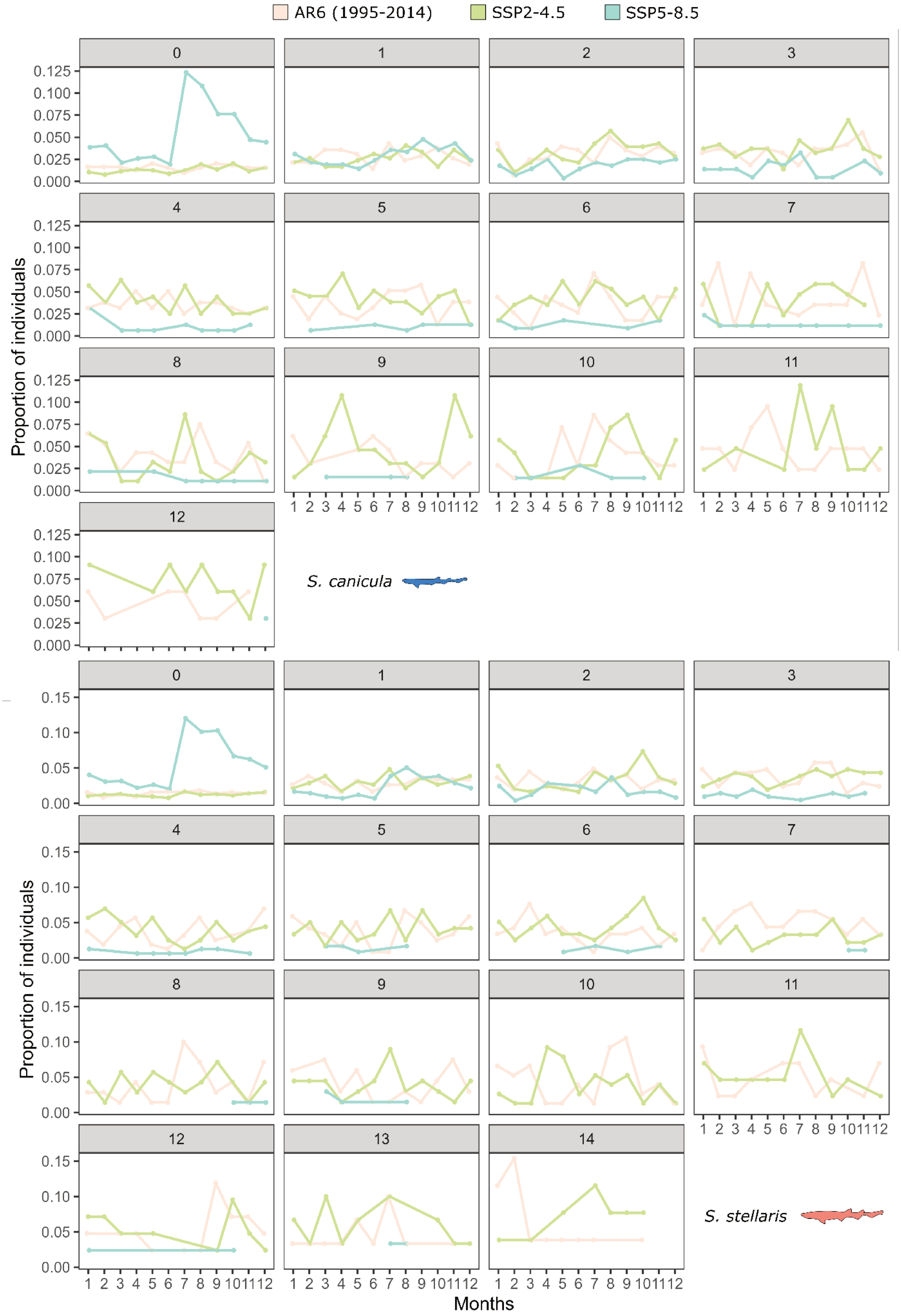


FIGURE S6. Proportion of individuals dying during simulations. The top panel with the blue shape corresponds to the data for *S. canicula* while the bottom panel with the red light shape corresponds to *S. stellaris*. Proportions of individuals dying during simulations by scenario are shown in beige (AR6 1994-2015), light green (SSP2-4.5) and light blue (SSP5-8.5) respectively.

Supplementary Tables

TABLE S1. Size of females with an egg emerging from the cloaca, observed opportunistically at fish auctions during the EOS

Species	Size (cm)
S. stellaris 	103
	90
	99
	94
	100
	101
	98
	102
	94
	101
	103
	94

TABLE S2. Age-specific p-value for *S. canicula* and *S. stellaris*

Age class	p-value for *S. canicula* 	p-value for *S. stellaris* 
0-1	0.680595189	0.241013107
1-2	0.590094852	0.5376230565
2-3	0.571482771	0.209531333
3-4	0.5589321	0.1761572425
4-5	0.551072946	0.1505214335
5-6	0.545612735	0.130743884
6-7	0.541622934	0.114061864
7-8	0.538679163	0.1009409475
8-9	0.53638145	0.089452017
9-10	0.534632017	0.0796852265
10-11	0.533382885	0.0714590295
11-12	0.532517859	0.0642573635
12-13	0.52055024	0.0580743355
13-14		0.0527735865
14-15		0.037923151

TABLE S3. Summary of the bioenergetics model predictions of the number of individuals surviving to each age.

Species	**Scenario**	**Age**	**Survival rate**
S. canicula 	AR6 1994-2015	0	0.8
		1	0.8225
		2	0.83738602
		3	0.84573503
		4	0.85407725
		5	0.82663317
		6	0.85410334
		7	0.85765125
		8	0.81327801
		9	0.87755102
		10	0.81976744
		11	0.83687943
		12	0.90677966
	SSP2-4.5	0	0.836
		1	0.84330144
		2	0.84113475
		3	0.8381113
		4	0.84909457

Species	Scenario	Age	Survival rate
		5	0.81279621
		6	0.83673469
		7	0.87456446
		8	0.84462151
		9	0.82075472
		10	0.81034483
		11	0.86524823
		12	0.82786885
	SSP5-8.5	0	0.327
		1	0.55351682
		2	0.66298343
		3	0.70833333
		4	0.82352941
		5	0.88571429
		6	0.85483871
		7	0.83018868
		8	0.79545455
		9	0.91428571
		10	0.8125

Species	Scenario	Age	Survival rate
		11	1
		12	0.96153846
S. stellaris 	AR6 1994-2015	0	0.802
		1	0.816708229426434
		2	0.854961832061069
		3	0.833928571428571
		4	0.850107066381156
		5	0.863979848866499
		6	0.854227405247813
		7	0.815699658703072
		8	0.861924686192469
		9	0.854368932038835
		10	0.767045454545455
		11	0.844444444444444
		12	0.807017543859649
		13	0.869565217391304
		14	0.8375
	SSP2-4.5	0	0.831
		1	0.817087845968712

Species	Scenario	Age	Survival rate
		2	0.852724594992636
		3	0.839378238341969
		4	0.84156378600823
		5	0.858190709046455
		6	0.823361823361823
		7	0.878892733564014
		8	0.866141732283465
		9	0.85
		10	0.812834224598931
		11	0.855263157894737
		12	0.861538461538462
		13	0.857142857142857
		14	0.864583333333333
	SSP5-8.5	0	0.23
		1	0.491304347826087
		2	0.566371681415929
		3	0.65625
		4	0.738095238095238
		5	0.774193548387097

Species	Scenario	Age	Survival rate
		6	0.75
		7	0.888888888888889
		8	0.8125
		9	0.692307692307692
		10	1
		11	1
		12	0.777777777777778
		13	0.714285714285714
		14	1

TABLE S4. Summary of the bioenergetics model predictions of the age-specific reproductive output.

Species	Scenario	Age	Mean	Standard deviation
S. canicula 	AR6 1994-2015	0	0.0318727050183599	0.0972390598294839
		1	0.111746987951807	0.166784755272224
		2	0.275508021390374	0.280213822100653
		3	0.655306553911205	0.467926322766163
		4	1.32638820638821	0.768807198862712
		5	2.2625671641791	1.09486415672131
		6	3.08394366197183	1.4325627325463
		7	3.94323651452282	1.71315045495946
		8	4.81628140703518	1.82721520220187
		9	5.21818181818182	2.06069644008569
		10	5.6372027972028	2.12936888275972
		11	5.90566666666667	2.19243494325194
		12	5.97504587155963	2.22837452129026
	SSP2-4.5	0	0.0281323877068558	0.0874683318691547
		1	0.105682451253482	0.174573461452064
		2	0.248213689482471	0.271508817301548
		3	0.58072	0.399979310086152
		4	1.24225352112676	0.567329008434349

Species	Scenario	Age	Mean	Standard deviation
		5	2.05173789173789	0.717980580489552
		6	3.05017182130584	0.953319231203553
		7	4.16790513833992	1.04285358992199
		8	4.99962790697674	1.08418704250825
		9	5.57785310734463	1.17111345663003
		10	6.13666666666667	1.17331161242874
		11	6.55154471544715	1.13467264906013
		12	6.84384615384615	1.11920247931007
	SSP5-8.5	0	0.026628242074928	0.0875939634739414
		1	0.0791623036649215	0.150281594779274
		2	0.21	0.259009997609723
		3	0.311460674157303	0.284539302932261
		4	0.78	0.478827069325493
		5	1.68875	0.729756428162469
		6	2.29283018867925	0.96848092264776
		7	3.62090909090909	1.12389649896267
		8	4.536	1.23514038259053
		9	5.04	1.34753299079849
		10	5.87	1.45488703901585

Species	Scenario	Age	Mean	Standard deviation
		11	6.40769230769231	0.84308152721932
		12	6.4624	1.06902323018102
S. stellaris 	AR6 1994-2015	0	0.00188228155339806	0.00815982373230326
		1	0.010119335347432	0.0178201458565097
		2	0.0243433098591549	0.0278526626978572
		3	0.0542790697674419	0.0435048010888097
		4	0.0962706766917293	0.061365507779357
		5	0.166247093023256	0.0856116051146126
		6	0.266564189189189	0.124919428682616
		7	0.373185185185185	0.152142477084256
		8	0.469811594202899	0.177909648337908
		9	0.565661016949152	0.198116667605355
		10	0.652108695652174	0.202625168480956
		11	0.692153846153846	0.203308480384578
		12	0.754336956521739	0.185233459890925
		13	0.788333333333333	0.182099011529442
		14	0.81675	0.192621923009507
	SSP2-4.5	0	0.00172651605231867	0.00752670631595961
		1	0.011	0.0189555281235876

Species	Scenario	Age	Mean	Standard deviation
		2	0.0246792452830189	0.0290797286199778
		3	0.0469512195121951	0.0395166012000508
		4	0.0933268765133172	0.0546226435067615
		5	0.152543661971831	0.0711892534826068
		6	0.237081911262799	0.0953550329487822
		7	0.324221789883268	0.11610832021585
		8	0.432255605381166	0.132293804041639
		9	0.521261780104712	0.137550544030659
		10	0.598928571428571	0.147907235861428
		11	0.677	0.125510317084519
		12	0.7363125	0.125369582014915
		13	0.7755	0.105773541612556
		14	0.807506024096385	0.114702411726827
	SSP5-8.5	0	0.0012992125984252	0.00643030739020219
		1	0.0054051724137931	0.0130150270662505
		2	0.0169714285714286	0.023665526464821
		3	0.0275	0.026194628010059
		4	0.04640625	0.0487739085293132
		5	0.081125	0.0652635543143271

Species	Scenario	Age	Mean	Standard deviation
		6	0.122833333333333	0.0731848987958903
		7	0.160875	0.074158276679006
		8	0.248769230769231	0.0837179330113465
		9	0.286	0.066
		10	0.410666666666667	0.105794612339192
		11	0.44	0.0888552193177193
		12	0.504428571428571	0.161345237656045
		13	0.528	0.121249742267767
		14	0.561	0.138048904378122

TABLE S5. Bioenergetics growth model parameters obtained from individual weights-at-age for AR6 conditions (1995-2014) (calibration). compared to growth parameters from weights-at-age from the fitted Von Bertalanffy growth curve and parameters from individual measurements from field data.

Species	Model	Linf	K	t0
S. canicula 	Individual measurements from field data.	76.0	0.14	-1.13
	Von Bertalanffy growth curve	75.8	0.14	-1.10
	Individual weights-at-age for AR6 (1995-2014) conditions	72.8	0.15	-1.10
S. stellaris 	Individual measurements from field data.	137.1	0.10	-1.75
	Von Bertalanffy growth curve	140.1	0.10	-1.92
	Individual weights-at-age for AR6 (1995-2014) conditions	120.4	0.14	-0.78

TABLE S6. Summary of the bioenergetics model predictions of average and individual weights-at-age.

Species	Scenario	Age	Mean weight	Standard deviation
S. canicula 	AR6 1994-2015	1	25.73	4.13
		2	69.21	15.11
		3	137.16	34.62
		4	223.39	62.23
		5	327.36	91.46
		6	433.89	129.08
		7	541.90	164.57
		8	649.57	198.32

Species	**Scenario**	**Age**	**Mean weight**	**Standard deviation**
		9	763.53	224.89
		10	861.86	265.68
		11	946.75	300.35
		12	1018.82	339.03
		13	1060.30	365.20
	SSP2-4.5	1	24.52	1.56
		2	66.00	4.44
		3	131.31	8.86
		4	217.94	15.49
		5	320.21	25.29
		6	431.42	37.86
		7	547.60	55.09
		8	663.49	72.98
		9	774.00	98.31
		10	887.69	127.39
		11	990.22	155.91
		12	1101.41	182.58
		13	1186.58	207.99
	SSP5-8.5	1	18.48	2.86

Species	Scenario	Age	Mean weight	Standard deviation
		2	49.65	8.84
		3	100.22	18.62
		4	171.19	30.46
		5	260.61	42.78
		6	361.35	61.19
		7	470.47	82.26
		8	580.36	104.96
		9	697.18	124.48
		10	814.84	150.15
		11	919.13	173.02
		12	1033.66	200.15
		13	1128.87	221.83
S. stellaris 	AR6 (1994-2015)	1	54.17	3.94
		2	329.57	55.31
		3	583.66	113.33
		4	919.99	187.99
		5	1317.38	282.52
		6	1777.99	392.53
		7	2270.40	521.85

Species	Scenario	Age	Mean weight	Standard deviation
		8	2773.74	686.88
		9	3349.72	832.18
		10	3906.33	986.45
		11	4507.09	1101.74
		12	5085.85	1223.42
		13	5700.97	1364.88
		14	6199.90	1565.62
		15	6611.42	1729.44
	SSP2-4.5	1	53.19	1.61
		2	318.21	28.00
		3	560.07	58.91
		4	870.10	102.52
		5	1244.52	152.46
		6	1667.28	217.34
		7	2120.80	295.78
		8	2607.34	378.43
		9	3126.38	461.59
		10	3631.33	547.89
		11	4114.08	644.14

Species	Scenario	Age	Mean weight	Standard deviation
		12	4571.14	743.36
		13	5040.24	821.95
		14	5518.87	892.86
		15	5889.64	959.29
	SSP5-8.5	1	39.20	3.29
		2	221.14	44.16
		3	385.30	86.40
		4	591.20	153.22
		5	846.40	228.28
		6	1142.45	297.48
		7	1419.84	324.75
		8	1803.47	383.53
		9	2256.36	393.95
		10	2552.53	304.12
		11	2906.47	352.95
		12	3255.79	402.63
		13	3583.49	501.55
		14	3879.27	619.34
		15	4112.16	663.27

Source	**Species**	**Condition**	**weight**	**length**	**ICES area**	**Year**
Coulon et al. (2024a)	*S. canicula*	control	3.5	10.4	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.9	10.4	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.4	10.2	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	4	11	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.6	10	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.6	10.4	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.8	10.7	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.8	10.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	2.9	9.1	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.8	9.5	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.8	9.1	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.8	10.4	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.7	9.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	4.1	10.4	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	4.2	10.2	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.6	9.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.7	9.3	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.9	10.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.7	10.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.8	9.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.6	11.5	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	4.1	9.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.4	10.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.8	9.5	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.8	10.7	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.8	9.7	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.4	9.5	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.4	9.4	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.6	9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.6	9.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.7	10.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.9	10.6	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.1	9.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	4	9.2	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.9	9.7	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	4	10.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.9	9.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.1	9.4	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.5	8.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.8	9.2	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.9	11.3	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.5	9.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.5	10.1	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.3	8.6	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	0.9	5.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	0.8	6.9	27.7.e	2022

Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	1.2	7	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	2.5	9.1	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	3.4	10.5	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	2.9	7.6	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.5	9.1	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	4	9.5	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.4	9.5	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.8	9.3	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.9	9.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	3.8	10.6	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	1.9	8.3	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	control	4	10.1	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.7	9.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.3	10.1	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.4	9.7	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	3.7	9.1	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.7	8.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.4	10.9	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	3.4	8.8	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.5	9.6	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	3.5	9.7	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP5-8.5	3.4	10	27.7.e	2022
Coulon et al. (2024a)	*S. canicula*	SSP2-4.5	3.7	10.4	27.7.e	2022
Coulon, personnal communication	*S. stellaris*	control	23.257	18.2	27.7.e	2022
Coulon, personnal communication	*S. stellaris*	control	22.856	17.7	27.7.e	2022
Coulon, personnal communication	*S. stellaris*	control	23.014	17.9	27.7.e	2022
EOS	*S. stellaris*	control	4020	98	27.7.f	2014
EOS	*S. stellaris*	control	5500	108	27.7.f	2014
EOS	*S. stellaris*	control	5200	108	27.7.f	2014
EOS	*S. stellaris*	control	5720	106	27.7.f	2014
EOS	*S. stellaris*	control	3120	90	27.7.f	2014
EOS	*S. stellaris*	control	4080	98	27.7.f	2014
EOS	*S. stellaris*	control	3800	98	27.7.f	2014
EOS	*S. stellaris*	control	4760	97	27.7.f	2014
EOS	*S. stellaris*	control	4420	97	27.7.f	2014
EOS	*S. stellaris*	control	4260	97	27.7.f	2014
EOS	*S. stellaris*	control	4520	96	27.7.f	2014
EOS	*S. stellaris*	control	3940	94	27.7.f	2014
EOS	*S. stellaris*	control	3580	93	27.7.f	2014
EOS	*S. stellaris*	control	3540	91	27.7.f	2014
EOS	*S. stellaris*	control	3740	90	27.7.f	2014
EOS	*S. stellaris*	control	4180	100	27.7.f	2014
EOS	*S. stellaris*	control	3620	89	27.7.f	2014
EOS	*S. stellaris*	control	1300	68	27.7.f	2014
EOS	*S. stellaris*	control	2120	73	27.7.f	2014

EOS	*S. stellaris*	control	1940	73	27.7.f	2014
EOS	*S. stellaris*	control	1640	72	27.7.f	2014
EOS	*S. stellaris*	control	1600	72	27.7.f	2014
EOS	*S. stellaris*	control	1580	72	27.7.f	2014
EOS	*S. stellaris*	control	1980	71	27.7.f	2014
EOS	*S. stellaris*	control	1620	70	27.7.f	2014
EOS	*S. stellaris*	control	1600	70	27.7.f	2014
EOS	*S. stellaris*	control	1560	70	27.7.f	2014
EOS	*S. stellaris*	control	1680	69	27.7.f	2014
EOS	*S. stellaris*	control	3480	90	27.7.f	2014
EOS	*S. stellaris*	control	1940	68	27.7.f	2014
EOS	*S. stellaris*	control	1870	75	27.7.f	2014
EOS	*S. stellaris*	control	1800	67	27.7.f	2014
EOS	*S. stellaris*	control	1220	67	27.7.f	2014
EOS	*S. stellaris*	control	1120	64	27.7.f	2014
EOS	*S. stellaris*	control	1300	63	27.7.f	2014
EOS	*S. stellaris*	control	1140	63	27.7.f	2014
EOS	*S. stellaris*	control	1700	61	27.7.f	2014
EOS	*S. stellaris*	control	1200	61	27.7.f	2014
EOS	*S. stellaris*	control	1120	60	27.7.f	2014
EOS	*S. stellaris*	control	920	60	27.7.f	2014
EOS	*S. stellaris*	control	900	57	27.7.f	2014
EOS	*S. stellaris*	control	1600	69	27.7.f	2014
EOS	*S. stellaris*	control	2780	83	27.7.f	2014
EOS	*S. stellaris*	control	3360	88	27.7.f	2014
EOS	*S. stellaris*	control	2920	88	27.7.f	2014
EOS	*S. stellaris*	control	3640	87	27.7.f	2014
EOS	*S. stellaris*	control	3020	87	27.7.f	2014
EOS	*S. stellaris*	control	2980	87	27.7.f	2014
EOS	*S. stellaris*	control	2960	87	27.7.f	2014
EOS	*S. stellaris*	control	3140	86	27.7.f	2014
EOS	*S. stellaris*	control	3060	86	27.7.f	2014
EOS	*S. stellaris*	control	3080	85	27.7.f	2014
EOS	*S. stellaris*	control	2400	85	27.7.f	2014
EOS	*S. stellaris*	control	1760	75	27.7.f	2014
EOS	*S. stellaris*	control	2520	84	27.7.f	2014
EOS	*S. stellaris*	control	1860	75	27.7.f	2014
EOS	*S. stellaris*	control	2680	83	27.7.f	2014
EOS	*S. stellaris*	control	2320	83	27.7.f	2014
EOS	*S. stellaris*	control	2340	81	27.7.f	2014
EOS	*S. stellaris*	control	2220	80	27.7.f	2014
EOS	*S. stellaris*	control	2000	79	27.7.f	2014
EOS	*S. stellaris*	control	2280	78	27.7.f	2014
EOS	*S. stellaris*	control	2200	78	27.7.f	2014
EOS	*S. stellaris*	control	2280	76	27.7.f	2014
EOS	*S. stellaris*	control	2100	76	27.7.f	2014
EOS	*S. stellaris*	control	1920	76	27.7.f	2014

EOS	*S. stellaris*	control	2840	84	27.7.f	2014
EOS	*S. stellaris*	control	3080	83	27.7.h	2014
EOS	*S. stellaris*	control	5020	102	27.7.h	2014
EOS	*S. stellaris*	control	2200	76	27.7.h	2014
EOS	*S. stellaris*	control	2760	85	27.7.h	2014
EOS	*S. stellaris*	control	2940	85	27.7.h	2014
EOS	*S. stellaris*	control	2720	86	27.7.h	2014
EOS	*S. stellaris*	control	4260	97	27.7.h	2014
EOS	*S. stellaris*	control	4780	98	27.7.h	2014
EOS	*S. stellaris*	control	630	51	27.7.d	2020
EOS	*S. canicula*	control	548	55	27.8.a	2021
EOS	*S. canicula*	control	788	58	27.8.a	2021
EOS	*S. canicula*	control	754	59	27.8.a	2021
EOS	*S. canicula*	control	754	54	27.8.a	2021
EOS	*S. canicula*	control	684	58	27.8.a	2021
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EOS	*S. canicula*	control	674	57	27.8.a	2021
EOS	*S. canicula*	control	540	51	27.8.a	2021

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EOS	*S. canicula*	control	700	57	27.8.a	2021
EOS	*S. canicula*	control	754	59	27.8.a	2021
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EOS	*S. canicula*	control	678	55	27.8.a	2021
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EOS	*S. canicula*	control	640	52	27.8.a	2021
EOS	*S. canicula*	control	792	57	27.8.a	2021

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EOS	*S. canicula*	control	706	58	27.8.a	2021
EOS	*S. canicula*	control	876	59	27.8.a	2021
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EOS	*S. canicula*	control	720	58	27.8.a	2022
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EOS	*S. canicula*	control	810	56	27.8.a	2022
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EOS	*S. canicula*	control	510	53	27.8.a	2022
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EOS	*S. canicula*	control	810	57	27.8.a	2022
EOS	*S. canicula*	control	550	51	27.8.a	2022
EOS	*S. canicula*	control	690	56	27.8.a	2022

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EOS	*S. canicula*	control	700	58	27.8.a	2022
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EOS	*S. canicula*	control	700	56	27.8.a	2022
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EOS	*S. canicula*	control	1030	63	27.8.a	2022
EOS	*S. canicula*	control	930	61	27.8.a	2022
EOS	*S. canicula*	control	670	56	27.8.a	2022
EOS	*S. canicula*	control	730	58	27.8.a	2022
EOS	*S. canicula*	control	800	58	27.8.a	2022
EOS	*S. canicula*	control	810	58	27.8.a	2022
EOS	*S. canicula*	control	1010	66	27.8.a	2022
EOS	*S. canicula*	control	840	60	27.8.a	2022
EOS	*S. canicula*	control	690	56	27.8.a	2022
EOS	*S. canicula*	control	730	58	27.8.a	2022
EOS	*S. canicula*	control	770	56	27.8.a	2022
EOS	*S. canicula*	control	850	58	27.8.a	2022
EOS	*S. canicula*	control	810	57	27.8.a	2022
EOS	*S. canicula*	control	635	58	27.7.h	2022
EOS	*S. canicula*	control	655	62	27.7.e	2022
EOS	*S. canicula*	control	725	62	27.7.h	2022
EOS	*S. canicula*	control	692	55	27.8.a	2022
EOS	*S. canicula*	control	782	56	27.8.a	2022
EOS	*S. canicula*	control	828	61	27.8.a	2022
EOS	*S. canicula*	control	742	56	27.8.a	2022

EOS	*S. canicula*	control	644	58	27.8.a	2022
EOS	*S. canicula*	control	652	58	27.8.a	2022
EOS	*S. canicula*	control	828	58	27.8.a	2022
EOS	*S. canicula*	control	752	57	27.8.a	2022
EOS	*S. canicula*	control	798	60	27.8.a	2022
EOS	*S. canicula*	control	684	55	27.8.a	2022
EOS	*S. canicula*	control	768	56	27.8.a	2022
EOS	*S. canicula*	control	708	59	27.8.a	2022
EOS	*S. canicula*	control	834	58	27.8.a	2022
EOS	*S. canicula*	control	862	59	27.8.a	2022
EOS	*S. stellaris*	control	860	62	27.7.e	2022
EOS	*S. stellaris*	control	1155	65	27.7.e	2022
EOS	*S. stellaris*	control	1600	70	27.7.e	2022
EOS	*S. stellaris*	control	2820	82	27.7.e	2022
EOS	*S. stellaris*	control	900	60	27.7.e	2022
EOS	*S. stellaris*	control	920	62	27.7.e	2022
EOS	*S. stellaris*	control	3595	89	27.7.e	2022
EOS	*S. stellaris*	control	680	54	27.8.a	2022
EOS	*S. stellaris*	control	1000	62	27.7.e	2022
EOS	*S. stellaris*	control	380	44	27.7.e	2022
EOS	*S. stellaris*	control	5360	108	27.7.e	2022
EOS	*S. stellaris*	control	2770	85	27.7.e	2023
EOS	*S. stellaris*	control	4195	95	27.7.e	2023
EOS	*S. stellaris*	control	4500	98	27.7.e	2023
EOS	*S. stellaris*	control	5435	101	27.7.e	2023
EOS	*S. stellaris*	control	4820	97	27.7.e	2023
EOS	*S. stellaris*	control	5445	101	27.7.e	2023
EOS	*S. stellaris*	control	6230	106	27.7.e	2023
EOS	*S. stellaris*	control	4250	91	27.7.e	2023
EOS	*S. stellaris*	control	4085	94	27.7.e	2023
EOS	*S. stellaris*	control	1500	67	27.7.h	2023
EOS	*S. stellaris*	control	4325	92	27.7.h	2023
EOS	*S. stellaris*	control	280	41	27.7.e	2023
EOS	*S. stellaris*	control	1330	68	27.7.e	2023
EOS	*S. stellaris*	control	1000	61	27.7.e	2023
EOS	*S. stellaris*	control	1075	62	27.7.e	2023
EOS	*S. stellaris*	control	605	54	27.7.e	2023
EOS	*S. stellaris*	control	655	52	27.7.e	2023
EOS	*S. stellaris*	control	1980	79	27.7.e	2023
EOS	*S. stellaris*	control	3725	93	27.7.e	2023
EOS	*S. stellaris*	control	4375	100	27.7.e	2023
EOS	*S. stellaris*	control	650	57	27.7.e	2023
EOS	*S. stellaris*	control	1825	78	27.7.e	2023
EOS	*S. stellaris*	control	1180	64	27.7.e	2023
EOS	*S. stellaris*	control	695	55	27.7.e	2023
EOS	*S. stellaris*	control	465	48	27.7.e	2023
EOS	*S. stellaris*	control	680	53	27.7.e	2023

EOS	*S. stellaris*	control	1445	70	27.7.e	2023
Mahé et al. (2018)	*S. canicula*	control	620	57	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	660	58	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	400	49	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	580	54	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	760	59	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	620	55	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	700	57	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	720	57	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	820	59	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	860	58	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	238	46	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	326	51	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	260	46	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	580	60	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	25	21	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	204	42	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	306	48	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	222	43	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	398	52	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	276	46	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	276	46	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	226	43	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	45	25	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	172	39	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	302	47	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	324	48	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	250	44	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	220	42	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	560	57	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	226	42	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	21	19	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	18	18	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	435	52	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	435	52	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	33	22	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	33	22	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	302	46	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	25	20	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	200	40	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	710	61	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	676	60	27.7.d	2015
Mahé et al. (2018)	*S. canicula*	control	416	51	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	306	46	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	250	43	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	250	43	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	268	44	27.7.e	2014

Mahé et al. (2018)	*S. canicula*	control	252	43	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	875	65	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	797	63	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	254	43	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	87	30	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	480	53	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	258	43	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	382	49	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	278	44	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	408	50	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	318	46	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	210	40	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	522	54	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	650	58	27.7.d	2013
Mahé et al. (2018)	*S. canicula*	control	346	47	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	470	52	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	31	21	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	358	47	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	37	22	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	752	60	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	462	51	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	550	54	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	590	55	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	282	43	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	890	63	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	820	61	27.7.d	2013
Mahé et al. (2018)	*S. canicula*	control	510	52	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	613	55	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	438	49	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	496	51	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	526	52	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	500	51	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	280	42	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	632	55	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	956	63	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	350	45	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	694	56	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	743	57	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	633	54	27.7.d	2014
Mahé et al. (2018)	*S. canicula*	control	449	48	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	968	62	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	942	61	27.7.e	2014
Mahé et al. (2018)	*S. canicula*	control	840	57	27.7.d	2013
Mahé et al. (2018)	*S. stellaris*	control	435	50	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	192	38	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	652	57	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	454	50	27.7.d	2015

Mahé et al. (2018)	*S. stellaris*	control	2240	85	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	460	50	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3186	95	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	238	40	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1176	68	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	240	40	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1080	66	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	472	50	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	124	32	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1040	65	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	566	53	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4530	106	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	396	47	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1100	66	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	480	50	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	400	47	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	5000	109	27.7.d	2013
Mahé et al. (2018)	*S. stellaris*	control	1840	78	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3880	100	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	3140	93	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2004	80	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	154	34	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	215	38	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	655	55	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	252	40	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	200	37	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	142	33	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1820	77	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	780	58	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	1000	63	27.7.d	2013
Mahé et al. (2018)	*S. stellaris*	control	1760	76	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	320	43	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	120	31	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	830	59	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	240	39	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	970	62	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4580	104	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	122	31	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1730	75	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	426	47	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3640	96	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	1130	65	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2270	82	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4820	105	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	1145	65	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1560	72	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1990	78	27.7.d	2015

Mahé et al. (2018)	*S. stellaris*	control	1000	62	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	3840	97	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	780	57	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	630	53	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3300	92	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2180	80	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2180	80	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1400	69	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	1800	75	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	674	54	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	972	61	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	200	36	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	1290	67	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	128	31	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4700	103	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	1416	69	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	76	26	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3380	92	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1690	73	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1690	73	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3274	91	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3860	96	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	690	54	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	772	56	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4400	100	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	960	60	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	2460	82	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	784	56	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1670	72	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	830	57	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	310	41	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	5070	104	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	48	22	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	440	46	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	636	52	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3310	90	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	3100	88	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	270	39	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4160	97	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	642	52	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2280	79	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2120	77	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	514	48	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1884	74	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	3740	93	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4000	95	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	584	50	27.7.d	2015

Mahé et al. (2018)	*S. stellaris*	control	4980	102	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	3660	92	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2410	80	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	5940	108	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	880	57	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4490	98	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	1960	74	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2980	85	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2680	82	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	2680	82	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	1740	71	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	610	50	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	4320	96	27.7.e	2014
Mahé et al. (2018)	*S. stellaris*	control	820	55	27.7.d	2013
Mahé et al. (2018)	*S. stellaris*	control	1360	65	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	2740	82	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	4270	95	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2670	81	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	5840	105	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	2566	79	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	660	50	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	4530	95	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2610	79	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	5599	99	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	1190	54	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	6660	95	27.7.d	2015
Mahé et al. (2018)	*S. stellaris*	control	2840	58	27.7.d	2014
Mahé et al. (2018)	*S. stellaris*	control	570	33	27.7.d	2015

IV- Conclusion

Nous avons évalué les effets des températures projetées pour la fin du 21ème siècle selon les scénarios SSP2 et SSP5 sur la croissance individuelle, la maturation, la production d'œufs et la dynamique des populations des petites et grandes roussettes en Atlantique Nord-Est. Nos résultats montrent que même le réchauffement modéré prévu dans le cadre du scénario SSP2 a eu des effets notables sur la maturation des individus des deux espèces. En revanche, le réchauffement plus sévère prévu par le scénario SSP5 a entraîné des impacts négatifs significatifs, en particulier pour la grande roussette, dont les populations pourraient s'effondrer localement, révélant ainsi une vulnérabilité accrue par rapport à la petite roussette.

Les modèles individus-centrés que nous avons développés ont fourni un cadre solide pour traduire des informations physiologiques limitées sur la croissance individuelle, en réponses significatives sur la dynamique des populations de requins ovipares. Cependant, l'élaboration de ces modèles a révélé des lacunes significatives concernant la reproduction des requins. Par exemple, la taille à maturité de la grande roussette dans l'Atlantique Nord-Est demeure inconnue, ce qui a nécessité l'utilisation d'un *proxy* dans ce chapitre. De même, les effets de la température sur la fertilité des requins sont particulièrement mal documentés. En conséquence, le quatrième et dernier chapitre de cette thèse se concentre sur les impacts potentiels encore inexplorés du réchauffement global sur la fertilité des élasmobranches. Ce chapitre propose une recherche bibliographique approfondie et examine les implications écologiques et évolutives associées à cette pression thermique.

CHAPITRE 4 : Les impacts inexplorés du réchauffement global sur la fertilité des élasmobranches

I- Préambule

Les impacts du réchauffement global sur la fertilité des élasmobranches restent largement inexplorés. Ce chapitre s'appuie sur une revue bibliographique étendue, compilant des études menées à l’échelle mondiale, tout en en tirant des enseignements applicables aux élasmobranches du nord-est de l'Atlantique.

II- The unexplored impact of global warming on elasmobranch fertility

Auteurs : Noémie Coulon, Anne Lizé, Eric Feunteun, Alexandre Carpentier

Résumé : L'intensification des changements climatiques pose des risques sans précédent pour la biodiversité, avec des impacts profonds sur la dynamique des populations de tous les taxons. La fertilité, un facteur critique pour la persistance des populations, est particulièrement sensible au stress thermique, et atteint souvent ses limites avant que la mortalité ne se produise. Alors que les limites de tolérance thermique ont été largement étudiées, les limites de fertilité thermique, qui définissent le seuil au-delà duquel les organismes deviennent stériles, restent sous-explorées, en particulier chez les ectothermes. Les élasmobranches (requins et raies), présentent de faibles taux de reproduction et une maturité sexuelle tardive ce qui les rend très sensibles aux pressions anthropiques. Cette perspective passe en revue les impacts potentiels de l'augmentation des températures océaniques sur la fertilité des élasmobranches, en se concentrant sur les traits reproductifs clés tels que la gamétogenèse, le stockage des spermatozoïdes, la fécondation et le développement de la progéniture. Nous soulignons les conséquences écologiques et évolutives de ces stress thermiques sur la fertilité, identifions les lacunes critiques dans les connaissances et appelons à une recherche urgente sur les réponses de ces espèces vulnérables dans un monde qui se réchauffe.

Mots clés : fertilité ; gamètes ; raie ; réchauffement global ; requin

The unexplored impact of global warming on elasmobranch fertility

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Abstract

The intensification of climate change poses unprecedented risks to biodiversity, with profound impacts on population dynamics across taxa. Fertility, a critical factor for population persistence, is particularly sensitive to thermal stress, often experiencing limits before mortality occurs. While thermal tolerance limits (CTLs) have been widely studied, the thermal fertility limits (TFLs), which define the threshold beyond which organisms become sterile, remain underexplored, particularly in ectotherms. Elasmobranchs, including sharks and rays, exhibit low reproductive rates, late sexual maturity, and diverse reproductive modes, making them highly susceptible to global warming. This perspective reviews the potential impacts of rising ocean temperatures on elasmobranch fertility, focusing on key reproductive traits such as gametogenesis, sperm storage, fertilization, and offspring development. We highlight the ecological and evolutionary consequences of these thermal stresses, identify critical knowledge gaps, and call for urgent research into the fertility responses of these vulnerable species in a warming world.

Keywords

Fertility; gametes; global warming; ray; shark; skate

The rapid acceleration and intensification of current climate changes pose significant risks to a multitude of organisms across various environments. In response to climate change, profound shifts in population dynamics are observed in insects (Halsch et al., 2021), birds (Pearce-Higgins et al., 2015; Spooner et al., 2018), mammals (Paniw et al., 2021), as well as amphibians (Blaustein et al., 2010), and marine species ranging from phytoplankton to fish and marine mammals (Hastings et al., 2020). The stability of populations is fundamentally dependent on the reproductive success of individuals, as only offspring that survive to reproductive maturity and offspring production contribute meaningfully to the next generation. Among factors involved in climate change and directly affecting organism survival, maximum temperatures are key (Román-Palacios & Wiens, 2020). Critical thermal limits (CTLs), define the breadth of temperatures over which the organisms can tolerate at least short exposure are normally indexed by one of two metrics, upper and lower LT_{50} or CT_{max} and CT_{min} (Bennett et al., 2021; Cowles & Bogert, 1945). These limits are relatively straightforward to determine, making them a popular metric for measuring species physiological tolerance to extreme temperatures (Lutterschmidt & Hutchison, 1997). CTLs have been widely studied across different taxa and ontogenetic stages (e.g. Moyano et al., 2017; Terblanche et al., 2017), and these studies provide helpful information on how temperatures impact physiological and ecological limits of species, for example, geographical distribution (Bennett et al., 2021; Gerick et al., 2014; Khaliq et al., 2017 ; Sunday et al., 2012). However, for sexually reproducing organisms and particularly ectotherms, fertility (see lexicon in Box 1) limits can be reached before the onset of mortality, with sublethal temperatures hindering organisms to reproduce (Kellermann et al., 2012, Walsh et al., 2019, van Heerwaarden & Sgrò 2021). Thermal fertility limits (TFLs), defined as the extent and duration of thermal stress beyond which individuals become sterile (Walsh et al., 2019), are typically lower than CTLs, and can potentially have detrimental consequences on populations persistence (Domenech & Fricke 2022; Parratt et al., 2021; van Heerwaarden & Sgrò, 2021). Studying the capacity of organisms to cope with increasing temperatures has become an important research area, particularly within the climate change context (Parmesan 2006; Walsh et al. 2019; Parratt et al. 2021; Sales et al.

2021). TFL has been documented in several species, such as mammals (Hafez, 1964), birds (Schou et al., 2021), insects (Chakir et al., 2002, Conrad et al., 2017; Domenech & Fricke, 2022), and reptiles (Cowles & Burleson, 1945).

In sexually reproducing organisms, fertility results from a complex interplay of physiological, developmental, and behavioral processes across the various stages of sexual reproduction. These stages include gametogenesis, followed by mate searching in species with separate sexe, and eventually courtship and copulation. After copulation, fertilization of the ova can be delayed, with spermatozoa being stored in female sperm storage organs for varying durations (Birkhead & Moller, 1993; Holt & Fazeli, 2016): from less than a day in some mammals (Rodger & Bedford, 1982), to weeks in birds (Sittman & Abplanalp, 1965), and even in years in reptiles (Levine et al., 2021). Then, sperm quality, quantity, and its ability to compete with sperm from other males are critical factors influencing fertility (Simmons, 2002). Similarly, female ovum quality and quantity are key determinants of fertilization success. Post-zygotic development encompasses cellular differentiation and the formation of essential structures, through complex interactions between the embryo and its environment. Ultimately, fertility involves both the qualitative and quantitative production of offspring.

In aquatic environments, the specific heat capacity of water causes rapid changes in ectotherm tissue temperatures, which can directly impact on physiological and behavioral traits of organisms. In teleost fish, prolonged exposure to high temperatures significantly reduces the number of germ cells in both sexes (Byerly et al., 2005; Strüssmann et al., 1998). In males, it impacts sperm quality (da Silva Castro et al., 2024; Dadras et al. 2019; Mehlis & Bakker 2014; Pinheiro et al. 2021), while in females, it hinders oocyte maturation (Concannon et al., 2021; Gillet et al., 2011; Vikingstad et al., 2016) or impairs offspring development (Guzman et al., 2023). Still, their cohort biomass per recruit grows substantially from offspring to adult sizes, enhancing density-dependent regulation and providing a buffer against external disturbances such as environmental changes (Andersen, 2019). Additionally, their high population turnover increases the likelihood of producing individuals better adapted to changing environmental conditions, assuming the offspring survive (Kopp & Matuszewski, 2013; Sydeman et al., 2015). In contrast, the impact of global warming on species producing few eggs or offspring per reproductive boots, could have critical consequences for population persistence. Rays, skates and sharks (i.e. elasmobranchs) generally have slow growth, large adult size, late sexual maturity and low reproductive rates (Hoenig & Gruber 1990). For example, the spiny dogfish (*Squalus acanthias*) reaches sexual maturity at around ten years of age, exhibits bi-annual ovarian cycles, and produces litters of as few as ten individuals (Castro, 2009). Elasmobranchs also have evolved diverse reproductive modes, ranging from oviparity (egg-laying) to aplacental and placental viviparity (live-bearing). Oviparity is found in skates (Rajiformes), and in several families of sharks (e.g. Scyliorhinidae, Heterodontidae, Orectolobidae) (Wourms et al., 1988). Viviparity is characteristic of all rays and about 70% of shark species (Gelsleichter et al., 2024). Despite these various reproductive systems, all elasmobranchs have internal fertilization, where the male mates with the female using one of his paired claspers (intromittent copulatory organs) to transfer sperm to the female reproductive tract (Conrath & Musick, 2012). Additionally, in some species of elasmobranchs, the female can store the sperm for a prolonged period of time (Pratt 1993, Jordan et al., 2021).

The low reproductive rate of elasmobranchs, as well as their various reproductive traits may make them particularly vulnerable to rapidly rising ocean temperatures. While several elasmobranchs are already at high risk of extinction due to direct anthropogenic pressures (Dulvy et al., 2021), the potential impact of global warming on their fertility have never been documented. In this perspective, we provide a detailed assessment of the potential effects of global warming on elasmobranch fertility by exploring specific reproductive traits such as the gametogenesis, mate searching, gamete storage, fertilization, post-zygotic development, and offspring production. We also consider the potential ecological and evolutionary impacts in response to thermal pressure. Finally, we identify gaps and uncertainties in our understanding of the processes involved in fertility, as well as taxonomic and geographical variations.

BOX 1

Standardized terminology for fertility

The ability of an organism to produce viable offspring (Walsh et al. 2019). It can be measured through various metrics such as number of individuals producing live offspring, live sperm/eggs, number of offspring, sperm count, sperm viability, sperm morphology or sperm swimming speed, egg count or egg viability, gamete DNA damage, gonad deformation/size (Bretman et al. 2024). Fertility is ultimately constrained when conditions result in an individual being unable to produce any offspring (i.e., sterility).

Gametogenesis

Elasmobranchs display a diverse array of reproductive cycles that are intricately timed and environmentally sensitive. Males typically exhibit an annual spermatogenesis cycle, peaking at specific times of the year, while females can have longer and more variable reproductive cycles (Awruch, 2015). The reproductive cycle of female elasmobranchs is defined by the frequency of breeding and consists of two periods: vitellogenesis and gestation. These periods can occur concurrently or consecutively, and their duration is variable, collectively determining the length of the reproductive cycle (Awruch, 2015). Some females exhibit annual (Yamaguchi et al., 2021), biennial (Castro, 2000; Baremore and Hale, 2012), or triennial cycles. For example, the genus *Rhizoprionodon*, *Mustelus*, and some *Sphyrna* species display annual cycles with concurrent vitellogenesis and gestation, producing one brood each year (Castro, 2009). In contrast, sand tiger shark (*Carcharias taurus*) females have a biennial reproductive cycle with discontinuous ovulation (Castro, 2009), while the tope shark (*Galeorhinus galeus*) and the tiger shark (*Galeocerdo cuvier*) are suggested to have a triennial cycle (Nosal et al., 2021; Theron et al., 2001; Whitney and Crow, 2007).

Environmental conditions, particularly temperature, play a significant role in shaping these reproductive patterns (Hoffmayer et al., 2013). For instance, in the gummy shark (*Mustelus antarcticus*), there are notable differences in the reproductive cycles across different regions of southern Australia (Walker, 2007). In the western regions, the ovarian and parturition cycles tend to be annual, suggesting that these sharks go through a complete reproductive cycle every year (Walker, 2007). In contrast, the reproductive cycles are biennial in the eastern regions, with sharks completing their reproductive cycle every two years (Walker, 2007). These variations are primarily attributed to environmental differences between the regions. The western areas might offer more favorable conditions, such as higher or more constant water temperatures and abundant food resources, which can support the energy-intensive processes of vitellogenesis and gestation within a single year. On the other hand, the eastern regions may experience more fluctuating or less optimal environmental conditions, necessitating a longer period for females to sequester energy and transfer it to developing oocytes (Nosal et al., 2021). These conditions could include variations in sea temperatures, prey availability, and habitat quality, which collectively influence the reproductive timing and success of *M. antarcticus* populations in these distinct geographic locations (Walker, 2007). Conversely, species such as the Alaska skate (*Arctoraja parmifera*), that inhabit polar waters or deep ocean environments where temperature and prey availability remain stable, seem to exhibit continuous reproductive cycles throughout the year (Matta, 2015).

Moreover, the peak times for spermatogenesis and ovulation may not coincide within a year, leading to potential mismatches in reproductive timing. Spermatogenesis often peaks at a different time than ovulation in elasmobranchs. For example, in males of finetooth shark (*Carcharhinus isodon)*, spermatogenesis occurs from March to April while females ovulate from May to June (Higgs et al., 2020). This temporal mismatch means that the availability of mature sperm does not align with the availability of mature eggs, reducing the likelihood of successful fertilization in species where females could not store sperm for months. Hormonal fluctuations, including transient increases in testosterone and dihydrotestosterone in males, and estrogen and progesterone in females, correlate with these reproductive phases (Gelsleichter et al., 2024; Manire et al., 1995; Mull et al., 2010; Rasmussen et al., 1999; Theron et al., 2001; Tricas et al., 2000). Temperature is one of the main factors influencing endocrine regulation, playing a crucial role in the hormonal fluctuations that control spermatogenesis and ovarian follicle development (Elisio et al., 2019; Heupel et al., 1999; Nozu et al., 2018; Mull et al., 2008). For instance, Dobson and Dodd (1977) found that temperature changes can significantly alter the rate of spermatogenesis and sperm quality in the small-spotted catshark (*Scyliorhinus canicula*), potentially leading to lower sperm counts and reduced fertility if temperatures deviate from the optimal range. Similarly, Castro et al. (1988) demonstrated that fluctuations in water temperature can accelerate or decelerate the development of ovarian follicles in the chain catshark (*Scyliorhinus retifer)*. Warmer temperatures may hasten follicle development, leading to earlier ovulation, while cooler temperatures might delay the process. Therefore, the increasing and unpredictable temperatures associated with climate change could disrupt the balance of the elasmobranch endocrine system, leading to mismatches in reproductive timing and reduced reproductive success (Gelsleichter et al., 2024). For example, elevated temperatures might cause a premature surge in estrogen and progesterone levels in females, triggering ovulation before males reach peak sperm production. Conversely, cooler temperatures might delay these hormonal changes, resulting in a misalignment of reproductive cycles.

Searching for mates and copulation

Male and female elasmobranchs generally live separately for most of the year, grouping only during specific annual sexual aggregations. For example, the silky sharks (*Carcharhinus falciformis*) only gather at the southern tip of the Baja California Peninsula in June and July (Whitehead et al., 2022). Similarly, *C. isodon* sharks are observed in the mating areas of South Carolina when surface water temperatures rise above 20°C in late April and early May (Castro, 1993). Despite these predictable patterns, the timing of these gatherings can be inconsistent, with males and females not always arriving at breeding sites simultaneously. For instance, nurse shark (*Ginglymostoma cirratum*) males typically arrive in May and June and leave in July, while females arrive every two or three years (not simultaneously) in June (Pratt et al., 2022). The timing and location of these sexual aggregations are closely tied to environmental factors such as temperature and prey availability. Adults of the narrownose smooth-hound (*Mustelus schmitti*), for example, are found predominantly at aggregation sites that are significantly warmer than non-aggregation ones (Elisio et al., 2017). Likewise, courtship behaviors of the basking shark (*Cetorhinus maximus)*, such as torus formations, are closely associated with thermal fronts between May and July, indicating that these individuals aggregate in prey-rich areas before engaging in courtship (Sims et al., 2000; Sims et al., 2022). However, the warming of ocean temperatures and the increased unpredictability of prey availability due to climate change pose significant threats to those searching for mates. Rising temperatures could disrupt the timing and distribution of prey, potentially altering the environmental cues that sharks and rays depend on for their aggregations and mating behaviors. Moreover, increased variability in temperature may lead to mismatches in the timing of elasmobranch arrivals at breeding sites, decreasing mating opportunities and reproductive rates, which could adversely impact their reproductive success.

In addition, females often exhibit strong fidelity to specific breeding sites, which play a crucial role in their reproductive success (see review of Heupel et al., 2007). For example, Tiger Beach (Bahamas) is a renowned aggregation site for *G. cuvier* females (Sulikowski et al., 2016). Similarly, *G. galeus* females demonstrate triennial migration and site fidelity to La Jolla (California, USA) (Nosal et al., 2021). This strong site fidelity makes these species particularly vulnerable to habitat loss and degradation. Essential breeding grounds such as mangroves, seagrass beds, and coral reefs provide food resources, and optimal environmental conditions for reproduction (Speed et al., 2011). However, these habitats are increasingly threatened by human activities and climate change (Gilman et al., 2008; James et al., 2023). For instance, climate change-induced shifts in ocean temperatures and acidification can degrade the quality and distribution of these key areas, further compromising their reproductive success. Moreover, the loss of these critical habitats exacerbates the challenges faced by migratory species. If traditional breeding sites become unsuitable or are lost, elasmobranchs may be forced to undertake longer migrations in search of new sites. This increased travel may raise their energy expenditure.

The ultimate solution to reproductive constraints that make finding a partner exceedingly difficult may lie in the facultative use of parthenogenesis. Notably, changes from sexual reproduction to female-producing parthenogenesis (also called thelytoky) have been observed in the wild for the endangered bonnethead shark (*Sphyrna tiburo*) and the critically endangered smalltooth sawfish (*Pristis pectinata*) (Chapman et al., 2007; Fields et al., 2015). Examples in captivity also exist both in oviparous and viviparous species (Dudgeon et al., 2017; Feldheim et al., 2010; 2016; Harmon et al., 2016; Portnoy et al., 2014; Wyffels et al., 2021). Parthenogenesis may occur more frequently in conditions of low population density, where females face a heightened risk of reproductive failure due to the difficulty of finding mates. As climate change continues to exacerbate challenges related to mate availability—by disrupting habitat, altering population dynamics, and intensifying environmental stressors—the potential for parthenogenesis could increase. Most studies suggest that parthenogenesis occurs in cartilaginous species by terminal fusion automixis, the restoration of diploidy by fusion of the egg with a polar body (Harmon et al., 2016; Feldheim et al., 2010, 2016; Fields et al., 2015). This mechanism often results in elevated or complete homozygosity in offspring. However, gametic duplication also leads to elevated homozygosity and in most cases cannot be disregarded as the potential mechanism of parthenogenesis (Booth & Schuett, 2016). By contrast, genetic and flow cytometric analysis of a female whitetip reef shark (*Triaenodon obesus*) and her stillborn pup indicated that the pup was genetically haploid (Portnoy et al., 2014). While the parthenogenetic mechanism remains to be clarified and may be different according to species, a nearly complete homozygosity or haploidy can significantly compromise viability and reproduction of the clonal offspring, with direct implications for maternal fitness. Additionally, all parthenogenetically generated sharks reported to date were females, indicating that male is the heterogametic sex in these species. In scenarios where opportunities to find mates are limited, the production of homozygous or haploid clonal females could skew the sex ratio. If these clonal females are able to reproduce, this could trigger a downward spiral, making it progressively harder to find male partners. In addition, facultative asexual reproduction theoretically accelerates the accumulation of recessive deleterious mutations in offspring, thereby greatly reducing their fitness. Although facultative asexual reproduction may serve as a last resort for passing on genes in the absence of mating opportunities, the persistence of this reproductive strategy would require that the offspring produced are capable of reproduction.

Sperm storage and sperm quality

Sperm storage is shaped by selective pressures acting on male traits, such as the ability of sperm to remain viable over extended periods, and female traits, including the capacity to maintain and preserve sperm (Orr & Zuk, 2012). Female sperm storage has been documented in 32 species of both viviparous and oviparous sharks and skates (Bester-van der Merwe et al., 2022). Since males and females spend most of their time apart, female sperm storage strategies may ensure fertilization despite the spatial and temporal separation of sex. For instance, mated females of the clearnose skate (*Rostroraja eglanteria*) are capable of storing sperm and producing fertile eggs for up to six months after insemination (Luer & Gilbert, 1985; Luer et al., 2009). In species like the Atlantic sharpnose shark (*Rhizoprionodon terraenovae)*, the sperm is stored for weeks or months in the female reproductive tract, allowing fertilization to occur shortly after ovulation (Pratt, 1993). Females of the nomadic sharks, such as the blue shark (*Prionace glauca),* the dusky shark (*Carcharhin*us *obscurus*), *G. cuvier* or the dusky smooth-hound (*Mustelus canis)* possess specialized tubules surrounded by a secretory matrix, playing a crucial role in the storage and protection of sperm (Hamlett et al., 2002; Moura et al., 2011; Musick & Ellis, 2005). This adaptation also allows repeated fertilization over time (Pratt, 1993; Whitney & Crow, 2007). During this storage period, clasper gland secretions transmitted alongside the sperm to a female may provide essential nutrients to maintain the viability of the sperm within the female oviducal gland (Luer et al., 2009). Additionally, secretions from the male alkaline gland stimulate sperm motility, potentially enhancing the migration of sperm to the oviducal glands, thereby increasing the chances of successful fertilization (Luer et al., 2009).

In males, two distinct types of sperm aggregates have been characterized: spermatophores and spermatozeugmata (Pratt & Tanaka, 1994). Spermatophores consist of sperm embedded within a gelatinous or proteinaceous matrix, which serves to protect the sperm and enhance its viability until it is released (Moura et al., 2011). These structures have been observed in several species, including the bigeye thresher shark (*Alopias superciliosus*), C. *taurus*, the great white shark (*Carcharodon carcharias*), the shortfin mako (*Isurus oxyrinchus*), and the porbeagle (*Lamna nasus*) (Pratt & Tanaka, 1994). Although the production of spermatophores may require more energy and resources compared to non-aggregated sperm, their gelatinous structure helps to maintain the sperm's position, thereby increasing the likelihood of encountering an ovum. In contrast, spermatozeugmata refers to sperm structures that may or may not be surrounded by a protective capsule or matrix. These structures exhibit greater variability in their composition and are found in a broader range of species, including *Carcharhinus* species *S. acanthias*, *P. glauca*, *R. terraenovae*, and the scalloped hammerhead (*Sphyrna lewini*) (Pratt & Tanaka, 1994). While the morphological variability of spermatozeugmata may enable species to adapt to environmental conditions to some extent, their lack of protection can make them more susceptible to environmental damage, ultimately reducing their viability.

In the context of global warming, the significance of sperm storage strategies becomes increasingly apparent. Storing sperm increases the chances of fertilization, particularly when mate encounters are scarce. This problem is exacerbated if these encounters do not coincide with the period when males are actively attempting copulation (Willson & Smith, 2017) or producing sperm with the highest percentage of motile spermatozoa (Wyffels et al., 2020). Species capable of long-term sperm storage would thus seem to have a reproductive advantage if interactions with the opposite sex were to decrease. However, as temperatures rise, the quality of stored sperm in both males and females may deteriorate. Sperm quality—encompassing factors such as motility, fertilizing ability, and velocity—is known to be temperature-dependent (Alavi et al., 2005). For example, in humans, the average scrotal temperature is typically 2 to 4 °C lower than core body temperature, and an increase of 1 to 1.5 °C of the scrotal temperature can adversely affect sperm production and lead to morphological abnormalities (Hamerezaee et al., 2018). Elasmobranchs possess semen with unique features that allow for long-term movement and survival within the female reproductive tract, resembling mammalian sperm morphology and behavior. Any rise in body temperature in elasmobranchs could directly diminish the quality of both the sperm and the associated proteins responsible for their preservation and function, as observed in mammals. Additionally, female sperm storage processes, such as the female production of glucose-rich uterine fluid that enhances the duration of sperm motility (Minamikawa & Morisawa, 1996), are influenced by variations in plasma levels of key temperature-dependent hormones, including testosterone, 17β-estradiol, and progesterone (Gonzalez De Acevedo & Gelsleichter, 2021). Elevated temperatures can disrupt these hormonal levels, potentially affecting stored sperm viability and motility. Thereby, females may store sperm of initially poor quality and fail to maintain it effectively, leading to reproductive cycles that can span two or three years but ultimately prove unsuccessful. Moreover, polyandry, or the practice of females mating with multiple males, is widespread among elasmobranchs (Bester-van der Merwe et al., 2022). This frequently results in litters sired by different males, as seen in species like *G. cirratum*, where each pup in a single litter may have a different father (Heist et al., 2011; Saville et al., 2002). While the indirect genetic benefits of multiple mating are well-documented across various taxa, the specific advantages for female elasmobranchs remain largely unresolved

(Bester-van der Merwe et al., 2022). Females may benefit from polyandry in populations in which infertile males are common, or through an improved fertility (Kvarnemo & Simmons 2013). It may also reduce female monopolization by males, and thus weaken male focused sexual selection (Kvarnemo & Simmons 2013). Nevertheless, polyandry is also costly in terms of mate searching, competition for mates, sexually transmitted diseases, and male damage, potentially leading to sexual conflict (Birkhead & Møller 1998). In the context of rising temperatures, these competitive dynamics could play an increasingly important role in sexual selection, with alterations of pre- and post-copulatory sexual strategies (Birkhead & Møller 1998).

Post-zygotic development and offspring production

Female elasmobranchs employ a diverse array of strategies to supply developing embryos with essential nutrients. These strategies range from relying solely on the nutrients contained within ovulated eggs to establishing intricate connections between the mother and offspring (Hamlett et al., 1993). Because offspring of oviparous species develop outside the mother's body, a female's only opportunity to provide nutrition to embryos is via the egg yolk. In viviparous species, maternal investment into offspring falls across a spectrum of energetic investment that female elasmobranchs make in their young. Lecithotrophy, also known as yolk-sac lecithotrophy, describes a reproductive strategy where embryos develop internally within the mother's uterus but receive no supplemental nutrition beyond the initial yolk provided by the egg. In contrast, histotrophy, predominantly observed in Myliobatiformes (e.g. the giant manta, *Mobula birostris)* and some viviparous Carcharhinidae such as *C. carcharias* (Sato et al., 2016), involves specialized uterine structures that secrete nutrient-rich histotroph, or uterine milk, offering a significant increase in maternal energetic investment (Bester-van der Merwe et al., 2022; Wosnick et al., 2022). In Lamniformes, females ovulate unfertilized eggs during gestation that are consumed by developing embryos within the uterus (Pratt, 1993). This process, known as oophagy, allows mothers to transfer substantial lipid resources to their offspring via the consumed eggs. A rarer form of maternal investment, adelphophagy, is characterized by embryos cannibalizing their siblings and is notably observed in the Odontaspididae family, which combines both oophagy and adelphophagy strategies (Gilmore et al., 1983). Placentotrophy, a derived characteristic found only in certain Carcharhinidae (e.g. *P. glauca*), including some species within the Triakidae family (e.g. *M. canis*) and all members of the Hemigaleidae, Carcharhinidae, and Sphyrnidae families, involves a more developed connection between embryos and the mother's uterus through a yolk-sac placenta (Bester-van der Merwe et al., 2022).

Elasmobranchs are suspected to use temperature as a cue during the reproductive season (Hight & Lowe, 2007). They may seek out warmer waters or alter their activity to optimize the thermal environment for embryonic development, thereby potentially shortening the gestation period (Bansemer & Benneth, 2009; Jirik & Lowe, 2012; Nosal et al., 2014; Speed et al., 2012). For example, pregnant females of the Atlantic stingray (*Hypanus sabinus)*, a viviparous species, preferred water temperatures that were 1°C higher than those favored by their non-pregnant counterparts. This slight increase in temperature was sufficient to reduce gestation time by approximately two weeks (Wallman and Bennett, 2006). Similarly, it is hypothesized that oviparous species likely utilize higher temperatures to accelerate embryo development (Wheeler et al., 2020). For instance, the spiny skate *(Bathyraja spinosissima)* seems to actively exploit the elevated temperatures of hydrothermal vent environments to "incubate" their embryos (Salinas-de-León et al., 2018). However, while moderate increases in temperature can be beneficial for gestation and incubation, excessively high temperatures may pose significant risks. The anticipated rise in global temperatures due to climate change could lead to thermal stress, adversely affecting the health and survival of both embryos and adults. In teleost fish, high stress levels are linked to an increase in cortisol in lipid reserves provided to embryos, leading to developmental dysfunction and reduced offspring viability (Mccormick, 1999; Eriksen et al., 2006; Giesing et al., 2011; Åberg Andersson et al., 2011; Kleppe et al., 2013). As in teleost fish, excessive heat can significantly impair the efficiency of energy transfer from the mother to the embryo in elasmobranchs, whether through yolk provisioning (e.g. Coulon et al., 2024), nutrient-rich histotroph, or uterine milk secretions. For oviparous species, increased temperatures might lead to higher daily egg production, potentially regulated by progesterone (Rasmussen et al., 1999; Inoue et al., 2022), as seen in species like the thornback ray *(Raja clavata*), the blonde ray (*Raja brachyura*), and the spotted ray (*Raja montagui*; Holden et al., 1971). However, a higher frequency of egg-laying could elevate the energy demands on the female, potentially reducing maternal investment. This may manifest as a decrease in oocyte size (King et al., 2003; McCormick, 1998), which in turn could result in the production of smaller juveniles. Additionally, oviparous species experiencing a peak in egg-laying just before summer (Ellis & Shackley, 1997; Gao et al., 2022; Kang et al., 2013; Mabragaña et al., 2014) may face an increased embryo mortality during this critical period under the temperatures projected for the end of the century (Coulon et al., 2024). For viviparous species, since female hormone levels—key regulators of embryonic development stages (McComb et al., 2005; Sheldon et al., 2018)—are influenced by temperature fluctuations, changes in temperature are likely to affect the duration of these developmental stages. Furthermore, while global temperatures rise, regions experiencing intense upwelling that causes significant cooling could also lead to increased risks of unsuccessful births (Lesniak et al., 2015) or acute mortality in juveniles (Carlisle et al., 2015).

A strategy to better align elasmobranch gestation with the constraints imposed by environmental variations might involve the expression of embryonic diapause. This phenomenon, wherein embryonic development is temporarily suspended for several months at the blastodisc stage (Lessa, 1982; Morris, 1999), may help elasmobranchs synchronize their reproductive cycle with optimal environmental conditions, thereby enhancing reproductive success and adapting to fluctuating environmental factors. For a comprehensive review of embryonic diapause, see Waltrick et al. (2012). This strategy has been observed or confirmed in several elasmobranch orders, including Myliobatiformes, Rhinopristiformes, and families such as Carcharinidae (e.g., the Pacific spadenose shark, *Scoliodon macrorhynchos*, Zhao et al., 2022), and Priostiophoridae. For example, the gestation period of the Naru eagle ray (*Aetobatus narutobiei*) lasts approximately 12 months, which includes a 9.5-month obligate embryonic diapause during overwintering and seasonal migrations (Yamaguchi et al., 2021). Furthermore, the eastern fiddler ray (*Trygonorrhina fasciata*) gives birth in late autumn, even as water temperatures decrease to reach their lowest point in early spring. This timing could be advantageous if the main dietary components for newborns are particularly abundant during this period, providing a critical resource boost for the developing juveniles (Marshall et al., 2007). While the precise mechanisms underlying embryonic diapause in elasmobranchs remain unclear, Waltrick et al. (2014) demonstrated that testosterone levels are elevated throughout most of the diapause period in the Australian sandbar shark (*Rhizoprionodon taylori*). This finding suggests that testosterone may play a crucial role in maintaining this paused state of embryonic development. Moreover, the observed increase in plasma testosterone from the end of diapause to the onset of active development implies that androgens might be involved in terminating diapause and initiating development (Waltrick et al., 2014). Consequently, a moderate increase in temperature could alter hormonal regulation of embryonic diapause duration. This could create a mismatch between the timing of offspring emergence and the availability of their prey or potentially result in developmental anomalies due to accelerated growth (Luer & Wyffels, 2022). However, embryonic diapause may be facultative and vary among different populations of the same species, depending on their latitudinal distribution. For example, there are notable differences in the reproductive biology of *R. taylori* between individuals from the southern end of their range in eastern Australia and those from northern Australia (Taylor et al., 2016; Simpfendorfer, 1992). The southern individuals exhibit an annual breeding cycle that includes an embryonic diapause lasting 7 to 8 months. In contrast, these southern individuals have an average fecundity almost double that of their northern counterparts. Here, the female's longer reproductive cycle could be counterbalanced by higher fecundity. Since embryonic diapause is not a universal trait within all elasmobranch species, it is likely that this reproductive strategy has evolved independently across different species (Waltrick et al., 2012). Further research is needed to elucidate the mechanisms of diapause and to investigate its prevalence and role in various elasmobranch species.

Finally, females exhibit site-specific gestation, incubation and birthing behaviors (Baremore & Hale, 2012; Bejarano-Alvarez et al., 2011; Mull et al., 2010; Smith et al., 2021). For example, Feldheim et al. (2017) demonstrated that out of 55 females of *P. pectinata*, nine have consistently given birth in the Charlotte Harbor estuary in Florida (USA) for a decade or more. However, as global temperatures rise, the environmental conditions of these sites are likely to be disrupted. For example, rising sea temperatures could alter the thermal and oxygen profiles of these habitats, making them less suitable for the juveniles (Crear et al., 2020). This is especially critical for oviparous species, as rising temperatures and decreasing oxygen levels in the oceans could significantly increase embryonic mortality rates, as observed in *S. canicula* (Coulon et al., 2024; Musa et al., 2020). Similarly, changes in salinity due to altered rainfall patterns and freshwater inflow could affect the suitability of these sites (Cerutti-Pereyra et al., 2024). In addition to temperature and salinity changes, climate change is likely to impact prey availability, further compromising the survival of newborn elasmobranchs, which rely on these areas not only for protection but also for access to preys (Heithaus, 2007).

Future of elasmobranch fertility research

We have reviewed 77 articles to provide a comprehensive perspective on the largely unexplored impact of global warming on elasmobranch fertility. Our analysis reveals a notable increase in the number of publications on this topic from 1980 to 2020 (Figure 1). Among these studies, a significant proportion—one-third (26 out of 80)—were conducted in FAO zone 31 (central-western Atlantic) (Figure 1). This is followed by FAO zones 21 (North-western Atlantic) and 77 (central-western Pacific), with 11 studies each, indicating a primary focus on regions around North and Central America. Interestingly, despite the extensive monitoring history of fish populations in FAO zone 27 (Northeast Atlantic), which is among the longest and most comprehensive, only 6 studies have been conducted on elasmobranch fertility in this area. It is particularly concerning that the southern ocean is not represented in the studies, as this region hosts elasmobranchs with the highest functional and phylogenetic uniqueness globally (Pimiento et al., 2023). This implies that species in this area may exhibit highly specific responses compared to others. Moreover, significant research gaps are evident in the waters around Africa, especially in the North-western and South-eastern regions, which are known for their high species richness (Lucifora et al., 2011). Current understanding suggests that reproduction is generally aseasonal in deep-sea, pelagic, and tropical non-migratory elasmobranch species, likely due to the relatively stable water temperatures in these environments. Conversely, some prolonged oviparous species are hypothesized to exhibit partial seasonality in their reproductive patterns. In subtropical coastal regions, reproduction appears to be more distinctly seasonal, influenced by migratory patterns related to temperature fluctuations and food availability (Penfold & Wyffels, 2019). However, these hypotheses remain largely untested and warrant further investigation to fully understand their validity across various environments. Moreover, 22% of the studies (17 out of 77) were conducted in aquarium settings (Figure 1). While aquariums may not be ideal for studying large pelagic or migratory species, they offer valuable insights into the effects of global warming on the fertility of smaller, sedentary species that cannot avoid temperature changes through dispersion or migration (Feldheim et al., 2022). In terms of reproductive modes, oviparous species are underrepresented in the studies, comprising less than a quarter (19 out of 83) of the research focus (Figure 2). However, species of 23 families have been examined, resulting in a rich diversity in, environmental adaptations, and life-history traits (Figure 2). Regarding fertility stages, the majority of research has concentrated on gametogenesis, post-zygotic development, and offspring production, with 28, 28, and 22 mentions respectively (Figure 2). This distribution underscores a substantial gap in our understanding of the critical processes occurring between gamete production and embryo establishment.

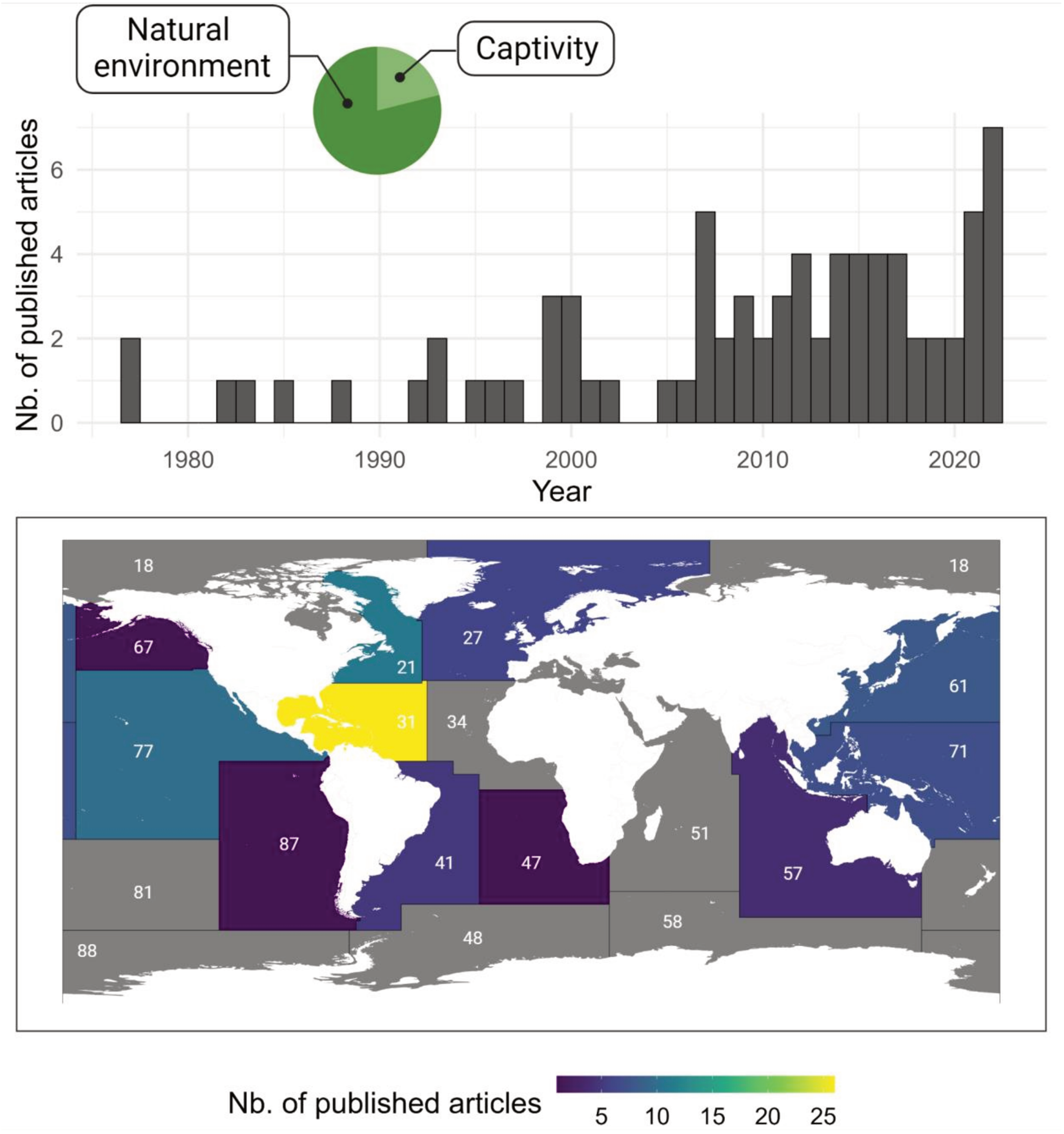

FIGURE 1. Distribution of scientific articles addressing the effects of temperature on elasmobranch fertility over time, in natural environments or captivity (top panel), and categorized by FAO zones of the study areas (bottom panel). The FAO zones are labeled in white on the map

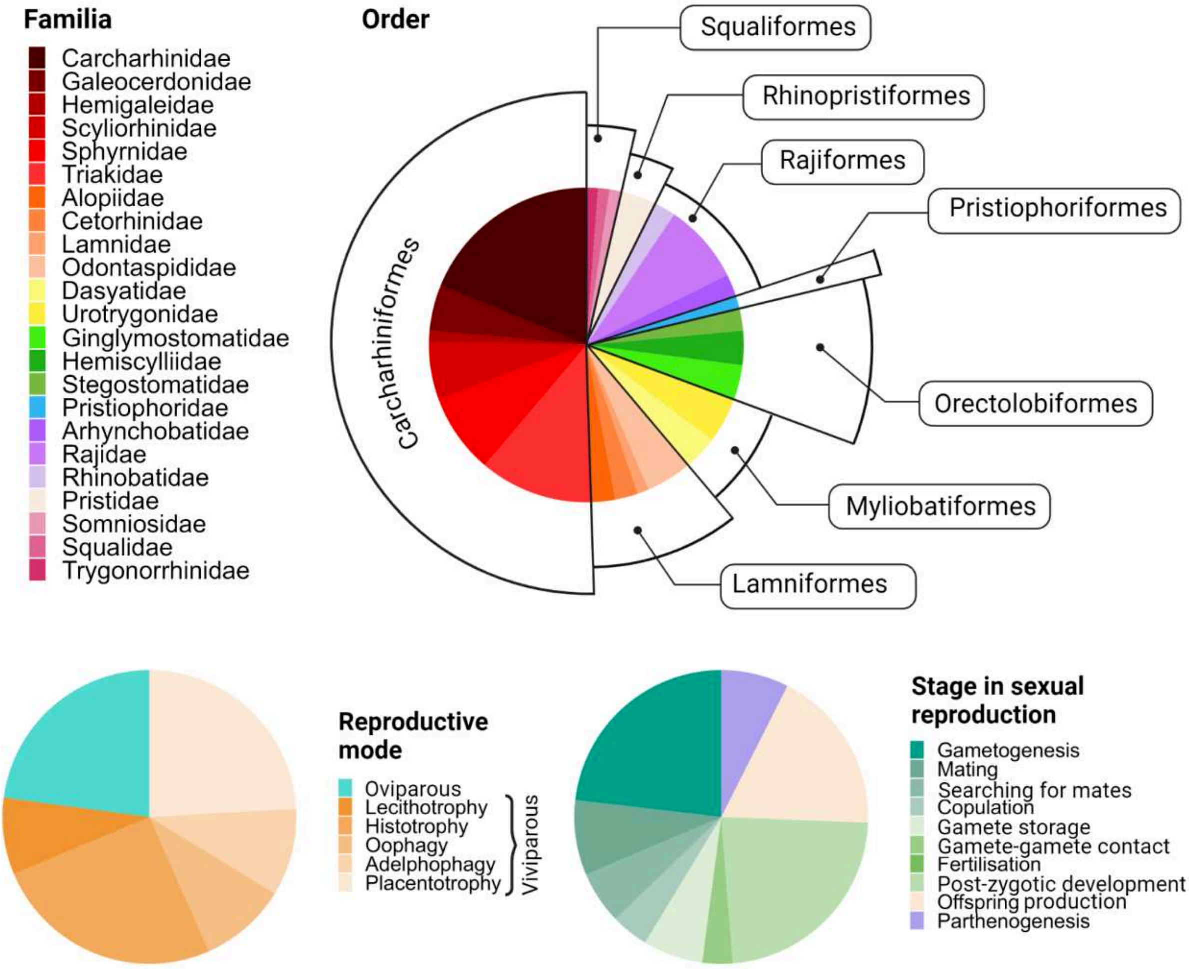

FIGURE 2. Distribution of scientific articles addressing the effects of temperature by elasmobranch order and family (top panel), reproductive mode (bottom left panel), and stage of sexual reproduction (bottom right panel).

Conclusion

Rays, skates, and sharks display diverse reproductive strategies, with each stage potentially affected by temperature changes, posing a threat to their reproductive success and long-term population stability. More research is required on both behavioral and physiological aspects to fully understand the impact of global warming on elasmobranch reproduction. Key areas of focus include how temperature affects mate searching, courtship, and copulation, as well as sperm storage and gamete compatibility.

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SYNTHÈSE ET PERSPECTIVES

Les objectifs principaux de cette thèse étaient d'évaluer les effets du changement climatique sur les élasmobranches d'Atlantique Nord-Est en combinant des approches expérimentales et de modélisation. Plus spécifiquement, elle visait à :

1. **Étudier les réponses physiologiques individuelles** des élasmobranches face aux variations de température et de niveaux d'acidification prédites par le GIEC, en utilisant des expériences en milieu contrôlé.
2. **Modéliser les dynamiques de population** et les trajectoires de survie de certaines espèces cibles sous ces mêmes scénarios climatiques prédits par le GIEC, afin de mieux comprendre leur résilience ou vulnérabilité face à ces conditions changeantes.
3. **Explorer les interactions entre les traits d’histoire de vie et les pressions environnementales**, notamment en ce qui concerne la reproduction et la survie des jeunes stades de développement.
4. **Évaluer les impacts potentiels sur la structure des assemblages** d'élasmobranches, en tenant compte des changements dans la distribution et l’abondance des espèces, et de leurs conséquences sur les fonctions écosystémiques.

Cette synthèse met en lumière les principales réponses observées, des individus aux assemblages d’espèces et propose des perspectives pour les recherches futures, en vue de mieux appréhender les dynamiques écosystémiques et les actions de conservation nécessaires face aux changements globaux.

L’exposition des embryons de petite roussette à deux scénarios de réchauffement et d'acidification des océans prévus d'ici la fin du 21ème siècle a révélé leur vulnérabilité face aux températures estivales élevées (Coulon et al., 2024b, **Chapitre 2**). Notre étude a montré que les effets combinés de l'augmentation de la température et de la baisse du pH varient significativement selon le scénario climatique envisagé. Alors que les embryons soumis au scénario « SSP2 : Middle of the Road » (Fricko et al., 2017) ont présenté des impacts relativement limités en termes de taux d'éclosion et de croissance, près de 89 % des embryons exposés au scénario « SSP5 : Fossil-fuelled Development (Taking the Highway) » (Kriegler et al., 2017) n'ont pas éclos. Le pic de mortalité a été observé en août, lorsque les températures étaient les plus élevées (~23°C dans le scénario SSP5, comparé à ~19°C pour les températures historiques (1995-2014) et ~21°C dans le scénario SSP2). Ce résultat suggère une réponse non linéaire ainsi qu’un seuil critique de +4°C, au-delà duquel les effets néfastes de la température sur les organismes deviennent manifestes. Ce seuil est cohérent avec les températures seuils pour le développement embryonnaire allant de 3 °C à 5 °C au-dessus de la température historique documentée chez le requin chabot-bambou (*Chiloscyllium punctatum*) (Rosa et al., 2014), le requin chabot-ocellé (*Hemiscyllium ocellatum*) (Gervais et al., 2018), la raie hérisson (*Leucoraja erinacea*) (Di Santo, 2015) et le requin de Port Jackson (*Heterodontus portusjacksoni*) (Vila Pouca et al., 2019). Pour préciser ce résultat, il serait pertinent de concevoir un protocole expérimental intégrant une gamme plus large de températures et/ou des pics de température. De plus, étant donné que la mortalité est restée très élevée au cours de la première semaine d'acidification, il est crucial de déterminer si cette mortalité résulte d'une réponse retardée, potentiellement liée à un effet dose de la température, ou si elle est directement causée par l'acidification elle-même. Il serait donc pertinent d'examiner les effets combinés de températures stables et de niveaux d'acidité variables afin d'identifier d'éventuels effets synergiques, même si la température semble constituer le principal facteur de stress pour les embryons de petite roussette. Cette observation est en accord avec les travaux de Di Santo (2015), qui montrent que les effets conjoints de l'acidification et du réchauffement sont similaires à ceux du réchauffement seul, l'acidification exacerbant toutefois les impacts du réchauffement. Il serait également pertinent d'exposer des embryons de petites roussettes issus de populations de la façade Atlantique, voire de Méditerranée, afin de tester l'hypothèse d'une variabilité phénotypique des normes de réponse. Une telle approche permettrait d'explorer les différences potentielles dans la manière dont ces populations s'adaptent aux variations environnementales, reflétant des adaptations locales, comme cela a été démontré chez les embryons de requin de Port Jackson (Gervais et al., 2021). Ces résultats pourraient fournir des informations précieuses pour comprendre la capacité d'adaptation de l'espèce face au changement climatique

En comparant les trajectoires individuelles de développement, nous avons identifié le moment précis où les embryons qui n'ont pas éclos ont commencé à diverger de ceux qui ont survécu (Coulon et al., 2024b, **Chapitre 2**). Le pic de mortalité a été observé au $5^{ème}$ stade de développement des embryons (Musa et al., 2018). À ce stade, les filaments branchiaux commencent à s'internaliser et les embryons transforment leurs branchies externes en branchies internes (Pelster et Bemis, 1992). Dans notre dispositif expérimental, nous avons maintenu une saturation stable en oxygène, indépendamment des températures, pour éviter une augmentation significative de la mortalité embryonnaire (Musa et al., 2020). Ainsi, l'augmentation de la mortalité observée pourrait être attribuée à une incapacité des embryons à consommer suffisamment d'oxygène pendant la transition de leurs branchies. Nous avons également constaté un taux de consommation du vitellus plus faible et plus précoce, associé à un taux de croissance réduit. Cela suggère que les embryons exposés au scénario SSP5-8.5 avaient des besoins énergétiques plus élevés et plus précoces, ainsi qu'une mauvaise conversion entre le vitellus et le tissu corporel, ce qui pourrait entraîner un jeûne. Par conséquent, les voies métaboliques des lipides (Wen et al., 2013 ; Bernal et al., 2020) et le développement des branchies (Takata et al., 2018), particulièrement critiques au 5ème stade embryonnaire, nécessitent une étude moléculaire et (sub)cellulaire plus approfondie, notamment en ce qui concerne la biogenèse membranaire. Les semaines durant lesquelles les trajectoires de croissance des embryons SSP5-8.5 dévient de la norme devraient être particulièrement ciblées pour des investigations futures. De plus, notre approche individuelle a révélé que certains embryons dont les trajectoires de croissance déviaient de la norme pouvaient encore éclore. Bien que l'origine de ce changement phénotypique reste, elle mérite également une attention particulière, car la diversité génétique des individus pourrait aider les populations à faire face aux pressions environnementales aiguës (Forsman et Wennersten, 2016). Il serait donc pertinent d'explorer les raisons de la survie de ces individus et d'analyser l'impact de cette sélection sur la structure génétique des populations.

La forte mortalité observée chez les embryons exposés aux conditions prévues par le scénario SSP5-8.5 soulève des questions cruciales concernant la dynamique des populations de la petite roussette. Une telle mortalité soulève des questions sur la viabilité de l'espèce, qui pourrait être gravement menacée dans ce scénario. Toutefois, il est crucial d'évaluer quantitativement cette situation, notamment pour déterminer comment les paramètres démographiques de l'espèce pourraient être affectés par la diminution observée des taux de survie juvénile. Il est possible, par exemple, que cette diminution ne soit pas aussi préjudiciable qu'on pourrait le penser, compte tenu des traits d’histoire de vie de l'espèce, qui possède une fécondité relativement élevée par rapport aux autres élasmobranches. Pour approfondir cette analyse, nous avons comparé les dynamiques de population de la petite roussette à celles d'une espèce phylogénétiquement proche, la grande roussette, en utilisant des modèles individu-centrés prenant en compte les contraintes physiologiques de ces espèces face à la température (**Chapitre 3**). Bien qu’elles partagent un mode de vie démersal similaire, la grande roussette se distingue par une fécondité plus faible et une aire de répartition plus restreinte, suggérant une moindre tolérance aux variations de température. Nos résultats indiquent que même un réchauffement modéré, tel que prévu dans le scénario SSP2-4.5, retarderait l’âge à maturité deux espèces. En revanche, le réchauffement plus sévère prévu par le scénario SSP5-8.5 entraînerait des impacts négatifs significatifs, notamment pour la grande roussette, dont les populations pourraient s'effondrer en Atlantique Nord-Est, révélant ainsi une vulnérabilité accrue au réchauffement global par rapport à la petite roussette. Dans les scénarios AR6 (1994-2015) et SSP2-4.5, plus de la moitié des individus atteignent la maturité entre 9 et 10 ans, tandis que dans le scénario SSP5-8.5, il faut attendre la 13^{e} année. D'une part, le nombre d'individus atteignant la maturité est extrêmement faible ; d'autre part, la maturité n'intervient que deux ans avant l'espérance de vie de l'espèce.

Le **Chapitre 2** (Coulon et al., 2024b) et le **Chapitre 3** ont mis en évidence l'influence significative des températures estivales sur la survie des premiers stades de vie des petites et grandes roussettes, soulignant que la taille initiale des cohortes joue un rôle crucial dans la dynamique des populations des deux espèces. Ce phénomène a également été observé chez plusieurs autres élasmobranches (Kinney et Simpfendorfer, 2009), comme par exemple chez la raie brunette (*Raja undulata*) (Elliott et al., 2020). Pour les scénarios AR6 (1994-2015) et SSP2-4.5, le taux de survie était relativement élevé, allant de 80% à 83% pour les deux espèces. Cependant, dans le cadre du scénario SSP5-8.5, le taux de survie a considérablement diminué, tombant à 33% pour la petite roussette et seulement 23% pour la grande roussette. Cette constatation est particulièrement préoccupante étant donné que les roussettes ne produisent que quelques dizaines d'œufs par an, la grande roussette pondant 3 à 6 fois moins d'œufs que la petite roussette (Ellis et Shackley, 1997 ; Pecuchet et al., 2017). Dans le cadre du scénario SSP5-8.5, ces deux espèces pourraient réagir en déplaçant leurs zones de frai vers des eaux plus profondes ou en migrant vers des régions plus froides (Coulon et al., 2024a, **Chapitre 1** ; Sundby et Nakken, 2008). Le suivi spatio-temporel des sites de ponte pourrait faciliter la détection des déplacements des zones fonctionnelles des espèces, permettant de mettre en œuvre des stratégies de conservation plus efficaces, comme par exemple la réduction de la dégradation des habitats (chalutage de fond, extractions minière, pollution), voire leur mise sous protection. Les roussettes pourraient également ajuster leurs périodes de frais maximales aux mois où les températures sont plus clémentes, comme le printemps ou la fin de l'été (Rogers et Dougherty, 2019 ; Pankhurst et Munday, 2011). Cette plasticité phénologique pourrait conférer un avantage sélectif à certains individus, permettant à leurs descendants de bénéficier de conditions environnementales plus favorables. Cependant, les espèces à distribution côtière restreinte, telles que la grande roussette, risquent d'atteindre leurs limites de tolérance thermique plus rapidement. En raison de leur habitat en eaux peu profondes, elles sont particulièrement vulnérables en cas de dépassement de ces limites dès le printemps et jusqu'à l'automne. Pour mieux comprendre ces dynamiques, il serait pertinent d'incuber des œufs de roussettes à différents moments de la saison reproductive, afin d'évaluer l'impact de la temporalité de la ponte sur le succès d'éclosion et la survie des juvéniles. Ces données expérimentales pourraient enrichir les modèles de dynamique des populations individu-centrés tels que ceux développés dans le **Chapitre 3** afin d'en préciser les sorties sur la persistance des espèces dans un contexte de réchauffement global.

Les modèles individu-centrés développés dans le **Chapitre 3** ont établi un cadre solide pour transformer des données physiologiques limitées à la croissance individuelle en informations pertinentes pour la dynamique des populations de requins ovipares. Toutefois, leur élaboration a révélé d'importantes lacunes dans notre compréhension des capacités de reproduction des requins dans l'Atlantique Nord-Est. Des paramètres essentiels, tels que la taille à maturité et la fécondité des femelles, demeurent mal connus, ce qui complique l'évaluation de la dynamique des populations. Par exemple, dans cette région, la taille à maturité de la grande roussette reste inconnue et a été approximée à partir de la taille du plus petit individu observé en criée avec un œuf émergeant du cloaque. En raison de ces lacunes, de la dégradation du statut de conservation de nombreuses espèces en Atlantique Nord-Est (Coulon et al., 2023 ; Walls et Dulvy, 2021), et du risque de décalage temporel entre les effets du changement climatique et leurs impacts sur les dynamiques de population, dû à la lenteur du renouvellement de ces dernières, il est essentiel d’adopter un principe de précaution lors de l'élaboration de mesures de gestion. Parallèlement, il est essentiel de relancer les études fondamentales sur la biologie des raies et des requins afin de mieux comprendre leurs stratégies de reproduction, leurs capacités de dispersion et leur plasticité phénotypique face aux nombreux changements environnementaux attendus. Ces changements incluent non seulement des facteurs abiotiques, comme ceux que nous avons explorés, mais aussi des facteurs biotiques, tels que les réseaux trophiques et la compétition interspécifique résultant des modifications des aires de distribution des espèces détectées dans le **Chapitre 1** (Coulon et al., 2024a). Les débarquements de ces espèces le long de la façade Manche-Atlantique des côtes françaises pourraient fournir le matériel biologique nécessaire pour définir les stades de maturité des femelles. De plus, les campagnes scientifiques de chalutage de fond menées annuellement sur le plateau continentale européen (ICES, 2022) offriraient l’opportunité de corréler les stades de maturité des individus disséqués avec ceux des individus vivants, grâce à des techniques d'imagerie non invasive (Whittamore et al., 2010). L'utilisation combinée de ces approches permettrait d'étudier un gradient latitudinal de maturation. De telles études pourraient également offrir une meilleure compréhension des effets de la température sur la reproduction des requins, un domaine particulièrement mal documenté. De plus, des interactions renforcées entre la communauté scientifique et les aquariums pourraient faciliter le suivi temporel des individus maintenus en captivité, soit à des températures fixes, soit en suivant les variations saisonnières.

La recherche bibliographique approfondie menée dans le **Chapitre 4** a par ailleurs démontré l’intérêt d’une telle collaboration pour explorer les impacts du réchauffement global sur la fécondité des raies et des requins avec 22 % des études (17 sur 77) réalisées en aquarium. Bien qu’ils ne fournissent pas le cadre idéal pour étudier les grandes espèces pélagiques ou migratrices, ils pourraient apporter des informations précieuses sur les effets du réchauffement global sur la fertilité des espèces sédentaires plus petites (Feldheim et al., 2022), comme la petite roussette ou les raies benthiques côtières. De plus, il est particulièrement remarquable de constater que, malgré l’existence d'un des systèmes de surveillance des populations de poissons les plus anciens et complets dans l'Atlantique Nord-Est, avec un suivi annuel de la Mer du Nord depuis 1963 (ICES, 2023), seules six études ont été menées pour examiner les stratégies reproductives des élasmobranches dans cette région. Concernant les modes de reproduction, les espèces ovipares sont sous-représentées dans la littérature, constat d’un manque important d’intérêt pour ce groupe, alors qu’il concerne pour les eaux de France métropolitaine, 7 des 59 espèces de requins et l'ensemble des Rajiformes (25 espèces) (Bisch et al., 2024). Bien que cette thèse de doctorat se concentre sur les élasmobranches d’Atlantique Nord-Est, il est instructif de considérer les résultats de recherches menées dans différentes zones géographiques. Par exemple, Castro et al. (1988) ont montré que les fluctuations de la température de l'eau peuvent influencer le développement des follicules ovariens chez la roussette maille (*Scyliorhinus retifer*), en accélérant ou ralentissant ce processus. Des températures élevées pourraient entraîner une augmentation prématurée des niveaux d'œstrogène et de progestérone chez les femelles, déclenchant ainsi l'ovulation avant que les mâles n'atteignent leur pic de production de spermatozoïdes. Il est également important de noter que les hormones reproductives jouent un rôle crucial dans le stockage du sperme chez les mâles et les femelles (Bester-van der Merwe et al., 2022), une stratégie observée chez plusieurs espèces de l'Atlantique Nord-Est et notamment la petite roussette. Toute élévation de la température corporelle chez les élasmobranches pourrait diminuer directement la qualité des spermatozoïdes ainsi que celle des protéines associées à leur préservation et à leur fonction, comme c’est le cas chez les poissons téléostéens (Alavi et al., 2005). Ces exemples mettent en évidence un véritable goulot d'étranglement dans le processus de production de juvéniles dans le contexte du réchauffement global, un phénomène qui dépasse la simple équation reliant la température à la production d'œufs définie dans le **Chapitre 3**. En effet, la recherche bibliographique suggère que les variations de température influencent non seulement la quantité d'œufs produits, mais aussi des aspects fondamentaux tels que la gamétogenèse, la rencontre des partenaires, le stockage des gamètes ou bien encore le développement post-zygotique.

Enfin, la modélisation des habitats favorables pour neuf espèces de requins, réalisée dans le **Chapitre 1** (Coulon et al., 2024a), a révélé que les effets potentiels à observer d'ici la fin du siècle sur les individus et la dynamique des populations reposent sur des observations historiques à l'échelle de ces espèces conduites entre 1997 et 2020. Bien que la période d'étude soit relativement courte, elle suffit à montrer la sensibilité des élasmobranches dans l'Atlantique Nord-Est au changement climatique jusqu'à l'échelle des assemblages d'espèces. Parmi les neuf espèces de raies et de requins analysées, cinq se trouvent déjà à la limite supérieure de leur niche thermique. En outre, six de ces espèces ont connu des modifications de l'adéquation de leur habitat, se traduisant par une expansion de leur aire de répartition vers le nord ou l'est, ou encore une migration vers des eaux plus profondes, parfois confinées, comme le plateau des Hébrides ou la fosse norvégienne. Il serait pertinent de prolonger cette étude en intégrant aux projections les seuils de tolérance thermique des embryons, afin de déterminer avec précision la taille des habitats favorables non seulement pour les adultes, mais aussi pour les sites de ponte des différentes espèces (Mbaye et al., 2020). En effet, les femelles montrent souvent une forte fidélité à des sites de reproduction spécifiques, qui jouent un rôle essentiel dans leur succès reproductif (voir la revue de Heupel et al., 2007). Cette fidélité accentue leur vulnérabilité face à la perte et à la dégradation des habitats, aggravées par les changements environnementaux. L'identification de ces zones critiques pourrait ainsi permettre de réduire, dès à présent, les pressions anthropiques directes qui affectent ces habitats.

Par ailleurs, les modifications de l'adéquation des habitats ont entraîné des changements notables dans l'assemblage des traits bio-écologiques des espèces de raies et de requins (Coulon et al., 2024a, **Chapitre 1**). Premièrement, un décalage en profondeur des assemblages en Mer du Nord et en Mer Celtique a été détecté entre 1997 et 2020. La migration des espèces vers des eaux plus profondes est une réponse directe aux changements climatiques (Dulvy et al., 2008 ; Punzón et al., 2016) qui pourrait avoir entraîné des modifications dans le fonctionnement des écosystèmes. En effet, nous avons également détecté une baisse du niveau trophique des assemblages d'élasmobranches, notamment en Mer du Nord. Ces espèces occupant les plus hauts niveaux trophiques de l'Atlantique Nord-Est (Coulon et al., 2023), cette étude met en lumière l'importance d'étudier la dynamique du réseau trophique dans le contexte du changement climatique (Albouy et al., 2014 ; Halouani et al., 2016 ; Nagelkerken et al., 2020 ; Sagarese et al., 2017). Ces résultats suggèrent également que la structure et le fonctionnement des écosystèmes de l'Atlantique Nord-Est pourraient être profondément transformés d'ici à la fin du siècle. Il serait pertinent de prédire ces changements, mais plusieurs obstacles compliquent cette démarche. Tout d'abord, bien que le modèle HMSC développé soit performant pour prédire les habitats favorables aux espèces dans la zone d'étude entre 1997 et 2020, il n'est pas certain que les données soient suffisamment robustes pour des projections à long terme (Ovaskainen et al., 2020). De plus, rien ne garantit que les niches écologiques actuellement observées reflètent celles du futur (Chevalier et al., 2024), notamment en raison du déplacement en profondeur des espèces. Face à ces perspectives, il serait plutôt crucial d'identifier les traits qui rendent certaines espèces plus vulnérables aux changements environnementaux, afin de cibler les groupes nécessitant des mesures de protection renforcées pour préserver la stabilité des écosystèmes. Parmi les traits d'histoire de vie observés, nous avons relevé une augmentation de la taille à maturité, accompagnée d'une légère diminution de la fécondité. Il semblerait que certaines espèces, comme l'émissole tachetée, de distribution lusitanienne, tire profit des changements globaux en cours (Sguotti et al., 2016). Cependant, en raison de la longue durée de vie des élasmobranches et de leur faible taux de renouvellement, il est possible que les effets du changement climatique soient retardés comme cela a pu être observé chez les oiseaux marins (voir par exemple : Thompson et Ollason, 2001). Un déclin pourrait ainsi se manifester dans les décennies à venir, notamment en raison d'échecs dans la reproduction (**Chapitre 4**) ou le recrutement (Coulon et al., 2024b, **Chapitre 2** ; **Chapitre 3**).

Les politiques climatiques actuellement en vigueur à l'échelle mondiale ne permettraient pas de limiter le réchauffement à 1,5°C ou 2°C, mais entraîneraient plutôt une augmentation médiane de +3,2°C d'ici 2100 (Lee et al., 2023). Même si les engagements pris par les États lors des conférences climatiques des Nations Unies étaient respectés, la hausse des températures se stabilise autour de 2,8°C (avec une fourchette de 2,1 à 3,4°C d'ici la fin du siècle). Ces projections excèdent les valeurs prévues par le scénario SSP2-4.5, tout en demeurant inférieures à celles du scénario SSP5-8.5. Dans ce contexte, si ces prévisions se réalisent, les raies et les requins de l'Atlantique Nord-Est seront exposés à des températures intermédiaires à celles étudiées dans cette thèse. Les résultats de ce travail offrent des informations précieuses pour mieux comprendre les effets du changement climatique sur ces espèces. Cette recherche explore non seulement l'impact des températures plus élevées sur les individus, mais aussi sur la dynamique à long terme des populations et des communautés. Ces connaissances sont essentielles pour guider les stratégies de conservation et de gestion des élasmobranches dans un contexte de réchauffement global, où des décisions éclairées devront être prises afin de limiter les impacts sur ces espèces déjà vulnérables.

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