PhD in Aquatic Biosciences // No. 60 - 2024

The cumulative impacts of climate change and fishing on marine communities

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FACULTY OF BIOSCIENCES AND AQUACULTURE

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A thesis for the degree of
Philosophiae Doctor (PhD)

PhD in Aquatic Biosciences no. 60 (2024)
Faculty of Biosciences and Aquaculture

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ISBN: 978-82-93165-59-0

Print: Trykkeriet NORD

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PREFACE

This thesis is submitted in fulfilment of the requirements for the degree of Philosophiae Doctor (PhD) at the Faculty of Biosciences and Aquaculture (FBA), Nord University, Bodø, Norway. The presented research was performed as part of the Stipendiat program. The studies carried out were financially supported by Nord University.

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Bodø, November 2023

ACKNOWLEDGEMENTS

I would like to thank my family for their continued support. I would also like to thank my main supervisor Mark Costello for his patience and guidance. I thank all of my co-authors for their collaboration and mentorship. This includes Donna Dimarchopoulou, Fabrice Stephenson, Arnaud Grüss, Cui Liang, as well as fellow PhD students and lab mates Zhiyuan Shi and Cesc Gordó-Vilaseca. Lastly, I thank co-authors and gracious hosts Daniel Pauly and Deng Palomares at the University of British Columbia for their hospitality and support.

GENERAL ABSTRACT

Marine water-breathing ectotherms are unable to regulate their internal temperature, but rather, are subject to the ambient environment that they inhabit. In turn, they are evolved to inhabit a range of temperatures, as well as areas with sufficient levels of dissolved oxygen content. As the ocean warms and deoxygenates in line with anthropogenic climate change, such changes can negatively impact the fitness of water-breathing ectotherms. In turn, marine ectotherms have been observed and are expected to respond to such environmental changes by reducing their maximum body size and shifting their geographic distribution, in order to track their thermal affinity, and preserve safe physiological conditions within the environment they inhabit.

Yet, observed changes in geographic distribution and body size of marine ectotherms do not occur uniformly between species or biogeographic regions. Variable changes in the size structure and species composition of marine communities in line with ocean warming has the potential to exert destabilising mechanisms on ecosystem function and services, including marine food web structure and fisheries catch. Concurrently, persistent fishing pressure can negatively impact the structure of marine food webs, as fisheries preferentially target large-bodied, high trophic level species. This intensive fishing pressure can reduce both the body- and population size of high trophic level species, further exacerbating any ocean-warming induced reductions in maximum body size or regional population declines resulting from shifting geographic distributions.

How exactly ocean-warming induced changes in body size and geographic distribution, alongside persistent fishing pressure will interact and thus effect marine ecosystems and ecosystem services remains unknown. In light of the potentially negative impact of these cumulative stressors, this thesis investigated changes in maximum body size across temperature gradients, and apparent ocean-warming induced shifts in geographic distribution of marine ectotherm populations within waters of Norway and

New Zealand. The overfishing of high trophic level species was also investigated in New Zealand.

Reductions in maximum body size within warmer temperatures were observed for the largest study species in both Norway and New Zealand, suggesting active, large-bodied species may be those most vulnerable to body size reductions with ocean warming. As well, while all study species in New Zealand reduced in maximum body size in warmer temperatures, several study species in Norway grew to larger body sizes in warmer water. These results provide novel insight, in that lower-latitude species are more likely to shrink with ocean warming, whilst some Arctic fish species may grow larger with intermediate ocean warming. This may be a result of Arctic species being released from thermal stress experienced at their temperature minima (i.e., below 0 °C), although, these species will eventually be limited in maximum size again with warmer ocean temperatures, as temperatures approach their species-specific maxima.

Instances of shifts in the geographic distribution of marine species were investigated using the Mean Temperature of the Catch index. This index infers geographic shifts of populations based on trends in fisheries catch of species within a certain area and time period. In New Zealand waters, results revealed that fisheries catch of pelagic-oceanic species is increasingly composed of smaller-bodied, tropical- and sub-tropical species, and decreasingly composed of large-bodied, cold-water pelagic species. In Norway, fisheries catch of demersal species was dominated by the increasingly abundant Atlantic cod (*Gadus morhua*). These results in Norway and New Zealand suggest that species from lower latitudes are shifting their distributions to higher latitudes (as reflected in fisheries catch), whereby position in the water column (i.e., pelagic species), or capacity as a predator (i.e., Atlantic cod) may increase the rate and extent to which species can shift their geographic distribution in line with ocean warming.

Overfishing of high-trophic level species was investigated in New Zealand using the adjusted Mean Trophic Level index. Results revealed signals of overfishing of high trophic level species within New Zealand shelf waters between 1950 and 2019. These results suggest that during a period of geographic expansion of fisheries across New Zealand's Exclusive Economic Zone, shelf water catch was composed of increasingly lower trophic level species, due to overfishing and subsequent population size decline of higher trophic level species. These results provide novel insight of overfishing in New Zealand waters that was previously elusive in similar analyses across a similar time period. In summary, by investigating these multiple stressors, the results from this thesis provided understanding into expected changes facing marine communities in line with cumulative impacts brought about by climate change and persistent fishing pressure.

SAMMENDRAG PÅ NORSK

Marine vannpustende ektotermer er ikke i stand til selv å regulere sin indre temperatur, men er heller styrt av temperaturen i miljøet de bor i. De er utviklet til å leve i forskjellige temperaturområder, så vel som områder med tilstrekkelige nivåer av oksygen oppløst i vannet. Etter hvert som havet varmes opp og oksygeninnholdet minker i takt med menneskeskapte klimaendringer, kan slike endringer ha en negativ påvirkning på de vannpustende ektotermenes fitness. Marine ektotermer er blitt observert til, og forventes å reagere på slike miljøendringer ved å redusere sin maksimale kroppsstørrelse og flytte seg geografisk i søken etter foretrukket temperatur og et miljø med trygge fysiologiske betingelser.

Likevel, observerte endringer i geografisk fordeling og kroppsstørrelse hos marine ektotermer er ikke alltid ens hos de forskjellige artene eller biogeografiske regionene. Slike varierende endringer i størrelsesstrukturen og artssammensetningen hos marine samfunn som følge av havoppvarmingen har potensiale til å utvikle seg til destabiliserende mekanismer på økosystemfunksjoner og -tjenester, inkludert strukturen i det marin næringsnettet og fiskefangst. Samtidig kan vedvarende fiskepress ha en negativ påvirkning på strukturen til det marine næringsnettet, ettersom fiskeriene fortrinnsvis retter seg mot store fiskearter på høyt trofisk nivå. Dette intensive fiskepresset kan redusere både kropps- og bestandsstørrelsen til arter på høyt trofisk nivå, og ytterligere forverre reduksjoner i maksimal kroppsstørrelse eller regional populasjonsnedgang som følge av geografisk forflytning eventuelt indusert av havoppvarming.

Nøyaktig hvordan endringer i kroppsstørrelse og geografisk fordeling indusert av havoppvarming, vil samhandle med vedvarende fiskepress og dermed påvirke marine økosystemer og økosystemtjenester, er fortsatt ukjent. I lys av den potensielt negative effekten av disse kumulative stressorerne, undersøker arbeidet i denne oppgaven endringer i maksimal kroppsstørrelse på tvers av temperaturgradienter, og tilsynelatende havoppvarmingsinduserte endringer i geografisk fordeling av marine

ektotermpopulasjoner i havområder i nærheten av Norge og New Zealand. Overfiske av arter på høyt trofisk nivå ble også undersøkt i New Zealand.

Reduksjon i maksimal kroppsstørrelse i løpet av perioder med økende temperatur ble observert på de største artene i studiet, både i Norge og New Zealand, noe som tyder på at aktive arter med stor kropp kan være mest påvirket av at havoppvarming fører til reduksjoner i kroppsstørrelse. I tillegg, mens alle artene i studiet i New Zealand fikk mindre maksimal kroppsstørrelse i varmere temperaturer, vokste flere studiearter i Norge til større kroppsstørrelser i varmere vann. Disse resultatene gir ny innsikt, i og med at arter på lavere breddegrader har stor sannsynlighet for å krympe som følge av havoppvarming, mens enkelte arktiske fiskearter kan vokse seg større som følge middels havoppvarming. Dette kan være et resultat av at middels oppvarming frigjør arktiske arter fra det termiske stresset de opplever fordi de lever nært deres temperaturminima (dvs. under 0 °C). Derimot, viss oppvarmingen fortsetter, vil også disse artene avta i maksimal størrelse igjen, etter hvert som temperaturen nærmer seg deres arts-spesifikke maksima.

Tilfeller av geografiske forflytning hos marine arter ble undersøkt ved å bruke den såkalte indeks for gjennomsnittstemperatur på fangst. Denne indeksen drar slutninger om geografiske forskyvninger av bestander basert på trender i fiskefangst av ulike arter innenfor et bestemt område og tidsperiode. I farvannet rundt New Zealand viste resultatene at fiskefangsten av pelagisk-oseaniske arter i økende grad er sammensatt av tropiske og subtropiske arter av mindre størrelse, og i minkende grad sammensatt av store pelagiske kaldtvannsarter. I Norge var fiskerifangsten av bunnfisk dominert av en stadig rikere forekomst av den atlantiske torsken (Gadus morhua). Disse resultatene i Norge og New Zealand antyder at arter fra lavere breddegrader flytter sin utbredelse til høyere breddegrader (som gjenspeiles i fiskefangsten), hvorved posisjon i vannsøylen (dvs. pelagiske arter), eller kapasitet som en generalist i diettvalget (dvs. Atlantisk torsk) kan øke hastigheten og omfanget arter kan endre sin geografiske utbredelse på i takt med havoppvarmingen.

Overfiske av arter på høyt trofisk nivå ble undersøkt i New Zealand ved å bruke en såkalt justert gjennomsnittlig trofisk nivåindeks. Resultatene avslørte tegn på overfiske av arter på høyt trofisk nivå i New Zealands sokkel-havområder mellom 1950 og 2019. Disse resultatene tyder på at i en periode der fiskeriene ble utvidet geografisk utover New Zealands eksklusive økonomiske sone, var fiskeriet i sokkel-havområdene sammensatt av fiske på arter på stadig lavere trofisk nivå, på grunn av overfiske og påfølgende nedgang i populasjon av arter på høyere trofisk nivå. Disse resultatene gir ny innsikt i overfiske av arter på høyt trofisk nivå i New Zealands sokkel-havområder fra 1950-tallet og utover, resultater som tidligere har manglet i lignende analyser av New Zealands fiskefangstdata over en tilsvarende tidsperiode.

Ved å undersøke disse tre individuelle stressorerne, gir resultatene fra denne oppgaven ny innsikt i forventede endringer som marine samfunn står overfor gjennom det kommende århundret med havoppvarming og vedvarende fiske. Slik innsikt i den variable responsen av endringer i kroppsstørrelse, geografisk fordeling og påvirkning på populasjonsnivå fra fiskepress, mellom ulike arter med variabel habitat-tilknytning og livshistorie, er nyttig fremover for å få til et godt vern og en god fiskeriforvaltning av slike grenseutvidende populasjoner i det marine biologiske mangfoldet.

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LIST OF PAPERS

Paper I: Lavin, C. P., Gordó-Vilaseca, C., Costello, M. J., Shi, Z., Stephenson, F., Grüss, A. (2022). Warm and cold temperatures limit the maximum body length of teleost fishes across a latitudinal gradient in Norwegian waters. *Environmental Biology of Fishes*, 105: 1415-1429. https://doi.org/10.1007/s10641-022-01270-4

Paper II: Lavin, C. P., Gordó-Vilaseca, C., Stephenson, F., Shi, Z., Costello, M. J. (2022). Warmer temperature decreases the maximum length of six species of marine fishes, crustacean, and squid in New Zealand. *Environmental Biology of Fishes*, 105: 1431-1446. https://doi.org/10.1007/s10641-022-01251-7

Paper III: Lavin, C. P., Pauly, D., Dimarchopoulou, D., Liang, C., Costello, M. J. (2023). Fishery catch is affected by geographic expansion, fishing down food webs and climate change in Aotearoa, New Zealand. *PeerJ*, 11:e16070. https://doi.org/10.7717/peerj.16070

Paper IV: Lavin, C. P., Dimarchopoulou, D., Gordó-Vilaseca, C., Palomares, M. L. D., Pauly, D., Costello, M. J. (2023). Mean temperature of the fishery catch does not correlate well with contemporaneous research trawl data in the Barents Sea (*Manuscript*).

1 INTRODUCTION

1.1 General overview

Anthropogenic climate change has seen the ocean warm above 1° C relative to pre-Industrial temperatures (IPCC 2023). As the ocean warms, dissolved oxygen levels have concurrently decreased, with a ~ 2 % decline in dissolved oxygen content within the global top 1000 m depth observed since the 1960s (Schmidtko et al. 2017; Ito et al. 2017; Breitburg et al. 2018; Oschlies et al. 2018). As the majority of marine animals are water-breathing ectotherms, such environmental changes may deleteriously impact individual-level fitness, as well as wider population- and ecosystem level processes (Poloczanska et al. 2016). Marine ectotherms inhabit geographic space that overlaps with their thermal niche and contains sufficient dissolved oxygen content required for aerobic metabolism (Deutsch et al. 2020). As oceans warm and deoxygenate, three universal responses are expected from water-breathing ectotherms in an attempt to avoid deleterious environmental conditions that may negatively impact their fitness. These responses include changes in phenology (Asch 2015), changes in body size (Gardner et al. 2011), and shifts in geographic distribution (Poloczanska et al. 2016).

Yet, it is observed that such responses do not occur uniformly across geographic regions or amongst species. For example, it is suggested that negative physiological impacts of ocean warming and deoxygenation will disproportionately impact larger individuals and species of water-breathing ectotherms (Forster et al. 2012). Species declines due to geographic shifts are projected to be highest in tropical, low latitude marine ecosystems. Consequently, marine ecosystems face variable and potentially destabilising changes with regards to food web structure (Tekwa et al. 2022), population-level replenishment (Barneche et al. 2018; Wilson et al. 2023), as well as ecosystem services such as fisheries catch (Free et al. 2019) at a global scale.

At the same time, anthropogenic stressors may interact with climate change related responses of marine organisms, further reducing species- or ecosystem-level stability and resilience (Gissi et al. 2021). Such stressors include but are not limited to habitat destruction and loss (Luypaert et al. 2020), excess nutrient input from terrestrial sources (Tait et al. 2023), pollution (Mearns et al. 2020), and destructive fishing practices such as overfishing or by-catch and discard related mortality (Pauly and Palomares 2005; Moore et al. 2013). For example, decades of intensive fishing pressure has seen the large-scale reduction in size of harvested stocks (Worm et al. 2009). Furthermore, due to market demands, it is often the largest individuals or species that are targeted by fisheries (Tsikliras and Polymeros 2014), which has led to reductions in both maximum size as well as abundance of large consumer species (Jackson et al. 2001). The pervasive overfishing of large, high trophic level species has led to some fisheries to increasingly target smaller, lower trophic level species, a term called ‘fishing down marine food webs’ (Pauly et al. 1998; Pauly and Palomares 2005). Instances of ‘fishing down’ can exert destabilising impacts on marine food webs, impacts that could be amplified by concurrent ocean-warming induced reductions in maximum size and shifts in geographic distribution of marine biodiversity.

An in-depth understanding of the potential cumulative impacts of climate change related responses of marine animals, as well as the effects of persistent fishing pressure are required in order to better inform mitigative or adaptive management of biodiversity and resources within the forthcoming century of ocean warming. It is therefore the aim of the present thesis to investigate several of the aforementioned stressors. This will be done individually for each stressor, with the intention that novel insights into individual processes can inform a more wholistic understanding of combined stressors within further research applications. Specifically, the present research aims to investigate changes in maximum body size of marine ectotherms across an environmental gradient within a portion of their realised distribution. Also, this research will investigate apparent instances of ‘fishing down marine food webs,’ as well as signals of shifting geographic distributions of species, as reflected in regional fisheries catch data. Lastly, a comparison between fisheries catch and research survey data will be done in order to investigate the extent to which fisheries catch data may reflect population-level changes in biomass in lieu of survey data, and also, the extent to which fisheries are adapting to potential ocean-warming induced changes in geographic distribution of biomass.

1.2 Maximum body size response of marine ectotherms under ocean warming and deoxygenation

For marine water-breathing ectothermic species, their body temperature will generally be determined by the ambient temperature which they inhabit (Jutfelt et al. 2021). This temperature thus serves as a key environmental variable that may influence their overall fitness, as well as geographic distribution (Ern 2019). This is also the case for dissolved oxygen in sea water, as water-breathing animals have a critical threshold above which they are able to maintain aerobic metabolism (Grieshaber et al. 1994). Overall, temperature and dissolved oxygen in sea water are closely linked to ectotherm fitness, as warmer water may contain less dissolved oxygen, whilst simultaneously increasing an animal's oxygen demands (Kielland et al. 2019). In turn, it is largely observed that marine water-breathing ectotherms adhere to the Temperature-Size Rule (TSR), which states that ectotherms will grow faster, sexually mature earlier, and reach a smaller maximum body size within warmer temperatures (Atkinson 1994). Therefore, observed and expected ocean warming and deoxygenation have the potential to ubiquitously impact the overall body size of populations of marine ectotherms. For example, results from Cheung et al. (2013a) analysing 600 species globally estimated assemblage-level reductions in maximum body weight upwards of 24 % under future ocean warming scenarios, highlighting the potential large-scale impacts of ocean-warming on marine ectotherm size. This thesis will discuss the TSR, including the scientific basis of this relationship, observations of the TSR between different species, as well as the implications of the TSR on marine populations and ecosystems within future ocean warming scenarios.

Across a water-breathing ectotherm's geographic distribution, species will generally be able to extract sufficient amounts of dissolved oxygen from sea water, in order to meet all demands imposed by the full range of activities required on a daily basis. This includes a range between maintaining standard metabolic rates (SMR), or metabolic rates at resting states, and maximum metabolic rates, or metabolic rates experienced at maximum exertion (MMR) (Atkinson et al. 2006). The difference between these two rates is known as a species' aerobic scope (Jutfelt et al. 2021), or metabolic scope (Claireaux and Chabot 2016). As such, species within adequate environmental conditions performing all necessary activities between resting and full exertion should still maintain a safety margin of aerobic scope that does not exceed their MMR for extended periods of time (Atkinson et al. 2006). Exceeding the safety margins of aerobic scope will push animals into anaerobic metabolism, which is not only less efficient at producing energy relative to aerobic metabolism, but also, will impose an oxygen deficit, which can result in deleterious impacts associated with fitness and growth (Hochachka and Somero 2002; Pörtner and Farrell 2008).

As ambient temperatures warm in line with ocean warming, water-breathing ectotherms experience increases in both SMR and MMR (Claireaux and Lagardère 1999). Temperature-induced increases in metabolic rate will therefore prompt higher dissolved oxygen demands (Fry 1971). Yet, as MMR will be constrained to a species-specific maximum level, as SMR increases with warmer temperatures, the overall aerobic scope of an animal will be reduced (Rubalcaba et al. 2020). A reduced aerobic scope implies that there is less excess energy available for performing fitness-related activities, including growth and reproduction (Pörtner and Knust 2007; Claireaux and Lefrançois 2007; Rubalcaba et al. 2020). Furthermore, as water-breathing ectotherms grow larger throughout their life span, the per unit of weight resource demands increase (Atkinson et al. 2006). Therefore, relatively more energy, and thus dissolved oxygen, is required to maintain aerobic scope at larger body sizes (Neubauer and Andersen 2019). Consequently, warmer temperatures increase overall metabolic rates and oxygen demand, and thus the amount of resources required to maintain metabolism, within a reduced arena of aerobic scope, which will disproportionately affect larger individuals that require more energy for metabolism. As a result, compensatory mechanisms are required by water-breathing ectotherms as they grow larger in order to maintain safe aerobic scope within warming temperatures. This can be achieved by reducing size-dependent dissolved oxygen demands, i.e., growing to a smaller maximum body size (Atkinson et al. 2006).

It is the limiting of growth to a smaller maximum body size in warmer temperatures (Atkinson 1994) that we highlight from the TSR within the context of this thesis. As previously mentioned, the TSR also states that animals will grow faster and sexually mature earlier (Atkinson 1994). It is as such that the TSR reflects a phenotypic response across different stages of ontogeny, and at differing levels of biological organisation (Verberk et al. 2021), although the scope of this thesis will focus on limitations of an animal's maximum size across temperature gradients. We will henceforth refer to species growing to a smaller maximum size in warmer temperatures as a negative 'temperature-size response' (Horne et al. 2015). While temperature-size responses are well observed across the majority of species that have been investigated (Atkinson 1994; Daufresne et al. 2009; Ohlberger 2013), the mechanisms underpinning this response remain unresolved. However, three hypotheses offer mechanistic explanations for the observed temperature-size responses in water-breathing ectotherms, including the 'Ghost of Oxygen-limitation Past' hypothesis, the 'Oxygen and Capacity-limited Thermal Tolerance' (OCLTT) hypothesis, as well as the 'Gill-oxygen Limitation Theory' (GOLT).

The Ghost of Oxygen-limitation Past hypothesis refers to the influence of evolutionary history on the prevalence of large-bodied individuals within a species (Verberk et al. 2021). As was previously discussed, larger bodied water-breathing ectotherms are disproportionately negatively affected by warming and deoxygenation. In turn, past events of extreme ocean warming or deoxygenation throughout evolutionary time scales could have selected for phenotypes that produce individuals of smaller maximum body size (Verberk et al. 2021). Such selection events could subsequently influence phenotypes of descendant generations (Grant et al. 2017). For example, fishes reared under warming conditions were found to grow to smaller maximum body sizes across multiple generations (Loisel et al. 2019). This selective pressure would ensure that genotypes have a canalized TSR in order to ensure preservation of aerobic scope across the range of temperatures and dissolved oxygen levels that species have evolved to inhabit (Verberk et al. 2021). According to this hypothesis, temperature and dissolved oxygen levels will therefore serve as cues to inform growth throughout an animal's lifetime, and animals that grow to smaller maximum body sizes in warmer or oxygen-poor waters will remain the favoured genotype (Verberk et al. 2021).

As opposed to the Ghost of Oxygen-limitation Past, both the OCLTT and GOLT focus less on the influence of evolutionary selection and more on the physiological limitations imposed at threshold temperatures located near the limits of a species' thermal niche. The OCLTT hypothesis highlights a species' environmental niche occupying conditions between pejus temperatures (pejus meaning 'worse') (Pörtner 2010). Between pejus temperatures, water-breathing ectotherms have optimal conditions allowing them to extract sufficient dissolved oxygen from water in order to maintain aerobic metabolism (Pörtner and Peck 2010). As temperatures approach pejus limits, a species' ability to maintain safe aerobic scope is limited by the amount of oxygen they can supply relative to temperature-dependent increases in demand (Pörtner and Peck 2010). As temperatures increase, and relative oxygen supplies decrease, hypoxaemia (i.e., low oxygen content of blood) and anaerobic metabolism occur, which can damage the structural integrity of molecules, leading to molecular denaturation (Pörtner and Peck 2010) and thus limits on somatic growth. The length of exposure to pejus temperatures or temperature beyond this limit will determine the response of organisms. Long term exposure to beyond-pejus temperatures can lead to death, while short term exposures will engage protective mechanisms such as anaerobic metabolism and antioxidative defences (Pörtner and Peck 2010). Ultimately, an adult's maximum size will be determined by the frequency of exposure to pejus temperatures. Animals living closer to their thermal maxima encounter pejus temperatures more often and will therefore maintain a narrower aerobic scope and have less excess energy available to service daily activities, growth and reproduction. As a result, they will grow to smaller maximum sizes, in order to reduce size- and temperature-dependent oxygen demands and in turn remain within a safe aerobic scope (Pörtner and Farrell 2008; Pörtner and Peck 2010).

The GOLT shares similarities with the OCLTT with regards to the role of temperature- and size-dependent oxygen demands influencing growth, but rather than emphasising pejus temperatures, the GOLT focuses on anatomical oxygen supply constraints. According to the GOLT, as the body of a water-breathing ectotherm grows in 3-dimensions towards an asymptotic size, the size of 2-dimensional gill structures gradually provides insufficient oxygen per unit of weight required to maintain growth (Pauly and Cheung 2018). In turn, to service oxygen demands within warmer temperatures in order to maintain a safe aerobic scope, animals grow to smaller maximum sizes, which will maintain a sufficient gill surface area to body weight ratio and thus the supply of oxygen per unit of weight (Pauly 2021). In line with both the OCLTT and GOLT, anaerobic metabolism and oxidative stress can negatively impact the quaternary structure of protein molecules (Pörtner et al. 2017; Pauly and Cheung 2018). Increased levels of protein denaturation caused by oxidative stress increases levels of catabolism (i.e., the breaking down of body tissue), and as levels of catabolism approach levels of anabolism (i.e., body tissue synthesis), growth will gradually cease (Pauly 2021), thus lending water-breathing ectotherms to temperature-dependent asymptotic maximum body sizes, as described in the TSR.

With multiple hypotheses engaging the mechanisms behind the TSR, the temperature- and size-dependent increases in oxygen demand for water-breathing ectotherms is well-observed and remains a central tenant of the TSR (Pörtner 2001; Pauly 2019; Verberk et al. 2021). Yet whether or not the availability and assimilation of resources for growth also impact the TSR remain unclear. Theoretically, temperature- and size-dependent increases in metabolic demands can be complemented by an increase in resources acquired (e.g., through increased feeding activity), or conversely, by a reduction in demand for resources (e.g., less locomotion for feeding) (Woods and Moran 2020; Verberk et al. 2021). Yet, it is possible that such compensations could incur a significant energetic cost to organisms as they limit their resources (e.g., dissolved oxygen or food) within increasingly warmer conditions (Verberk et al. 2021). Therefore, temperature-size responses may provide a mechanism for animals to avoid resource limitations concurrent with warming, as smaller individuals will maintain lower per unit weight resource demands, and they may be better suited to find food and match temperature-induced increases in dissolved oxygen demand relative to larger individuals (Atkinson et al. 2006; Neubauer and Andersen 2019; Verberk et al. 2021). It has also been suggested that within warming conditions, animals may be incentivised to have more frequent meals of smaller sizes (Jutfelt et al. 2021). After eating a meal, an animal's metabolic rate and thus dissolved oxygen demand will increase sharply during digestion, a process termed 'specific dynamic action' (SDA, Secor 2009). Within supra-optimal conditions, reducing SDA may assist animals to maintain aerobic scope. This transition to smaller meals may influence growth to a smaller maximum sizes within warmer temperatures to ensure aerobic scope protection (Jutfelt et al. 2021).

The proposed transition to smaller, more frequent meals, and its effects on maximum growth of marine ectotherms highlight the potential impacts that temperature-size responses can exert on marine ecosystems, in particular, food webs. Reductions in maximum adult body size can influence a species' feeding interactions, including foraging capacity and trophic position (Peters 1983; Coghlan et al. 2022). For example, with smaller maximum body sizes, the width of a fish's mouth gape will be reduced, thus, reducing the size of prey that predators are able to consume (Mihalitsis and Bellwood 2017). Reductions in body size can also influence which prey species will be large enough to survive predation (Persson et al. 1996). For example, if one prey species experiences a stronger, negative temperature-size response relative to other prey species, it may become more susceptible to predation from larger animals (Ahti et al. 2020). Accordingly, reductions in body size have also been linked with changes in swimming and foraging behaviour. Results from Walsh et al. (2006) found that smaller individuals of Atlantic silverside (*Menidia menidia*) were less willing to forage due to the threat of predation relative to larger individuals of the same species. Less willingness to forage may thus reduce acquired energy and overall fitness (Walsh et al. 2006; Ahti et al. 2020).

Changes in body size structure at different trophic levels of marine food webs can result in ecosystem-level changes (Gibert and DeLong 2014; Hočevar and Kuparinen 2021). The size-spectrum of an ecological community describes the total biomass of classes based on body size (Sprules and Barth 2015). In general (absent of fishing pressure), there is an inverse relationship between body size and biomass within marine communities, thus, larger bodied animals of higher trophic levels and long-lived are less abundant within marine ecosystems than smaller, shorter lived species of lower trophic levels (Blanchard et al. 2017). Yet, these animals are those that are disproportionately targeted by fisheries due to their higher market price (Tsikliras and Polymeros 2014), and in general, are more susceptible to overfishing (Sadovy de Mitcheson et al. 2020). Persistent fishing pressure can therefore reduce the maximum size of species (Hunter et al. 2015). This may exacerbate any maximum size reductions induced by ocean warming (Audzijonyte et al. 2016), as has been observed for menhaden (*Brevoortia tyrannus* and *B. patronus*) populations in the United States (Turner 2017).

A significant loss of biomass at high trophic levels can influence food web structure, possibly leading to trophic cascades, or the loss of predation pressure that propagates across trophic levels from the top-down (Baum and Worm 2009). An example of trophic cascade resulted from the loss of large bodied-sized, old-age structure of Atlantic cod (*Gadus morhua*) in eastern Canada, from a combination of overfishing, ecological and environmental changes (Swain and Benoît 2015). Following population collapse resulting from overfishing, adult age classes of cod in the region have been defined by younger sexual maturation and smaller body sizes (Olsen et al. 2004). The loss of predation pressure from abundant and large-bodied cod saw a proliferation of smaller-bodied fish and macroinvertebrates (Frank et al. 2005). Grazing from increasingly abundant smaller animals had a marked impact on the abundance of zooplankton and phytoplankton, which in turn was reflected in nutrient concentrations within areas of Labrador and Newfoundland (Frank et al. 2005).

The case of Atlantic cod in eastern Canada exemplifies a top-down trophic cascade brought about by the reduction of large-bodied predator biomass. Together, the combined stressors of fishing pressure and negative temperature-size responses truncating the size-distribution of populations can further impede population recovery (Olsen et al. 2004), as body size is also a determinant of reproductive output. For most non-mammalian marine animals, reproductive output scales hyperallometrically with body size (Hixon et al. 2014; Barneche et al. 2018). It is therefore recommended that fisheries management conserve older age structures of adult populations in order to ensure stable levels of spawning stock biomass (Froese et al. 2008). Accordingly, warming-induced reductions in maximum body size of marine ectotherms may result in decreased rates of per-capita reproductive output (Rijnsdorp et al. 2010; Baudron et al. 2014), which may ultimately impact population-level reproductive output (Ottersen and Holt 2023).

Body size is an important determinant of biological and ecological functions for marine ectotherms. In line with the TSR, ocean warming may lead to reductions in maximum size, which in turn may pose challenges to population-level replenishment as per-capita reproductive output decreases. Changes in size-spectra of a community can also negatively impact the transfer of energy between trophic levels, possibly leading to a re-structuring of marine food webs. As the potential externalities of maximum body size reductions for marine ectotherms are severe, an in-depth understanding of predicted and observed temperature-size responses is necessary to anticipate future changes.

While the mechanistic underpinning of the TSR remains unresolved (Pörtner 2001; Pauly 2021; Verberk et al. 2021), temperature-size responses have been observed in the majority of ectothermic species that have been investigated (Atkinson 1994; Daufresne et al. 2009). Yet, species of variable size, traits and milieu will be impacted by ocean warming and deoxygenation differently (Venegas et al. 2023). Accordingly, in order to advance our understanding of the possible ecological effects of temperature-size responses, research can transition from investigating whether or not a species adheres to the TSR, to what extent do different species of variable traits experience temperature-size responses. Such research can be accomplished in several ways. Laboratory experiments are done under controlled conditions that allow for direct investigation of temperature-size responses. A meta-analysis by Forster et al. (2012) reviewed temperature-size responses of 22 marine ectothermic species tested in laboratory settings. The authors found that negative temperature-size responses became stronger with increasing body size of study species (Forster et al. 2012). These results are in line with the observed size- and temperature-dependent increases in oxygen demands of water breathing ectotherms that underlines the TSR (Atkinson et al. 2006).

As previously mentioned laboratory experiments are highly controlled and provide direct insight into temperature-size responses. Although, they are usually completed in normoxic settings, with abundant food and a lack of predation pressure (Morrongiello et al. 2019). Investigating temperature-size responses of species in their natural setting may provide a more complete understanding of how these responses are expressed, incorporating factors such as recruitment and mortality, competition, predation risk and the availability of resources (Audzijonyte et al. 2020). Using research survey data, van Rijn et al. (2017) investigated temperature-size responses between 74 different fish species across a temperature gradient in the Mediterranean Sea. The authors considered three species-level traits which were body size, activity level and thermal affinity, and the influence of such traits on realised temperature-size responses (van Rijn et al. 2017). Results found that large, highly active species were those to display the strongest negative temperature-size responses. These results may have important implications at the community-level, as variable changes in body size between predator and prey species could result in size-based mismatches (van Rijn et al. 2017), or equally, active predatory species reducing in size may face increasing size-based competition with more sedentary species for common resources (Munday et al. 2001; van Rijn et al. 2017).

The results from van Rijn et al. (2017) support the tenants of the TSR, although conflicting evidence has challenged the universality of an expected negative temperature-size response concurrent to ocean warming. By analysing data from over 30,000 underwater visual transect surveys, Audzijonyte et al. (2020) investigated the temperature-size response of 335 coastal species spanning from tropical to temperate distributions along the coasts of Australia. The authors found that from those species displaying a temperature-size response, 97 species had negative responses, while 64 species had positive responses (i.e., larger in warmer temperatures) (Audzijonyte et al. 2020). Overall, tropical species were twice as likely to experience a negative temperature-size response relative to temperate species, while temperate species were equally likely to experience either positive or negative responses (Audzijonyte et al. 2020). Further, the maximum body length of species was positively correlated to their relative change in mean body length, i.e., smaller species were generally smaller in warmer waters while larger species were generally larger (Audzijonyte et al. 2020).

Overall, there are few studies that have robustly investigated the observed temperature-body size relationship across environmental gradients of wild marine ectotherm populations (van Rijn et al. 2017; Audzijonyte et al. 2020). Both van Rijn et al. (2017) and Audzijonyte et al. (2020) displayed the influence of temperature in determining maximum length, although contrasting results highlight the complexity and variability of temperature-size responses that may be expressed between species of different thermal affinities, habitat, body size and trophic position. Thus, while the effects of ambient temperature on ectotherm metabolism is well observed, how exactly further ocean warming will affect species and ecosystems through changes in animal body sizes remains unclear. This uncertainty demonstrates the need for further research to elucidate the variable expression of temperature-size responses between different marine species.

1.3 Shifts in geographic distribution of marine ectotherms in line with ocean warming and deoxygenation

In general, ocean temperatures warm at a slower rate than that of air temperatures over land, yet marine ectotherms have shifted their geographic distributions in line with warming faster than terrestrial ectotherms (Burrows et al. 2011). In part, across a species' geographic distribution, marine ectotherms inhabit temperatures at or near their thermal maxima (García Molinos et al. 2016), whilst fewer barriers to dispersal (relative to terrestrial ecosystems) allow species to geographically track their thermal affinity as oceans warm (Cheung et al. 2009; Pinsky et al. 2013). Yet, species have been shown to shift at variable rates and directions, in part due to variations in traits or life histories (Pinsky et al. 2013; Sunday et al. 2015). Overall, as species shift, the large-scale reorganisation of marine species has the potential to destabilise community structure (Huntington et al. 2020), fisheries catch potential (Cheung et al. 2010) and other ecosystem services. An in-depth understanding of species shifts in distribution is therefore crucial in order to inform conservation and fisheries management throughout future decades of ocean warming. This section will review the scientific basis for marine species' geographic shifts in distribution, as well as the variable extent of shifts observed between different species and biogeographic regions. This section will also discuss some of the observed and expected ecological outcomes of shifts, as well, how such shifts may be considered within management scenarios under further ocean warming.

As previously mentioned, marine water-breathing ectotherms inhabit a geographic distribution that overlaps with their evolved thermal niche (Sunday et al. 2012). More precisely, distributions will be found across a species' thermal range (STR), or the range of temperature between the minimum and maximum that the species can survive in (Burrows et al. 2019), as well, above a minimum threshold of dissolved oxygen content in order to maintain aerobic metabolism (Deutsch et al. 2015). The STR along with other biogeographical factors, including the availability of habitat, productivity levels, and competition, will determined a species' realised distribution (Costello and Chaudhary 2017). A species' thermal affinity can be calculated as the median temperature value that is observed across a species' geographic distribution (Burrows et al. 2019). In general, global oceans do not warm uniformly, but rather, local or regional isotherms (i.e., temperature fronts) may shift variably in direction or rate (termed 'climate velocity,' Burrows et al. 2011). In turn, species may thus shift their geographic distribution concurrent to prevailing climate velocities, in order to closely track their thermal affinity, and to avoid inhabiting environmental conditions that may negatively impact their fitness (Burrows et al. 2011; Pinsky et al. 2013; Brito-Morales et al. 2020).

Overall, the general expectation with ocean warming is that marine species will shift from lower to higher latitudes (see later text), yet species have been observed to shift in variable directions, or to deeper depths across their current distribution. Results from Dulvy et al. (2008) found that the North Sea assemblage of demersal fishes deepened by approximately 3 m per decade from 1980 to 2004. This deepening was uniform for the majority of species assemblages studied, whilst shifts in species' mean latitudes were heterogeneous (Dulvy et al. 2008). Results from Pinsky et al. (2013) found a southward mean latitudinal shift for the big skate (*Raja binoculata*) between 1968 and 2011. This "non-intuitive" shift was in the same direction as shifts in climate velocity (Pinsky et al. 2013), highlighting the influence of local climate velocities on realised shifts. Geographic shifts can also be significantly influenced by both the direction and strength of prevailing ocean currents (García Molinos et al. 2017). Results from García Molinos et al. (2022) investigating species' shifts found that species tracked closer their thermal affinity when prevailing ocean currents aligned with the direction of distributional shifts.

Variable species' traits and life histories have also been shown to influence the rate or extent of geographic shifts. Further results from García Molinos et al. (2022) found that position in the water column was a significant predictor of shifts in distribution, with greater distances associated with pelagic than bottom-associated species. Trophic category was also a significant predictor, with carnivorous and omnivorous species displaying greater distances shifted (García Molinos et al. 2022). Similar results from Sunday et al. (2015) investigating shifts found that a species' trophic position was the most important trait to influence the distance of range extension, followed by a species mobility (which largely indicates their position in the water column).

Aside from climate velocities and traits, ecological interactions have also been shown to significantly influence the extent of species' distributional shifts. Durant et al. (2023) investigated the presence and absence of two sympatric gadid species, the Atlantic cod and Atlantic haddock (*Melanogrammus aeglefinus*) across the North Sea and Barents Sea. The authors found that temperature and the location of cod had a negative effect on expansion of haddock into the Barents Sea. Similarly, haddock were seen to access areas of the North Sea during periods when cod were less abundant (Durant et al. 2023). These results suggest that the presence of a "predator wall" could limit an ocean-warming induced expansion of marine populations (Durant et al. 2023). Using spatially-explicit food web models, Tekwa et al. (2022) found that species' range shifts were slowed or reduced on account of trophic interactions, relative to single-species models. Results showed variation in range shift processes amongst species of different body sizes and trophic levels. For example, larger-bodied predators were shown to remain within historical habitat longer than smaller-bodied, lower trophic level species, as larger species received ecological subsidies from smaller species shifting, or "colonising" into new territories (Tekwa et al. 2022). Such results highlight the importance of trophic interactions to be considered in further research on shifting species distributions.

In turn, while variable shifts in geographic distribution are well observed between species and regions, the global, poleward shift of thousands of species has already been observed. Chaudhary et al. (2021) analysed global species richness across a latitudinal gradient for over 48,000 species since the 1950s. The authors found an increasing dip in species richness at equatorial latitudes across the time series, with bimodal (i.e., northern and southern hemisphere) increases of richness at mid-latitudes, indicating the large-scale shift of species away from low latitudes (Chaudhary et al. 2021). Overall, species found at lower latitudes live within warm, stable temperatures. Thus, their thermal range is relatively low (termed 'stenothermal' species). As oceans warm at low latitudes, tropical, stenothermal species can be rapidly exposed to temperatures exceeding their thermal maxima, prompting them to shift in order to remain within their thermal range (Yasuhara et al. 2020). The interaction of ocean warming and deoxygenation at lower latitudes will further expose water-breathing ectotherms to deleterious environmental conditions outside of their aerobic metabolic scope (Kielland et al. 2019), prompting shifts away from the area.

This process means that with future ocean warming and deoxygenation, a large-scale poleward shift of species from low to higher latitudes is predicted (Hodapp et al. 2023). Interestingly, species found within polar regions are also stenothermal, as they maintain stable and narrow temperature ranges (Peck 2016). As global ocean warming will impact polar regions, these animals will also need to track their thermal affinity in order to remain within suitable environmental conditions. Yet, polar species already inhabit some of the coldest and most well-oxygenated waters on Earth (Deutsch et al. 2020). Therefore, the predicted levels of global extinction for marine species under severe warming scenarios is highest for polar species (Penn and Deutsch 2022), as refuge areas containing suitable habitat for such species may eventually disappear. As opposed to stenothermal species, eurythermal species (i.e., wide temperature range species) are usually from temperate, mid-latitude distributions (Stuart-Smith et al. 2017). Their wide thermal range is in part due to such species experiencing wide seasonal fluctuations of temperature (Poloczanska et al. 2016). Evidence suggests that eurythermal species may be better equipped to quickly track isotherms and thus shift their geographic distribution relative to stenothermal species (Sunday et al. 2015).

In general, it is possible to demonstrate realised distributional shifts based on the geographic movement of a species' centroid of biomass distribution (Pinsky et al. 2013). However, the processes occurring at both the leading edge (i.e., expanding edge) and trailing edge (i.e., contracting edge) of a species' distribution may not be in equilibrium (Hastings et al. 2018). Overall, environmental conditions will still significantly influence the occurrence of range shifts at both edges. Within the context of this thesis, temperatures within the trailing edge of a species' distribution will likely become too warm to tolerate. Conversely, temperatures within the leading edge of a species' distribution will warm, presenting species with previously uncolonized territory that now maintains conditions within their thermal range (Sunday et al. 2012). Seasonality may still impact species throughout this process, in particular, at the leading edge of their distribution, where they may encounter winter temperatures outside of their thermal range, thus resulting in a seasonal shift back to lower latitudes. Although, gradual warming of ocean winter temperatures has seen species withstand overwintering temperatures within newly expanded territories, as was documented for Atlantic croaker (*Micropogonias undulatus*) in the Northwestern Atlantic (Hare and Able 2007).

At the trailing edge of a species' distribution, shifts will occur when a population's growth rate is negative (due to movement away from an area), or via local extinction, i.e., extirpation (Louthan et al. 2015). Species with narrow thermal ranges, low adult mobility (e.g., sessile or crawling species), low larval dispersal, as well as specialised species are those more likely to be extirpated (Nicastro et al. 2013; Smale and Wernberg 2013). In general, detecting extirpation within a species' trailing edge is difficult, due to possible cryptic habitat use of species, as well as imperfect detection abilities – hence, trailing edge shifts are far less documented than leading edge shifts (Poloczanska et al. 2013). Conversely, leading edge shifts of species' distributions are observed at a wider scale and at a faster rate (Poloczanska et al. 2013). Compared to confirming a species' complete local extirpation, recording a species within expanded territory may be easier and more cost-effective (García Molinos et al. 2022). As previously mentioned, adult mobility and position in the water column is strongly associated with a species' ability to expand the leading edge of their distribution (Sunday et al. 2015). Species found higher in the water column (e.g., pelagic) are considered more likely to expand, and at a faster rate, relative to demersal, crawling or sessile species (García Molinos et al. 2022). Trophic ecology may also influence a species' ability to expand, whereby predatory or omnivorous species have been observed to display a wider latitudinal expansion (Sunday et al. 2015; García Molinos et al. 2022). High trophic level predators are considered those best suited to shift their distribution, due to the availability of diverse prey types contained within newly expanded areas (Pinsky et al. 2020).

Importantly, species will only be able to expand their distribution if they are able to fully colonise newly accessed territory, either through settlement and positive population growth, or via persistent immigration (Bridle and Vines 2007). Yet, while ocean warming may facilitate the poleward expansion of species, other environmental factors at the leading edge of a species' distribution could limit their ability to successfully colonise new area. For example, the availability of aragonite in sea water necessary for scleractinian skeletal formation of coral organisms decreases with latitude, possibly limiting the ability of some tropical coral species to shift their distribution polewards (Jiang et al. 2015; Hoegh-Guldberg et al. 2017). For temperate fishes shifting polewards, irradiance has been considered a possible limitation to visual predation during winter periods at high latitudes (Varpe and Fiksen 2010). Conversely, if and when a species successfully colonises newly expanded territory, they have the potential to significantly impact regional food webs and ecosystem structure through novel competition or predator-prey interactions (Kortsch et al. 2015; Ellingsen et al. 2020; Johannesen et al. 2020).

In conclusion, this section has reviewed the scientific basis of geographic shifts in marine species' distributions in line with climate change related ocean warming. Overall, a global shift in species' distributions from low- to high-latitudes has been observed and is expected to continue. Nonetheless, it has also been observed that the direction and pace of local or regional climate velocities and ocean currents will influence the extent that species' shift, as well as the direction. Species' traits may also influence the extent of shifts, while expansion into recently habitable territory will depend on a species' ability to colonise and settle in that area. As such, variable shifts of different animals between trophic levels have the potential to disrupt regional food web structure as shifts occur. The multiple, combined effects and possible outcomes of large-scale geographic shifts of marine species must be considered within biodiversity and conservation management moving forward. Therefore, in order to better inform management, a more in-depth understanding regarding variable shifts in geographic distribution between different species, across biogeographic regions, requires further research.

1.4 Climate response and ecological effects of fisheries in changing marine communities

The previous sections outlined how changes in maximum body size as well as geographic distribution of water-breathing ectotherms can impact marine communities during the present period of rapid ocean warming. The current section will discuss how shifts in distribution, as well as regional oceanographic changes are expected to impact fisheries catch potential globally. Furthermore, climate change fisheries adaptation will be discussed as a response to said geographic shifts in species' distributions and thus fisheries catch potential. Lastly, the potential impacts of persistent fishing pressure, in particular, on large-bodied, high trophic level species, will be outlined as a cumulative stressor that may exacerbate ocean-warming induced responses of marine species.

Overall, current rates of ocean warming have been associated with reductions in dissolved oxygen content (Oschlies 2021), changes in ocean circulation and stratification (Peng et al. 2023), as well as shifts in the geographic distribution and availability of primary and secondary productivity (Bopp et al. 2013). Such changes in biological productivity may influence community-wide availability of biomass through the trophodynamic transfer of energy across marine food webs from the "bottom-up" (Stock et al. 2017). Ultimately, these changes, along with the aforementioned changes in body size and geographic distribution of fishes can directly influence regional levels of fisheries productivity and thus catch potential. A study by Cheung et al. (2010) projected global changes in fisheries catch potential for over 1000 stocks by mid-century across different climate change scenarios. Indeed, the authors found that a global re-distribution of catch potential would be driven primarily by range shifts as well as changes in primary production across regional scales (Cheung et al. 2010). Areas such as the tropics and semi-enclosed seas (e.g., Mediterranean Sea) would thus see a decrease in catch potential, whilst ocean warming, reductions in sea ice, and increased primary production, paired with poleward shifting species is predicted to increase catch potential at high latitudes (Cheung et al. 2010).

As changes have already been expressed in ocean temperatures and regional productivity, retrospective analyses may be able to elucidate the relationship between such changes and fisheries productivity. Free et al. (2019) modelled hindcast changes in maximum sustainable yield (MSY, or the theoretical maximum amount of catch that is considered to be sustainable), amongst 235 fished stocks, representing 124 species and approximately 33% of reported global fisheries catch, from 1930 to 2010, in line with temperature trends. Strong regional heterogeneity was observed in MSY changes, changes that were largely explained by temperature, displaying "winning" and "losing" regions (i.e., increasing or decreasing MSY, Free et al. 2019). Yet, the expected pattern of increased fisheries production at high latitudes and decreased production at low latitudes was not yet apparent in the author's results (Free et al. 2019). The authors concluded that contemporary shifts in geographic distribution of stocks are unlikely to have influenced regional fisheries catch potential thus far, but rather, other biophysical or oceanographic variables such as primary production, dissolved oxygen or habitat availability, as well as the influence of fisheries catch, may have driven observed changes (Free et al. 2019).

Utilising a different approach, analyses by Cheung et al. (2013b) looked directly at fisheries catch statistics from 1970 to 2006 across 52 Large Marine Ecosystems (LMEs) in order to investigate observed changes in fisheries catch composition in line with trends in ocean warming. This was done using the Mean Temperature of the Catch (MTC) index, or the mean preferred temperature of the fisheries catch assemblage across an area, weighted by catch. Effectively, a positive trend in MTC would indicate an increasing proportion of fishes of warmer thermal affinity recorded in the catch, or equally, a reduction of cold water fishes (Cheung et al. 2013b). Such results could indicate the geographic shift of species' distribution across areas, in line with oceanographic changes. The authors found a mean MTC increase of 0.19 °C per decade across the 52 LMEs to be significantly correlated with trends in ocean warming. Furthermore, regional variations saw MTC trends to be higher in non-tropical LMEs, as asymptotic MTC trends resulted from the reduction in catch of subtropical (i.e., cooler) species in tropical areas, whilst positive MTC trends in non-tropical LMEs resulted from increasing catch of species of generally warmer thermal affinity (Cheung et al. 2013b). These results suggest that global fisheries have already experienced changes in catch assemblages, changes that favour the catch of relatively warmer-water species at higher latitudes (Cheung et al. 2013b).

In line with the results from Cheung et al. (2013b), how changes in fisheries catch reflect realised shifts in species' distribution remains unclear. Within their initial application, the authors compared MTC trends calculated between scientific research survey data (i.e., using species abundance) and fisheries catch data for 55 common species in the North Sea. The authors found no difference in MTC trends, thereby supporting their use of a fisheries MTC as a proxy for changes in actual species abundance within the community (Cheung et al. 2013b). However, whether this relationship holds in other regions or fisheries management regimes aside from the North Sea remains unclear. The relationship between community abundance and fisheries catch therefore requires further investigation.

Moving forward, with expected increases in ocean warming and species shifts in geographic distribution, projections depict large-scale re-distribution of fished stocks. Results from Palacios-Abrantes et al. (2022) predicted that by 2030, global EEZs will experience up to a 59 % change in the proportion of catch of transboundary stocks (i.e., stocks shared between neighbouring EEZs). These results highlight the importance of both national and international fisheries management and governance, both at the trailing edge and leading edge of species' distributions. For example, the observed expansion of Atlantic mackerel (*Scomber scombrus*) distribution into the Icelandic EEZ saw the country quickly capture upwards of 18% of the entire fishery's total allowable catch (TAC, Spijkers and Boonstra 2017). This catch was done without consultation of the management authority of the stock, the North-East Atlantic Fisheries Commission, which is represented by Iceland, Norway, Denmark, Russia and the European Union, leading to disputes between countries (Spijkers and Boonstra 2017).

Fisheries management must also consider possible deleterious effects of harvest on populations that are experiencing range shifts. The previous example of mackerel in Icelandic waters highlights how mismanaged fisheries developing at the leading edge of a species' shifting distribution can compromise the sustainability of the wider stock (Gaines et al. 2018). Within the trailing edge of a species' distribution, it is recommended that fishing effort should be reduced on species that are decreasing in abundance due to geographic shifts. This can be done in order to reduce the likelihood of overfishing and in turn increase the resilience of populations to other climate change associated stressors (Szuwalski and Hollowed 2016; Gaines et al. 2018; Ojea et al. 2020; Free et al. 2020). Such climate change fisheries adaptation will remain of upmost importance as the geographic distribution of species and fisheries catch potential continues to shift at a global scale.

Of course, persistent fishing pressure has already exerted large-scale stress on marine species and communities, through overfishing, by-catch and discard, as well as habitat destruction (Jennings and Kaiser 1998; Howarth et al. 2014). Overall, for those species directly targeted by fisheries, many of their stocks are overfished – 35% of them globally in 2022, according to Food and Agriculture Organization of the United Nations (FAO 2022). It was also observed that the maximum body size of harvested species has gradually declined, as fisheries preferentially target the largest individuals or species within an assemblage (Jackson et al. 2001) since they generally maintain higher market value (Tsikliras and Polymeros 2014). These species which are large, long-lived, and of a high trophic level are also usually those most vulnerable to overfishing, as compared to smaller shorter-lived species (Sadovy de Mitcheson et al. 2020). As previously discussed, instances of overfishing high trophic level predators can lead to trophic cascades across marine food webs (Daskalov et al. 2007; Steneck 2012).

It has been suggested that the pervasive overfishing of large, high trophic level species has forced some regional fisheries around the globe to increasingly target smaller, lower trophic level species, a term called ‘fishing down marine food webs’ (Pauly et al. 1998; Pauly and Palomares 2005). Instances of ‘fishing down’ could exert destabilising impacts on marine food webs by further perturbing the availability and transfer of energy between trophic levels (Pauly et al. 1998). Fishing down has been investigated at global (Pauly et al. 1998; Pauly and Palomares 2005) and regional scales (e.g., Freire and Pauly 2010; Liang and Pauly 2020; Durante et al. 2020; Gough et al. 2022), largely through the use of the catch-weighted metric, the mean trophic level of the catch, or MTL (Pauly et al. 1998). Similar to the MTC, the MTL represents the catch-weighted mean trophic level of an assemblage of species contained within a fishery within a certain area. Therefore, decreases in MTL over time would indicate a decreasing proportion of higher trophic level species contained in the catch, or vice versa.

Nonetheless, it has been demonstrated that catch weighted metrics can be masked by a variety of factors, as will be discussed further (see Section 2.2.2). Therefore, instances of masking effects, as well as the utility of catch-weighted metrics like the MTC and MTL to reflect actual changes in abundance, requires further examination.

In conclusion, this section has outlined the observed and anticipated changes to fisheries catch potential in line with oceanographic changes and the subsequent response of marine species. Variable changes in fisheries productivity have already been observed at regional scales, whilst further ocean warming projects such changes to continue. As changes in primary and secondary productivity are complemented with shifts in species' distributions, management must adapt as fisheries catch potential may be redistributed across transnational boundaries. Furthermore, fisheries at the leading or trailing edge of shifting populations should consider their potential effects on stocks and wider populations. Climate change fisheries adaptation will react to changes in abundance as species arrive or shift away from traditionally fished areas. Lastly, pervasive fishing pressure has already exerted pressure on marine populations through overfishing and the preferential target of large-bodied, high trophic level species. This has been implicated in the widespread shift of fisheries catch from higher to lower trophic levels, termed fishing down marine food webs. The potential impacts of fishing down marine food webs can threaten the stability of marine community structure, a structure that may concurrently be affected by changes in body size and geographic shifts in animal distribution. The overall extent that shifts in geographic distribution and persistent fishing pressures have influenced regional fisheries must be investigated in-depth, in order to identify likely outcomes within future scenarios of continued ocean warming and fishing. Yet, identifying trends of fishing down or geographic shifts using fisheries catch data, as well as the potential masking effects and apparent utility of such indices, also requires further examination.

2 RESEARCH

2.1 Knowledge gaps and aims of thesis

As discussed previously, several knowledge gaps exist regarding multiple stressors exerted on marine ecosystems and ecosystem services. For example, how may the maximum body size and geographic distribution of different marine ectothermic species in different biogeographic regions change in response to ocean warming? Concurrently, to what extent has persistent fishing pressure negatively impacted the structure of marine food webs, in particular, through the overfishing of high trophic level species? As well, have fisheries management systems adjusted to such changes in marine populations already instigated by ocean warming and persistent fishing? The research aims of the present thesis are designed in order to address the aforementioned knowledge gaps. Filling these knowledge gaps would advance our field of understanding and in turn, better inform management systems required throughout the forthcoming century of climatic and oceanographic changes.

These research aims were addressed through four distinct objectives:

1) Investigating temperature-size responses of wild marine ectotherm populations (**Paper I and Paper II**)
2) Investigating signals of fishing down marine food webs in historical fisheries catch data (**Paper III**)
3) Investigating geographic shifts in distribution of marine ectotherms using fisheries catch data (**Paper III and Paper IV**)
4) Comparing trends in fisheries catch data and research survey data to assess response of fisheries and utility of catch-weighted metrics (**Paper IV**)

These research objectives were facilitated by analysing fisheries catch and research survey data between two countries within two distinct ecoregions: New Zealand and Norway. Both countries maintain a long history of fisheries (Mikalsen & Jentoft 2003, Smith 2013), and host unique marine communities that lie within oceanographic transition zones between ‘warm’ and ‘cold’ current systems. In the case of Norway’s Barents Sea territory, warm, saline Atlantic-origin waters flow north- northeast towards the Svalbard Archipelago where they meet cold, dense Arctic-origin waters flowing west- southwest (Lundesgaard et al. 2022). Across New Zealand waters, ocean temperatures are influenced by the inflow of warm, subtropical waters from the west-northwest and cold, subantarctic waters from the west- southwest (Kerry et al. 2023). The presence of oceanographic transition zones in New Zealand and Norway result in significant temperature gradients across both respective study areas. These gradients allowed investigation of the influence of ambient oceanographic conditions on particular response variables. Analysis of time series oceanographic data also allowed investigation of response variables in line with climate change related trends.

2.2 Research design and methodologies

Each research objective was addressed via distinct analyses. This section will briefly outline the methodologies deployed for each objective.

2.2.1 Temperature-size responses

Temperature-size responses were investigated using Generalised Additive Models (GAMs). Maximum length measurements of selected species were gathered from scientific surveys conducted in both Norwegian and New Zealand waters (Paper I and Paper II). For each study species, maximum length data points were derived from the longest recorded individual of that species within a trawl haul. In order to relate the animal’s maximum length to the ambient environment, long term temperature and dissolved oxygen content were assigned to each data point based on the geographic location (i.e., latitude and longitude) of the sample station. Thereafter, with maximum length as the response variable, and temperature (°C), dissolved oxygen (mg/l) and geographic location (a proxy variable for latent ecological or environmental variables) as explanatory variables, GAMs were fit for each species. From the GAM results, we predicted a species’ maximum length across their observed (i.e., from data points) temperature and dissolved oxygen range, as well, compared the amount of variation in maximum length explained by each variable. Furthermore, since it is well known that fishing pressure can negatively truncate a populations' maximum body length (Jackson et al. 2001), or conversely, reductions in fishing pressure can lead to an increase in population's maximum body size (Worm et al. 2009), we also investigated the influence of fishing pressure on maximum body size across the respective timeseries.

2.2.2 Fishing down marine food webs

The influence of fishing down marine food webs was investigated by deploying the Mean Trophic Level (MTL) index (Pauly et al. 1998) using New Zealand fisheries catch data from 1950 to 2019 (Paper III). The MTL assigns study species their trophic level (based on values reported to FishBase, Froese and Pauly 2021) and then calculates the mean trophic level of the species assemblage contained in fisheries catch within a certain area weighted by individual species catch (tonnes per year) (Pauly et al. 1998). Positive trends in MTL indicate an increasing proportion of catch composed of higher trophic level species, while negative trends indicate an increasing proportion of lower trophic levels. Negative MTL trends can therefore infer instances of fishing down marine food webs, as catch transitions from depleted stocks of large, high trophic level species to small, low trophic level species (Liang and Pauly 2017). Yet, the historical geographic expansion of fisheries across a large study area has been shown to mask trends in the MTL (Kleisner et al. 2014; Liang and Pauly 2020). Ideally, the MTL would be calculated on the exact same area and associated fish assemblage over time, but often fishery catch is reported from a large area within which fisheries vary spatially and/or temporally.

After calculating the MTL using fisheries catch data in New Zealand waters, this masking factors of geographic expansion was corrected for by further calculating the Fishing-in-Balance index (FiB) and the adjusted Mean Trophic Level index (aMTL) (Kleisner et al. 2014) using the same catch data. The FiB index identifies geographic expansion of fisheries, based on the assumption of constant trophic transfer efficiency between trophic levels (transfer efficiency = 0.1, Kleisner et al. 2014). If the MTL of fisheries catch increases by 1, this should yield a 10-fold reduction in catch, based on the assumption of trophic transfer efficiency. If the catch increases more than expected based on decreases in MTL, this indicates that catch came from adjacent stocks, thereby identifying a geographic expansion of fisheries into a new stock assemblage.

Using the results from the FiB, we then calculated the adjusted Mean Trophic Level (aMTL), or the mean trophic level for each unique stock assemblage. The aMTL calculates the maximum fisheries catch potential amongst each identified stock assemblage, based on the full range of trophic levels present within the catch dataset, as well as the constant assumption of trophic transfer efficiency (Liang and Pauly 2017). Once the maximum catch potential has been calculated amongst the distinct stock assemblages, the aMTL is then calculated for each assemblage. In summary, the FiB and aMTL indices calculate the mean trophic level between distinct species stock assemblages harvested during the geographic expansion of fisheries. By separating between species stock assemblages (and thus, between distinct habitats or fishing areas across the wider study area), apparent instances of fishing down that were otherwise masked in New Zealand's historical fishing catch records can be revealed (Kleisner et al. 2014).

2.2.3 Distributional shifts affecting fisheries catch

In order to investigate ocean-warming induced changes in fisheries catch in line with apparent shifts in geographic distribution or changes in biomass, we utilised the Mean Temperature of the Catch (MTC) index (Cheung et al. 2013b). By assigning species their mean preferred temperature (according to a global compilation of species distribution models, and adjusted for appropriate depth, sensu Froese and Pauly 2021), the MTC calculates the mean temperature of a species assemblage contained within fisheries catch of an area weighted by individual species catch (Cheung et al. 2013b). Yet, as previously mentioned, trends in catch-weighted indices like the MTC can be masked by a variety of factors, including the geographic expansion of fisheries across a large study area (Liang and Pauly 2017), or by the gear used to collect and harvest species of different habitat associations (Leitão 2015; La Peyre et al. 2021). In order to account for these masking effects, analysed data were grouped together by the fishing gear types used, as well as species' milieu, whereby MTC trends were recalculated between groups (Paper III, i.e., New Zealand). Further MTC analyses were restricted to 18 demersal species, i.e., captured using similar bottom-associated fishing gear (Paper IV, i.e., Norway).

2.2.4 Comparison of fisheries catch and research trawl data

Using 18 common demersal species, the MTC between fisheries catch data and research survey data in the Barents Sea from 2004 to 2019 (Paper IV) were compared. The Bray-Curtis dissimilarity index was also calculated annually for each dataset, and thereafter compared using a Mantel test, to investigate whether species turnover between the 2 species assemblages were correlated. These analyses allowed assessment of the utility of catch-weighted indices like the MTC to reflect changes in community composition. Simultaneously, these analyses allowed investigation of the extent to which fisheries in the Barents Sea may be adapting to ocean-warming induced changes in geographic distribution of species.

3 RESULTS

3.1 Temperature-size responses

The temperature-size responses of 10 and 6 water-breathing ectotherm species were investigated across an environmental gradient in Norway and New Zealand. The influence of temperature, dissolved oxygen content, and geographic location on maximum length were also investigated, in order to elucidate the importance of these variables in determining temperature-size responses. The study areas spanned 26 and 20 degrees latitude, 10 and 16.5 °C annual average temperature, and 2.5 and 4 mg/l dissolved oxygen, in Norway and New Zealand, respectively.

In Norway (Paper I), the 10 study species displayed 3 types of temperature-size responses. This included negative temperature-size responses (for spotted wolffish *Anarhichas minor*, cusk *Brosme brosme*, and Norway redfish *Sebastes viviparus*), positive temperature-size responses (for capelin, *Mallotus villosus*, Greenland halibut *Reinhardtius hippoglossoides*, golden redfish *Sebastes norvegicus*, daubed shanny *Leptoclinus maculatus*, and polar cod *Boreogadus saida*), and humped temperature-size responses (for Atlantic wolffish *Anarhichas lupus*, and beaked redfish *Sebastes mentella*) across their observed temperature ranges (Paper I, Figure 3). For all 10 study species, temperature, dissolved oxygen and geographic location were significant in determining maximum body length. Regarding the relative importance of each variables, geographic location was most important for all species, while temperature was more important than dissolved oxygen for 5 out of 10 species.

In New Zealand (Paper II), all 6 study species displayed negative temperature-size responses, whilst the largest overall study species, hoki (*Macruronus novaezelandiae*) displayed the largest negative temperature-size response (Paper II, Figure 5). For all New Zealand study species, temperature and geographic location were found to significantly influence maximum body length, whereby dissolved oxygen was significant for 4 species, including hoki, southern blue whiting (*Micromesistius* *australis*), orange roughy (*Hoplostethus atlanticus*), and New Zealand scampi (*Metanephrops challengeri*), thereby excluding Australasian snapper (*Pagrus auratus*) and New Zealand arrow squid (*Nototodarus sloanii*). By estimating the relative importance of model covariates, geographic location was in general the most important variable in determining maximum lengths of the study species. Following geographic location, temperature was in general more important in determining maximum body size versus dissolved oxygen availability.

Regarding the influence of fishing pressure on maximum body length, in Norway (Paper I), a ‘pseudo total mortality’ (pseudo-Z) value was calculated for each species by constructing a length-converted catch curve. As natural mortality (M) for wild marine animals is assumed constant, any apparent trends in total mortality would therefore be driven by fishing mortality (F, as $Z = M + F$) (Beverton & Holt 1956). Across the 30-year study period, no trends in pseudo-Z were observed, indicating there were no strong increases or decreases in fishing pressure. In New Zealand (Paper II), the influence of fishing was inferred via the maximum body sizes of species predicted and compared between a ‘past’ fishing period (1979-1998) and a ‘recent’ fishing period (1999-2021). This was done by separating the analysed data between these two periods and then predicting the species maximum body lengths across their observed environmental range. In general, species maintained the same relationship between temperature and maximum body length across the two periods. This indicates that the influence of fishing has not strongly impacted the maximum body length of study species across the study period.

3.2 Overfishing and its impact on high trophic level species

The instance of fishing down marine food webs was investigated using time-series fisheries catch data in New Zealand from 1950 to 2019 amongst 102 species (Paper III). By first calculating the MTL, our results are in line with those from Durante et al. (2020) who also calculated the MTL using fisheries catch data across the same study area, showing a steady increase in MTL until the 1990s, thereafter levelling off (Paper III,

Figure 3c). Further, results calculating the FiB index showed positive trends until the 1990s, then levelling off (Paper III, Figure 3d). Using the results from the MTL and FiB, we then calculated the aMTL of New Zealand fisheries catch from 1950 to 2019. Our results identified two discrete periods of geographic expansion of fisheries across the New Zealand EEZ, thus separating catch amongst three distinct stock assemblages. The first two stock assemblages represent the species found within shelf fisheries, maintaining lower trophic levels than the third stock assemblage, found in offshore waters. The two shelf water species assemblages displayed negative trends in aMTL until the 1990s, thereafter levelling off and slightly increasing in the 2000s. The third, offshore species assemblage displayed consistently high aMTL values and no signals of fishing down (Paper III, Figure 3e). As such, these results suggest that shelf water fisheries catch was affected by fishing down during the expansion of New Zealand's fisheries offshore from the 1950s onward.

3.3 Ocean-warming induced changes in distribution reflected in fisheries catch

The MTC was calculated amongst 102 study species in New Zealand from 1950 to 2019 (Paper III). Results present a strong, negative MTC trend until levelling off in the 1990s (Paper III, Figure 3b). Thereafter, New Zealand catch data was separated amongst the fishing gear used for capture, as well as species' milieu. Overall, for bottom-associated species and fisheries gear, MTC displayed strong negative trends until levelling off in the 1990s. Conversely, for pelagic associated gear and species, MTC trends were positive (Paper III, Figures 4 and 5). Therefore, results from New Zealand suggest that bottom-associated fisheries increasingly harvested colder-water species, whilst pelagic associated fisheries increasingly targeted warmer-water species across the study period. The MTC was also calculated amongst 18 demersal fish species in the Barents Sea region of Norwegian waters (Paper IV) from 2004 to 2019. Overall, MTC trends in the Barents Sea were flat across the time series (Paper IV, Figure 3), indicating no strong changes in the assemblage of species harvested in demersal fisheries across the study area and period.

3.4 Fisheries catch data inferring community assemblage change

The Barents Sea MTC (Paper IV) was also calculated from 2004 to 2019, amongst 18 demersal fish species, also using research trawl data, in order to compare trends with the calculated fisheries MTC trend. The research MTC trend was found to be positive, increasing 0.55 °C per decade across the study period. In turn, this trend was not significantly correlated to the fisheries MTC. Also, neither of the two MTC trends were significantly correlated with trends in ocean warming (Paper IV, Figure 3). Furthermore, results from the Mantel test investigating the correlation between the research and fisheries Bray-Curtis dissimilarity matrices was non-significant (Paper IV, Figure 4). These results suggest that the fisheries catch MTC calculated in the Barents Sea from 2004 to 2019 does not closely reflect changes in the demersal fish community composition.

Lastly, in order to assess the response of fisheries within the Barents Sea to apparent ocean-warming induced changes in geographic distribution of species, we compared the (log) slopes of species between research trawl and fisheries catch datasets. Only two species (spotted wolffish, Atlantic cod) had significantly correlated trends between fisheries catch and survey biomass (Paper IV, Figure 5). These two species represented 70 % of all fisheries catch (70 % cod, < 0.001 % spotted wolffish) and 40 % of research trawl biomass, respectively.

4 DISCUSSION, NOVELTY AND IMPLICATIONS

Overall, the present research has assessed temperature-size responses between variable species, signals of fishing down marine food webs, apparent instances of geographic shift reflected in fisheries catch, and finally, the utility of fisheries catch to reflect changes in community composition. First, by investigating the temperature-size response of several species, of variable habitat associations, between two countries within distinct ecoregions, our results revealed novel insight into how such responses are expressed by different marine ectotherms. In New Zealand (Paper II), we displayed the negative temperature-size responses of 2 invertebrate species, the New Zealand scampi and arrow squid. This was a novel contribution, as focus on the temperature-size response of marine organisms has largely focused on teleost fishes (Pauly 2019). We also observed that the 2 species with the widest observed temperature ranges, hoki and arrow squid, displayed the strongest negative temperature-size responses.

The largest New Zealand study species, hoki, displayed the strongest negative temperature-size responses. These results are in line with the literature, that reports large, active species may be most likely to experience strong negative temperature-size responses. In a laboratory setting, Forster et al. (2012) found that larger water-breathing ectotherms displayed stronger negative temperature-size responses. Within wild populations, van Rijn et al. (2017) also found that larger, more active species displayed the strongest negative temperature-size responses across their observed temperature gradients. Hoki is a large-bodied, high trophic level species that can be found in depths between 10-900 m, but is primarily found between 200-600 m (Stevens et al. 2012). Adult individuals are benthopelagic, whereby they complete circadian vertical migrations from the seabed to mesopelagic layers in order to feed on crustaceans and small fish (Bulman & Blaber 1986, Connell et al. 2010). Hoki's large body size and active feeding ecology would therefore suggest their vulnerability to strong negative temperature-size responses, which we have confirmed in our results.

In Norway (Paper I), the two largest species, spotted wolffish and cusk, also displayed the strongest negative temperature-size responses. These results suggest further that large-bodied marine ectotherms are more likely to experience negative temperature-size responses. In the case of spotted wolffish and cusk, both species are demersal. Overall, demersal and benthic habitats often experience low oxygen conditions, conditions that are expected to increase in frequency and intensity with further ocean warming (Diaz and Rosenberg 2008; Breitburg et al. 2018). Accordingly, benthic and demersal species are generally less vulnerable to hypoxia, relative to, for example, pelagic species, which rely on behavioural capabilities to swim away from areas experiencing hypoxia (Ekau et al. 2010; Roman et al. 2019). Therefore, our results showing strong negative temperature-size responses of demersal species, within dissolved oxygen conditions at or near saturation (in both the Norway and New Zealand study areas), suggests that body-size- and temperature-dependent oxygen demands strongly determine temperature-size responses, not ambient oxygen availability. This conclusion is in line with the TSR mechanisms identified in the OCLTT and GOLT. Nonetheless, it may be that less hypoxia-tolerant species could experience stronger negative temperature-size responses, even when oxygen-levels are at or near saturation. It is therefore recommended that further research investigate observed temperature-size responses of wild populations between more diverse taxonomic groups.

Moreover, 7 out of 10 Norwegian study species were found to grow to larger maximum body sizes in warmer water (Paper I, Figure 3). These 7 species inhabited extreme cold temperatures (< 0 °C) within a part of their observed geographic range, in contrast to the sub-tropical or temperate waters inhabited by New Zealand study species (Paper II). In fact, these results are also in line with the TSR mechanisms explained by OCLTT and GOLT. Both of these theories highlight the role of protein denaturation as temperatures approach the extreme end of a species’ thermal range (Pörtner and Knust 2007; Pauly 2021). Protein denaturation occurs when the quaternary structure of a protein is lost due to extreme temperatures, resulting in loss of function (Privalov

1990). Rates of protein denaturation have been shown to increase as temperatures approach both extreme warm and cold, known as either ‘heat denaturation’ or ‘cold denaturation’ (Privalov 1990; Graziano 2014; Sanfelice et al. 2015; Yan et al. 2018). Denatured proteins become ‘removed’ from the stock of live proteins, leading to increased catabolism or the breaking down of body tissue. In turn, denatured proteins require replacement via resynthesis, an energy intensive process that will lead to elevated metabolic rates (Pauly and Lam 2023).

For Antarctic fishes that inhabit extreme cold temperatures (e.g. < 0 °C), their observed elevated standard metabolic rates have been referred to as ‘metabolic cold adaptation’ (Wohlschlag 1962, 1964; Pauly 1979; White et al. 2012; Fraser et al. 2022). Our results in the Barents Sea represent the first contribution to the literature that suggests Arctic (i.e., not Antarctic) fishes are limited in maximum size due to metabolic cold adaptation applied within the TSR framework. This novel insight also means that some Arctic fishes can grow to larger body sizes with intermittent ocean warming as they are released from thermal stress limiting their growth at extreme cold temperatures.

Yet, while some Arctic species may grow to larger maximum body sizes with intermediate warming, they will eventually be limited in maximum size again, as ambient temperatures approach the warm extreme of their thermal range. This is exemplified by the hump-shaped temperature-size responses of Atlantic wolffish and beaked redfish across their observed temperature range in the Barents Sea (Paper I, Figure 3) (Figure 1). Such results further highlight the role of protein denaturation and limits to growth at extreme ends of a species’ thermal range, confirming the basis of the OCLTT and GOLT in explaining the TSR. In between these extremes, a ‘Goldilocks’ temperature may minimise the rate of protein denaturation relative to synthesis, allowing species to grow to their maximum body size potential (Somero 2022; Pauly and Lam 2023). For species inhabiting extreme cold temperatures, this temperature optimum may be higher than the temperature minimums they currently experience within certain parts of their distribution, as displayed in our results. Overall, our results investigating the temperature-size response of fishes in the Barents Sea contributed greatly towards the discussion-base of Pauly and Lam (2023) focusing on the role of protein denaturation and the TSR.

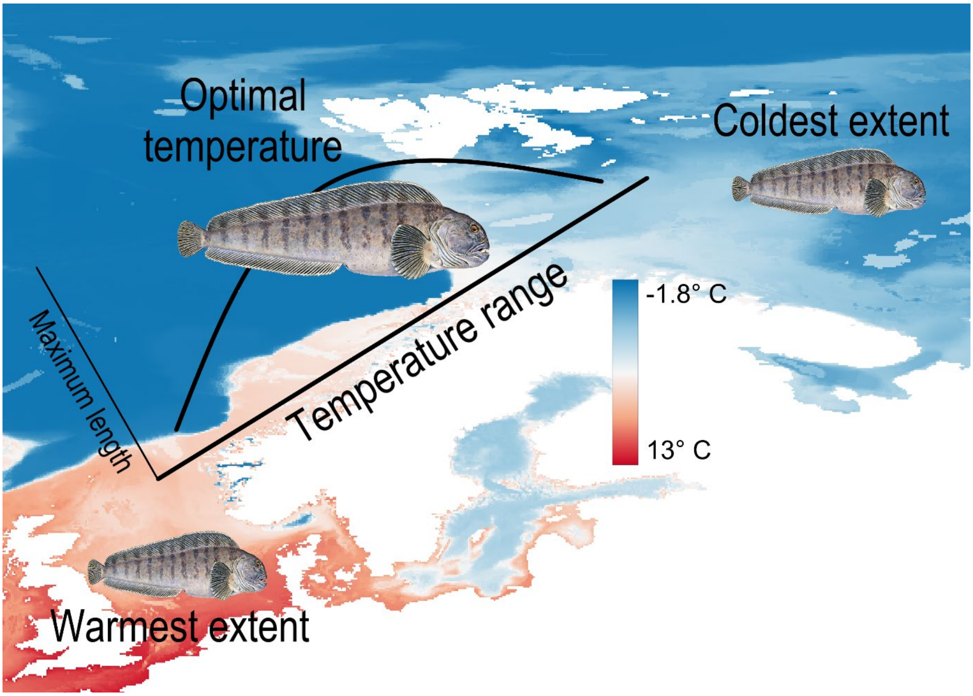

Figure 1. *Variation in maximum body length of the Atlantic wolffish (Anarhichas lupus) across the study area in Paper I. Atlantic wolffish was found to grow to smaller maximum body lengths within the warmest (9.0 °C) and coldest (-0.8 °C) extents of its observed distribution across the study area. Conversely, the species grows to the largest maximum body length within an intermediate temperature (~4 °C). Photo of Anarhichas lupus courtesy of Jan Fekjan and Artsdatabanken (CC).*

Moving forward, we then investigated the extent of fishing down reflected in New Zealand's fisheries catch from the 1950s onwards. Our results provided novel evidence suggesting the overfishing of high trophic level species, with catch subsequently shifting to lower trophic level species, within shelf water stock assemblages across the study period. As previously mentioned, Durante et al. (2020) also calculated the masked MTL of New Zealand fisheries, with similar results displaying a 'fishing up' of marine food webs from the 1970s until levelling off in the 1990s (Paper III, Figure 3c). Yet, we went on to account for the masking effect of geographic expansion of fisheries across the time series. As fishing effort in New Zealand expanded offshore, hoki came to dominate overall catch, leading to both an increase in MTL and also a decrease in MTC, as hoki is a deep, cold-water, high trophic level species (Figure 2). By applying the FiB and aMTL indices, we identified discrete species assemblages captured by fisheries across a geographic expanse in New Zealand's EEZ, in line with the assumptions of trophic transfer efficiency.

After calculating the aMTL between each species assemblage, our results revealed that fished stocks within shelf waters actually display signals of fishing down, contrary to the full, masked MTL trend (Paper III, Figure 3e, Stock Assemblage 1 and 2). These results are in line with the documented historical over-exploitation of New Zealand shelf fisheries throughout the late 20th century (Johnson and Haworth 2004). In fact, recognition of shelf fisheries overexploitation led New Zealand to implement a Quota Management System (QMS) in 1986, and since then, overall fisheries catch has been reduced in these waters (Durante et al. 2020). Despite this, there exists little empirical evidence documenting the deleterious impacts of persistent fishing pressure on New Zealand fish communities and food webs (Durante et al. 2020), therefore, our results have contributed novelty to the understanding of the historical impacts of New Zealand fisheries. As previously stated, large, high trophic level species are particularly sensitive to overfishing (Sadovy de Mitcheson et al. 2020). In turn, the combination of overfishing and reductions in maximum body size induced via ocean-warming could negatively impact the fitness of targeted species, and result in significant changes to the size-spectrum of marine food webs. For example, amongst our study species, results from both New Zealand papers (Paper II and Paper III) suggest evidence of overfishing (of their assemblage), as well as maximum body size reductions for Australasian snapper. This ecologically and economically important species inhabits coastal waters of New Zealand, whereby adult individuals feed on crabs, bivalves and smaller fish (Usmar 2012). Cumulative stressors including fishing-and ocean-warming induced reductions in population- and body-size could interact to deleteriously impact snapper fitness across their current distribution. Furthermore, New Zealand waters represent the southern-most distribution of this species (Froese and Pauly 2021). With little to no coastal shelf area available south of New Zealand (until Antarctica), if this species is unable to shift polewards within a warming New Zealand shelf, then maximising snapper genetic diversity in order to adapt to ocean warming should remain a top management priority. This would entail close monitoring of changes in body size distribution of the species, as well as biomass and fishing levels to further prevent overfishing of a stock that has already experienced such conditions (Johnson and Haworth 2004; Durante et al. 2020). The results from the present research have helped illuminate the necessity for such monitoring and precautionary management.

We also addressed the apparent negative MTC trend in New Zealand fisheries catch data across the same time period. The emerging dominance of deep, cold-water hoki during a period of fisheries geographic expansion led to a negative MTC trend that levelled off in the 1990s (Figure 2). By separating New Zealand's catch between fishing gear and species milieu, we found that pelagic-oceanic species and fishing gear types displayed positive trends in MTC across the study period (Paper III, Figures 4 and 5). We found that pelagic-associated MTC warming was driven by the reduction in the large-bodied, temperate Southern bluefin tuna (*Thunnus maccoyii*) and increase in the smaller-bodied, tropical skipjack tuna (*Katsuwomus pelamis*) and subtropical blue mackerel (*Scomber australasicus*) (Paper III, Figures 6c and 6d). These results suggest that with modest levels of ocean warming observed across the study area, Southern bluefin tuna reduced in abundance or shifted in geographic distribution away from New Zealand EEZ waters, based on their fisheries catch trends. Conversely, skipjack tuna and blue mackerel increased in abundance or shifted their distribution into the study area across the timeseries, also based on their fisheries catch trends. These results highlight the apparent variability of geographic shifts between species of different habitat associations, as MTC warming was only apparent for pelagic associated species. In turn, realised and expected shifts in distribution of pelagic-oceanic species should remain of fisheries and conservation management priority in New Zealand.

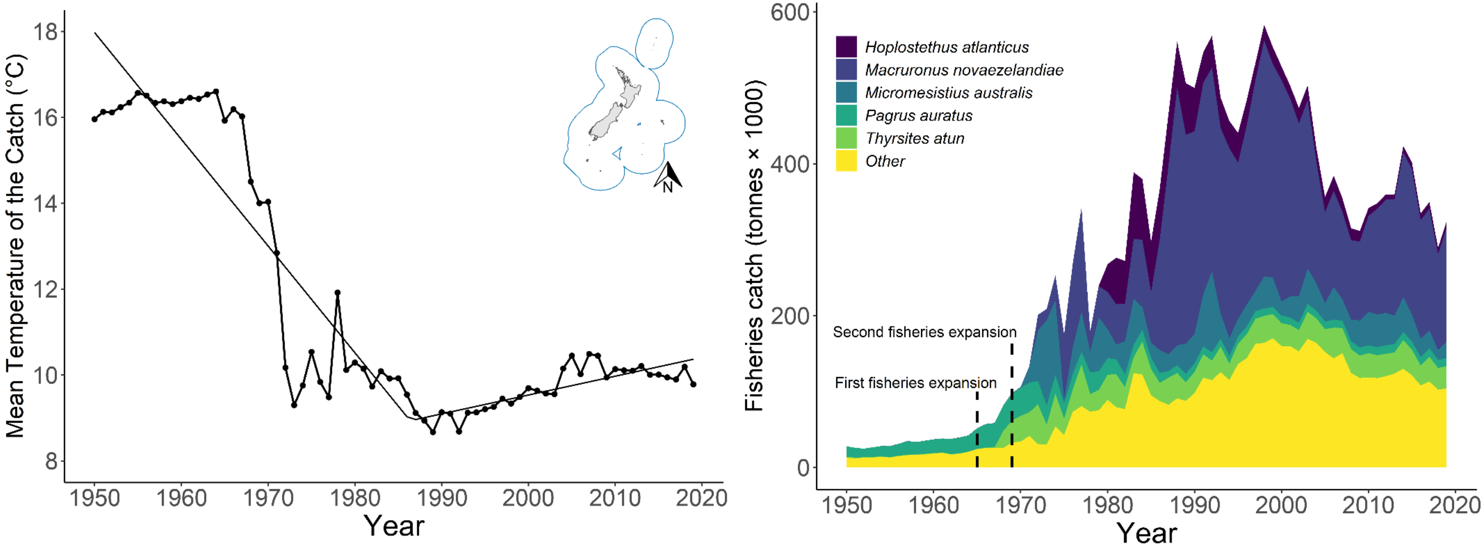

***Figure 2**. Results from calculating the Mean Temperature of the Catch (MTC, ° C, left) within the New Zealand Exclusive Economic Zone (inset, left) using fisheries catch data (tonnes × 1000, right) from 1950 to 2019 (Paper III). Highlighted species include orange roughy (Hoplostethus atlanticus), hoki (Macruronus novaezelandiae), southern blue whiting (Micromesistius australis), Australasian snapper (Pagrus auratus), snoek (Thyrsites atun) and all other species ('Other'). The years identified during which a geographic expansion of fisheries occurred, in line with results from the adjusted Mean Trophic Level (aMTL, Paper III) are also shown (1965 and 1969, right).*

Similarly, the fisheries catch MTC was calculated within shelf waters of the Barents Sea amongst 18 demersal species. Across the timeseries, we found no strong change in the MTC trend, as it increased 0.03 °C per decade (Paper IV, Figure 3) (Figure 3). The MTC calculated using fisheries catch data is intended to reflect changes in abundance of species within the community (Cheung et al. 2013b). Therefore, our results in Norway would suggest that none of the 18 study species displayed any shifts in geographic distribution or changes in abundance across the study area and period. By investigating catch of individual species, we found that the flat MTC trend in the Barents Sea was a result of catch dominated by Atlantic cod.

With the availability of research trawl data in the Barents Sea, we thereafter calculated the MTC amongst the 18 common species using biomass data from said research trawls (Figure 3). This allowed us to evaluate the utility of catch-weighted metrics like the MTC to reflect changes in species biomass abundance within the demersal fish community across the study area. Overall, the research trawl MTC increased 0.55 °C per decade, and was therefore not significantly correlated to the fisheries MTC trend (Paper IV, Figure 3) (Figure 3). These results are not in line with those from Cheung et al. (2013b), and suggest that the catch MTC may not always accurately reflect changes in abundance within the community. Lack of correlation between the two Barents Sea MTC trends may be due to differences in how animals are capture, e.g., using different gear in commercial fisheries versus scientific research trawls. For example, the mesh size of research trawls analysed was 22 mm (Johannesen et al. 2021), whilst bottom trawl fisheries in the area are required to use a minimum mesh size of 130 mm (Gullestad et al. 2015). In turn, the size selection of fishes between the two datasets is different, and therefore, may partly explain the lack of correlation between trends. This difference in gear has not been addressed within previous comparisons of fisheries and research trawl MTC trends (Cheung et al. 2013b; Tsikliras et al. 2015). Our results therefore illuminate this difference, and suggest that differences in gear should be considered in future application of the MTC.

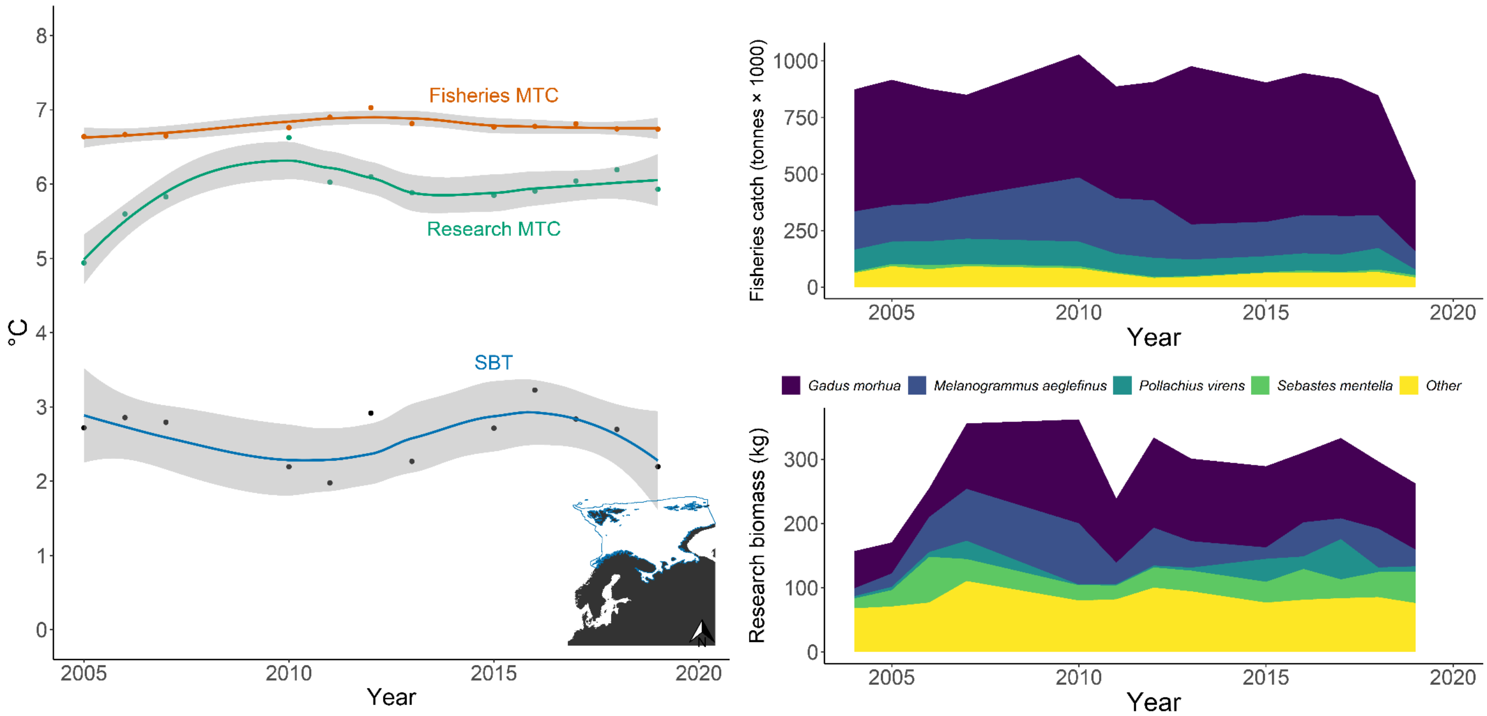

Figure 3*. Results from calculating the Mean Temperature of the Catch (MTC, ° C, left) between fisheries catch data and research trawl data in the Barents Sea (inset, left), along with trends in Sea Bottom Temperature (SBT, ° C, left) across the Barents Sea, from 2004 to 2019 (Paper IV). Also shown are trends in the fisheries catch (tonnes × 1000, top right) and research trawl biomass (kg, bottom right) per year for Atlantic cod (Gadus morhua), haddock (Melanogrammus aeglefinus), saithe (Pollachius virens), beaked redfish (Sebastes mentella) and all other study species (‘Other’) contained in analyses*

Furthermore, the Barents Sea fisheries MTC trend was strongly skewed by the commercial preference for cod. This effect has recently been highlighted in the Arabian-Persian Gulf, where the MTC trend abruptly changed due to increased catch of the largehead hairtail (*Trichiurus lepturus*) driven by international market demand (Alajmi et al. 2023). Within the full New Zealand MTC calculated amongst 102 species, this effect was also apparent due to the dominance of hoki within the catch. The presence of this effect suggests that MTC trends calculated using fisheries catch data only require caution during interpretation. In the instance that research survey data is available, it is recommended to compare MTC trends between fisheries catch and survey data. This comparison should be done amongst common species groupings gathered from similar gear types used to capture animals for fisheries or survey purposes (Leitão 2015). Although gear types will not be the exact same, as displayed in our Barents Sea MTC results, overlapping gear types (e.g., bottom trawls) between datasets may maximise comparability. In New Zealand, research survey data of pelagic species would facilitate comparison with our observed trends in pelagic-associated fisheries MTC warming, and thus, is recommended for further research and analysis.

Overall, the future application of catch-weighted indices like the MTC and MTL will require further comparison with available research survey data, pending availability. While some studies have attempted these comparisons (Branch et al. 2010; Cheung et al. 2013b; Tsikliras et al. 2015; Alajmi et al. 2023), the utility of such indices to reflect realised changes within marine communities has been challenged (Cressey 2010). For example, Branch et al. (2010) found low levels of correlation between the MTL calculated using fisheries catch data and the MTL calculated using ecosystem survey data across 25 LMEs. In the same study, Branch et al. (2010) presented the MTL for New Zealand fisheries, displaying the same masked MTL trend (via the geographic expansion of fisheries) that has also been identified by Durante et al. (2020) and the results in Paper III. This instance highlights not only the need for comparison with research survey data, but also, for methods to correct possibly masked trends with abundance-weighted indices. In the case of the MTL, the FiB and aMTL indices attempt to do so – it is therefore recommended within future application of the MTL to also apply the FiB and aMTL indices.

By comparing bottom-trawl fisheries catch and research trawl data of 18 common species, we were also able to assess the response of fisheries in the Barents Sea to apparent geographic shifts in species' distributions. We found that 2 out of 18 species had significant, positive correlations between research trawl biomass abundance and fisheries catch. This included spotted wolffish and Atlantic cod. For Atlantic cod, this species alone represented 70% of all fisheries catch, and 37% of all surveyed biomass (Figure 3). Within the context of Barents Sea demersal fisheries, the preference for cod could be interpreted as climate change adaptation in line with ocean-warming induced changes in distribution of species. Across the Barents Sea, the wide-spread 'borealization,' or shift in spatial distribution of boreal fish communities into the area, is reported to be underway since the early 2000s (Fossheim et al. 2015; Bergstad et al. 2018), in line with trends in regional ocean warming (Polyakov et al. 2017; Asbjørnsen et al. 2020; Csapó et al. 2021). This process was driven primarily by Atlantic cod and haddock, which display positive trends in biomass since 2004 in the Barents Sea, an area that both species access during feeding migrations in summer months (Johannesen et al. 2020). Accordingly, cod has become the single most abundant demersal fish species in the western Barents Sea in terms of biomass from 2012-2020 (Gjøsæter et al. 2023). Their recent increase in abundance within the area may be facilitated by cod's success as a predator, plus increasingly favourable environmental conditions via ocean warming (Ellingsen et al. 2020), paired with reductions in fisheries catch in the late 1990s and early 2000s designed to increase the stock size (Kjesbu et al. 2014). The latter instance highlights the role of fishing pressure in influencing potential ocean-warming induced shifts or changes in population biomass (Årthun et al. 2018; Palomares et al. 2020).

Further ocean warming will likely see the continued poleward shift of marine species' geographic distributions (Hodapp et al. 2023), including Atlantic cod. As such, the current example of increasingly abundant cod in the Barents Sea representing the preferred fisheries stock can be considered as climate change fisheries adaptation. In the Barents Sea, TAC quotas are agreed upon and ratified in both states through the Joint Norwegian-Russian Fisheries Commission (Howell et al. 2023). TACs are informed by annual stock biomass assessments, and are widely considered as precautionary (Hønneland 2014). Since 2004, officially reported catch of cod to the International Council for the Exploration of the Sea (ICES) between both Norway and Russia have generally followed precautionary TAC trends (Paper IV, Figure 8). In turn, fisheries management informed by annual stock biomass assessments can be considered innately adapted to climate change induced shifts in the geographic distribution of species' biomass.

Moving forward, 'climate-resilient' fisheries should regularly monitor trends in local or regional population biomass. Doing so can inform management decisions and fishing effort that will minimise the risk of overfishing species that are reducing in biomass abundance whilst concurrently maximising the catch potential of increasingly abundant species (Free et al. 2020; Eurich et al. 2023). In the Barents Sea, while cod may become increasingly dominant in regional fisheries (Mueter et al. 2021), that is not to say that it will not also require further management. Since 2020, cod has displayed relative reductions in biomass within the western Barents Sea, leading to a subsequent reduction in catch (Gjøsæter et al. 2023) (Figure 3). This may be due to the observed influence of hydrographic variation on Barents Sea cod stock size, including fluctuations in Atlantic water inflow and the Atlantic Multidecadal Oscillation (AMO, Årthun et al. 2018).

Overall, the research in the present thesis has investigated changes in body size as well as shifts in geographic distribution of marine water-breathing ectotherms. Importantly, how these two responses will interact under further ocean warming and fisheries scenarios requires further investigation. In their study analysing a global species assemblage of 600 marine fishes, Cheung et al. (2013a) estimated wide-spread reductions in body size by 2050 under high emissions scenarios. Within the same study, the authors accounted for the mediative effects of distributional shifts. Theoretically, if species are able to significantly shift their distribution in order to track their thermal affinity, then perhaps large-scale reductions in body size would not be required.

Nonetheless, after taking this into account, Cheung et al. (2013a) still predicted wide-spread body size reductions for species assemblages. The authors found that both ocean-warming induced increases in metabolic rate, as well as species' shifts in geographic distribution each explained approximately 50% of the observed assemblage body size reduction (Cheung et al. 2013a). Effectively, the process of geographic shifts that explained half of this variation was a result of smaller, low latitude fishes shifting to higher latitudes, composing a higher proportion of overall biomass (Cheung et al. 2013a). Since lower latitude species live closer to their thermal maxima relative to higher latitude species, they are more likely to experience negative temperature-size responses (Audzijonyte et al. 2020). This observation was also apparent in the present research, as New Zealand study species (Paper II) all experienced negative temperature-size responses, while the Norwegian study species did not (Paper I). Therefore, low-latitude species are projected to 'shrink' at a faster rate, whilst concurrently shifting their distribution polewards (Cheung et al. 2013a).

Growing to a smaller maximum body size occurs across an animal's ontogeny, whereby warmer water will signal to the animal to limit its growth following sexual maturation (Verberk et al. 2021) . Concurrently, warming water also signals to species to track their thermal affinity across geographic landscape (Pinsky et al. 2013). In turn, these two processes occur across both short-term (i.e., life-span) and long-term (i.e., evolutionary) time scales (Atkinson 1994; Loisel et al. 2019). Therefore, it is unlikely that observed changes in body size or shifts in geographic distribution mediate one another, but more likely, they occur simultaneously through an individual's lifetime and also across generations. In turn, it is possible that regional species assemblages may be increasingly composed of more abundant, smaller fishes (Coghlan et al. 2023), especially in sub-tropical or mid-latitude regions (Friedland et al. 2023).

In line with the aforementioned discussion, ocean-warming induced changes in assemblage-level body size can be driven by within-species changes (i.e., via temperature-size responses), or by compositional changes, either through the gain or loss of species or by changes in abundance (i.e., via distributional shifts) (Martins et al. 2023). Such findings have wide-spread implications regarding the functions and management of marine ecosystems throughout future ocean warming and fisheries scenarios. An increase in abundance of smaller fishes may lead to reductions in population-level reproductive output, as reproductive output in teleost fish scales hyperallometrically (Marshall et al. 2021). An increase in abundance of smaller fishes and macroinvertebrates can also impact the foraging dynamics of higher trophic level species including fishes, sea birds and marine mammals (Friedland et al. 2023). For example, smaller-bodied prey items may be more cryptic or elusive (Wardle 1975; Domenici and Blake 1997; Domenici 2001), as well, could contain less energy density per unit of weight (Thoral et al. 2021), which in turn can negatively influence predator species' energy expenditure per unit of food resource required (Johansen et al. 2001; Friedland et al. 2023). Furthermore, concurrent overfishing of top predators could induce mesopredator release of increasingly abundant, smaller fishes. This mesopredator release could result in suppression or extirpation of prey species, further altering the size-spectra of marine communities and thus challenging the functional integrity of food webs and trophic dynamics (Brown et al. 2004; Newsome et al. 2017).

These potentially negative outcomes may be induced by the cumulative impact of the individual processes investigated in the present thesis. This includes ocean-warming induced changes in body size and geographic distribution, at variable rates and extents between species and biogeographic areas, as well as overfishing of high trophic level species. Together, cumulative stressors exerted upon marine ecosystems could in turn threaten the innate, social and economic value of their services including biodiversity maintenance and fisheries production. In recognition of these potential outcomes, it will become increasingly necessary to monitor such changes throughout the forthcoming century of rapid climate change and ocean warming. The research deployed in the present thesis may assist in such monitoring, which will help inform the required management of marine biodiversity and food security moving forward.

5 CONCLUSION AND RECOMMENDATIONS

In conclusion, the research in the present thesis has investigated individual stressors that can interact cumulatively to impact marine communities as well as fisheries. First, results revealed that ocean warming is likely to reduce the maximum body size of water-breathing ectotherms, in particular, large, active species, as well as species at lower latitudes (relative to higher latitudes). Furthermore, these results suggest that some polar species may grow to larger maximum body sizes with intermediate ocean warming, as they may be released from thermal stress encountered at extremely low temperatures. Nonetheless, beyond intermediate warming, polar species may once again be limited in maximum body size as they approach the warm extent of their temperature range. While populations of marine ectothermic species have displayed concurrent reductions in body size and shifts in geographic distribution, how polar species will balance these responses should remain of high research priority, as the threat of extinction through loss of suitable environmental habitat is highest for polar species (Penn and Deutsch 2022).

Furthermore, while changes in body size or geographic distribution represent adaptive mechanisms of water-breathing ectotherms to rapid ocean warming, current emissions scenarios may lead to absolute ocean temperatures at high latitudes that have not been experienced by polar species over the past 55 million years (Sluijs et al. 2006; Brown et al. 2022). Hence, whether adaptive mechanisms such as shifts in geographic distribution and changes in body size are sufficient to prevent wide-spread extinction of polar species, within environmental changes not experienced over recent evolutionary history, should remain priority for further research.

In general, the present temperature-size response results are in line with the TSR mechanisms of the OCLTT and GOLT, which highlight the rate of protein denaturation occurring at species' thermal maxima. While these results have contributed valuable insight into the role of protein denaturation sensu the Temperature Size Rule (Pauly and Lam 2023), it is recommended that further research pursue the mechanistic underpinnings of the TSR at the physiological and biochemical level between species of variable biogeographic origins. Furthermore, how anticipated decreases in dissolved oxygen in sea water impact temperature-size responses between variable taxa should be prioritised, as levels of thermal stress and hypoxia tolerance will vary between species of different habitat associations and life histories (Shi et al. 2022).

While water-breathing ectotherms are likely to reduce in maximum size with ocean warming, historical fishing pressure has also been shown to reduce population- and body-size of fished stocks. In particular, high trophic level species have been depleted due to persistent market demands. Using the Mean Trophic Level, as well as the Fishing-in-Balance and adjusted Mean Trophic Level indices, we built upon previous research to reveal the gradual fishing down of marine food webs in shelf waters of New Zealand from the 1950s onward.

Concurrently, further ocean warming is expected to see the poleward geographic shift in distribution of marine ectothermic species at a global scale. Such shifts can occur in variable direction and extent between species of different life histories and habitat associations. For example, our results calculating the Mean Temperature of the Catch in New Zealand waters inferred an increasing proportion of smaller-bodied, tropical pelagic species (skipjack tuna, blue mackerel) encountered in New Zealand waters, whilst larger-bodied, temperate species such as Southern bluefin tuna decreased. Such results, along with the aMTL calculated in New Zealand, were inferred from fisheries catch data. Further validation of these results will require direct comparison with fisheries-independent research survey data, between datasets that have sampled overlapping habitats and using similar gear types, as was done for the Barents Sea demersal fish community in the present research.

While the majority of countries do not maintain fisheries-independent research surveys, our results here demonstrate their importance in monitoring the ongoing and expected poleward shift of marine species' distributions, as well as warming-induced changes in body size, throughout the coming century of climate change. Importantly, closely monitoring changes in the biomass distribution of species will help inform climate change adaptation of fisheries. While the preference for Atlantic cod in the Barents Sea skewed any apparent trends in the MTC, fisheries management for this species has been acutely informed by such biomass surveys. In turn, Norway and Russia have directed fishing effort towards the increasingly abundant cod, and away from sensitive, polar species reducing in biomass abundance. Like those fisheries analysed in the Barents Sea, global fishing effort should prioritise climate change adaption strategies that similarly reduce effort on locally- or regionally-reducing species. Close comparison of research survey data and fisheries catch data can facilitate such management.

Overall, the cumulative effects of body size reductions, shifts in geographic distribution, and persistent fishing pressure have the potential to reduce marine communities' resilience in the face of rapid anthropogenic climate change. While recent evidence has shown that both temperature-size responses and geographic shifts are likely to occur concurrently, the research in the present thesis has provided novel insight into how anticipated changes are likely to occur between variable species as well as biogeographic regions. Such insight highlights the need for in-depth monitoring of marine communities and ecosystems, as well as persistent fishing pressure. Doing so can help inform conservation and fisheries management that is necessary in order to preserve ecosystem services such as biodiversity and food security within the forthcoming centuries of climatic change.

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Paper I: Lavin, C. P., Gordó-Vilaseca, C., Costello, M. J., Shi, Z., Stephenson, F., Grüss, A. (2022). Warm and cold temperatures limit the maximum body length of teleost fishes across a latitudinal gradient in Norwegian waters. Environmental Biology of Fishes, 105: 1415-1429. https://doi.org/10.1007/s10641-022-01270-4

Environ Biol Fish (2022) 105:1415–1429
https://doi.org/10.1007/s10641-022-01270-4

Warm and cold temperatures limit the maximum body length of teleost fishes across a latitudinal gradient in Norwegian waters

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Received: 31 October 2021 / Accepted: 4 May 2022 / Published online: 21 May 2022

Abstract As the majority of marine organisms are water-breathing ectotherms, temperature and dissolved oxygen are key environmental variables that influence their fitness and geographic distribution. In line with the temperature-size rule (TSR), marine ectotherms in warmer temperatures will grow to a smaller maximum body size, yet the extent to which different species experience this temperature-size response varies. Here, we analysed the maximum body length of ten teleost fish species in line with temperature, dissolved oxygen concentration and geographic location (that encompasses multiple latent variables), across a broad (26°) latitudinal gradient throughout Norwegian waters. Our results showed that the two largest study species, spotted wolffish (*Anarhichas minor*) and cusk (*Brosme brosme*), display the strongest negative temperature-size response. We also observed smaller maximum body lengths for multiple species within the coldest extent of their temperature range, as well as parabolic relationships between maximum length and temperature for Atlantic wolffish (*Anarhichas lupus*) and beaked redfish (*Sebastes mentella*). The smaller maximum body lengths for high latitude species at both warm and cold temperature extremes of species' thermal ranges corroborate the temperature-size mechanisms of the gill-oxygen limitation theory (GOLT), whereby spontaneous protein denaturation limits growth at both warm and cold temperatures.

Keywords Temperature-size response · Gill-oxygen limitation theory (GOLT) · Cold denaturation · Ocean warming · Maximum body length · Generalised additive models (GAMs)

Introduction

Since the start of the twentieth century, mean global temperatures have increased approximately by 1.1 °C concurrently with increasing anthropogenic greenhouse gas emissions (IPCC 2021). In parallel, the geographic extent of low oxygen areas in global oceans has been expanding, whilst upper layer oxygen

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10641-022-01270-4.

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levels have decreased, likely by 0.5–3.3% at surface and sub-surface layers throughout the past 50 years (Schmidtko et al. 2017; Breitburg et al. 2018; Bindoff et al. 2019). As the majority of marine species are water-breathing ectotherms, such environmental changes may present deleterious impacts on individual fitness.

In general, the response of marine water-breathing ectotherms to ocean warming and deoxygenation includes shifts in their geographic distribution to track their thermal affinities (Poloczanska et al. 2016). This may result from the complex interaction of temperature and dissolved oxygen concentration in sea water, as oxygen demands of water-breathing ectotherms increase, whilst the availability of dissolved oxygen may decrease with warming, enhanced ocean stratification and the accelerated respiration of dissolved organic matter (Oschlies et al. 2018). It is also suggested that a response to warming and deoxygenation includes the reduction of body size (Gardner et al. 2011).

Across an ectothermic species' geographical range, intraspecific clines in body size are apparent along latitudinal gradients, whereby individuals are generally smaller in warmer conditions (Horne et al. 2015). According to the temperature-size rule (TSR), those individuals reared in warmer temperatures grow faster and mature at a smaller size (Atkinson 1994). Whilst this 'temperature-size response' has been well documented in wild populations of aquatic ectotherms (Daufresne et al. 2009), the mechanisms underpinning this response have remained debated (Pauly 2010, 2021; Lefevre et al. 2017) and several explanations have been offered to resolve this interaction between environment and growth (Deutsch et al. 2015; Pörtner et al. 2017; Clarke et al. 2021; Pauly 2021; Verberk et al. 2021).

The strength of temperature-size responses will vary between species, likely based on factors including typical body size (Rubalcaba et al. 2020), sensitivity to environmental changes (Forster et al. 2011; Hoefnagel and Verberk 2015), scope of thermal niche (García Molinos et al. 2016; Burrows et al. 2019; Brito-Morales et al. 2020), life history (Weber et al. 2015; Audzijonyte et al. 2020), geography (Deutsch et al. 2020; Clarke et al. 2021), feeding strategy and behaviour (Block et al. 2011) and physiology (Atkinson et al. 2006). Therefore, rather than testing, if an ectothermic species displays a temperature-size response at all, it may be useful to compare the degree of responses between species, in order to reveal factors associated with strong temperature-size responses (Verberk et al. 2021).

In the present study, we investigated the relation between the maximum body length (hereafter simply referred to as 'maximum length') of ten teleost fish species and ocean temperature and dissolved oxygen concentration. This was done by fitting generalised additive models (GAMs) to open-source long-term bottom trawl survey data collected in Norwegian shelf and offshore waters (Djupevåg 2021). The ten study species included one benthopelagic species, Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum 1792); two pelagic species, capelin (*Mallotus villosus*, Müller 1776) and golden redfish (*Sebastes norvegicus*, Ascanius 1772); one bathypelagic species, beaked redfish (*Sebastes mentella*, Travin, 1951); and six demersal species, Norway redfish (*Sebastes viviparus*, Krøyer 1845), cusk (*Brosme brosme*, Ascanius 1772), Atlantic wolffish (*Anarhichas lupus*, Linnaeus 1758), spotted wolffish (*Anarhichas minor*, Olafsen 1772), daubed shanny (*Leptoclinus maculatus*, Fries 1838) and polar cod (*Boreogadus saida*, Lepechin, 1774).

Whilst much of the temperature-size research on marine ectotherms has focused on warming and maturation, we investigated the influence of temperature, dissolved oxygen concentrations and geographic location (representing other latent environmental variables) on the maximum length of species, as the mechanisms between these responses may vary (Hoefnagel et al. 2018). In turn, we hypothesise that the largest study species will exhibit the strongest negative temperature-size response (i.e. smaller in warmer temperatures), as larger ectotherm species have been found to be more sensitive to increased temperatures and deoxygenation (Rodnick et al. 2004; Messmer et al. 2017; Rubalcaba et al. 2020).

Methods

Study area

The study area includes coastal and offshore waters of Norway, extending from the temperate North Sea, Skagerrak and the Norwegian Sea to the Barents Sea and southern portion of the Arctic Ocean along the northern shelf of Svalbard (Fig. 1). Spanning a latitudinal range from 56°N to 82°N, the study area is marked by a temperature gradient from an annual mean sea surface temperature (SST) of 10.7 °C in the North Sea, to 4.8 °C in the northern Barents Sea and southern Arctic Ocean (Gonzalez-Pola et al. 2019).

Trawl survey data

The survey data employed in the present study were collected during the Norwegian Institute of Marine Research's long-term bottom trawl surveys between 1980 and 2020 (Djupevåg 2021). These long-term trawl surveys provide data on the abundance of targeted species to inform stock assessments across

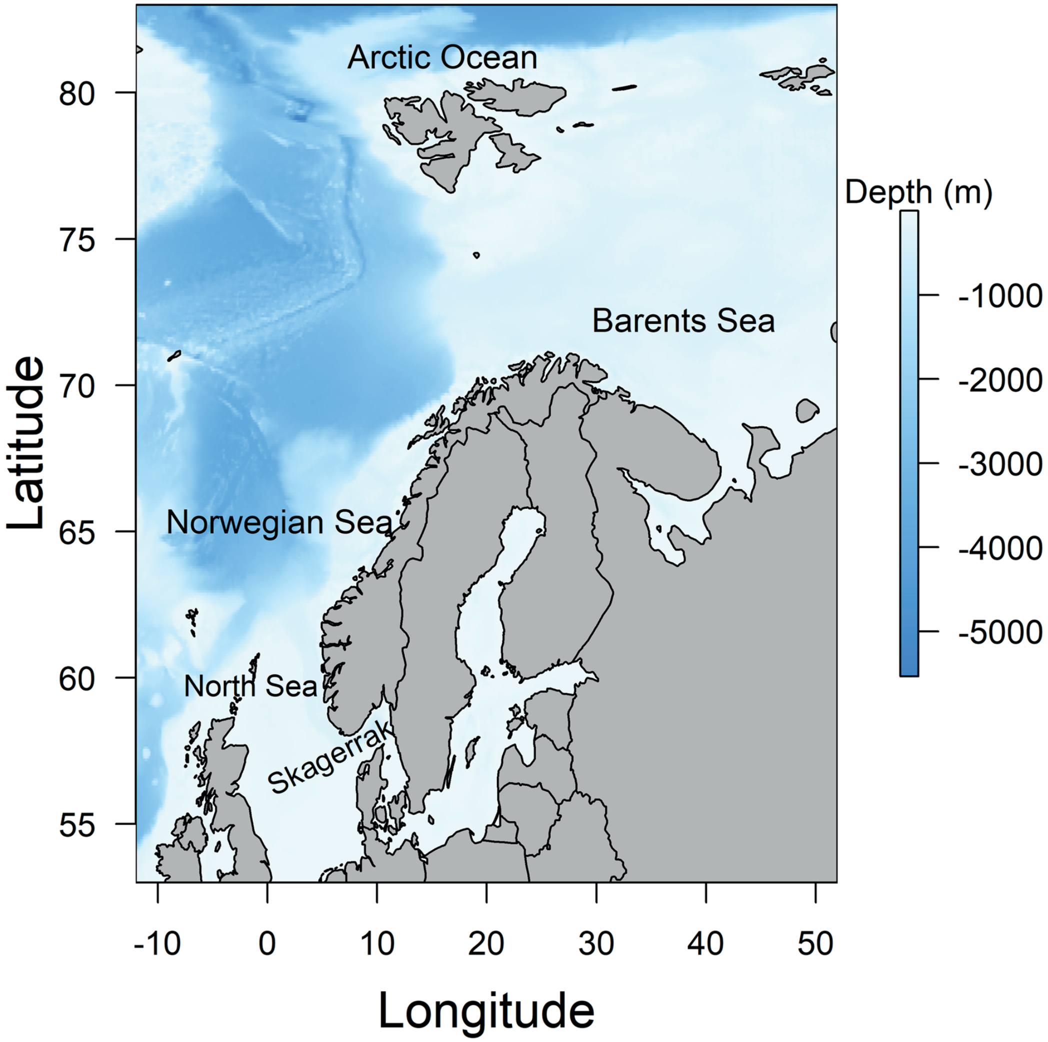


Fig. 1 Map of the study area, including the North Sea, Skagerrak, the Norwegian Sea, the Barents Sea and the southern portion of the Arctic Ocean. Bathymetry is displayed across the study area (m). This figure was created using the *raster* package (Hijmans 2021) in R (Team R Development Core 2021)

Norwegian waters (Djupevåg 2021). The survey data are publicly available via the Norwegian Marine Data Centre (https://doi.org/10.21335/NMDC-328259372).

To account for variation in sampling methods over the period 1980–2020, we restricted the data utilised in the present study to a single gear type and sampling method (‘shrimp trawl’, 15–35 mm mesh size) between 1990 and 2020. This provided us with a total of 256,788 records of 198 unique species caught in 22,262 research trawls (Fig. 2). The mean length of trawling events was 1.2 nautical miles. We selected those species that had more than 2000 records. This reduced our dataset to 239,902 records for 36 species. The information gathered from each record included the maximum length (total length (TL), cm) of fishes collected in a trawling event, the bottom depth of the trawl sample and geographic location of the start of the trawl station (latitude, longitude).

Environmental data and exploratory analyses

Mean temperature (°C) and dissolved oxygen concentration (mols/m^{-3}) at the maximum bottom depth of each raster cell (5 arcmin) were extracted from Bio-Oracle (Assis et al. 2018). Bio-Oracle environmental layers were produced via monthly averages of climate data between 2000 and 2014; thus, they represent the prevailing, long-term environmental conditions experienced by the study species. Environmental measurements were associated with maximum length records based on the latitude and longitude of sample location. For data analyses, longitude and latitude were expressed in Universal Transverse Mercator (UTM) coordinates, i.e. eastings and northings. For reporting purposes, the dissolved oxygen concentration values from Bio-Oracle were converted from mols/m^{-3} to mg/L using the unit conversions provided by the International Council for the Exploration of the Seas (ICES 2022).

We tested for multicollinearity between environmental covariates by calculating the Pearson’s correlation coefficient (r) between temperature, dissolved oxygen concentration, eastings and northings for the 36 selected species. Such multicollinearity analyses are necessary as regression models, including GAMs, are sensitive to highly correlated continuous variables (Guisan et al. 2002; Dormann et al. 2013). For the majority of the 36 species, the Pearson’s r between temperature and dissolved oxygen concentration was greater than 0.7. In order to avoid problems with model fit via multicollinearity, the relationship between temperature and dissolved oxygen concentration across the study extent was examined using a GAM, and the residuals from this model (henceforth ‘OxyResid’) were extracted and subsequently used as a covariate within our maximum length GAMs (Supplementary Fig. 1) (Leathwick et al. 2006; García et al. 2020). The OxyResid covariate indicates, at each sample site, the deviation in mean dissolved oxygen concentration that is expected at its given temperature, i.e. accounts for regional-scale variation in dissolved oxygen concentration (Leathwick et al. 2006).

The Pearson’s correlation coefficients were also calculated between temperature, OxyResid, eastings and northings for the environmental data pertaining to where each species was sampled. Pearson’s r’s greater than 0.7 in absolute value were considered indicative of multicollinearity, and species where this was the case were excluded from subsequent analyses. A total of ten species (67,029 records) had a Pearson’s r less than 0.7 in absolute value and were, therefore, included in maximum length GAM analyses (Table 1). Before fitting GAMs, we explored the distribution of the covariates included to visually identify outliers and subsequently removed them (Zuur et al. 2010). After this data treatment, the total number of records amongst the ten study species was reduced to 66,875 (Supplementary Figs. 2–11).

Study species

The ten species selected for maximum length GAM analyses include two pelagic species, one bathypelagic species, one benthopelagic species and six demersal species. Capelin is a pelagic, pan-Arctic planktivore species that represents an important prey item for piscivorous fish (Fall et al. 2018). Golden redfish is a pelagic, long-lived and late-to-mature Atlantic species that is found across shelf waters and the upper bathyal zone (Bakay 2017). Beaked redfish is a bathypelagic, long-lived species that inhabits deep-water habitats, as well as pelagic areas of continental slopes of the Atlantic Ocean (Cadrin et al. 2010). Greenland halibut is a benthopelagic flatfish species with circumpolar distribution that inhabits coastal fjords and bays, as well as slope areas of

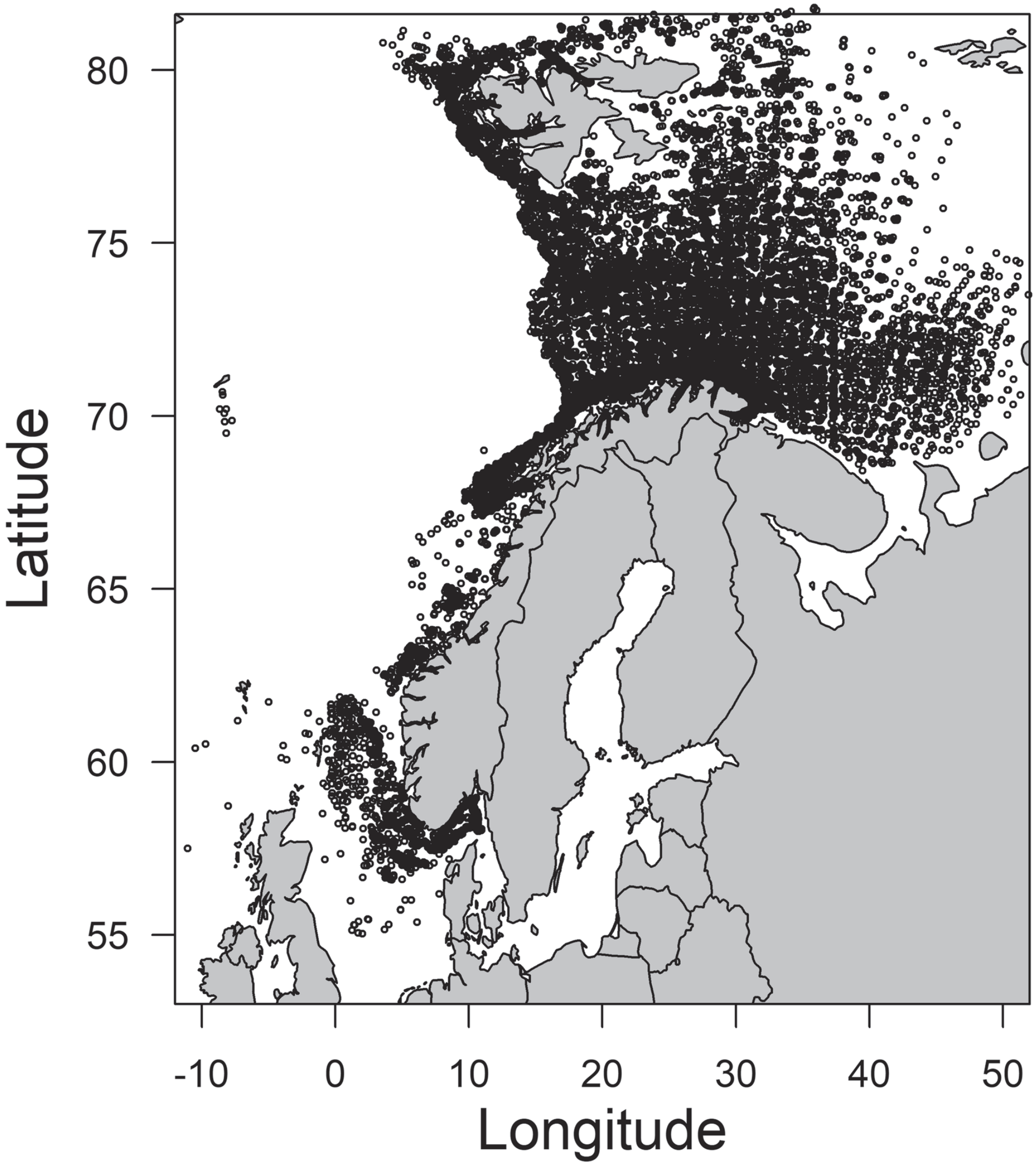


Fig. 2 Spatial distribution of the shrimp bottom trawl survey data collected between 1990 and 2020 that were used in the present study ($n=22{,}262$; Djupevåg 2021). This figure was created using the *raster* package (Hijmans 2021) in R (Team R Development Core 2021)

continental shelves (Giraldo et al. 2018). Norway redfish is a demersal species that occurs in Atlantic coastal and shelf waters and prefers structurally complex habitat, including boulder fields or sponge and coral habitat (Kutti and Fosså 2015). Cusk is a demersal Atlantic species that inhabits the upper slope

Table 1 The observed and reported maximum body length (total length (TL), cm) of study species. Reported maximum lengths: [1]Robins et al. 1986, [2]Frimodt 1995, [3]Orlov and Binohlan 2009, [4]Hureau and Litvinenko 1986, [5]Wilhelms, 2013, [6]Winters 1970, [7]Muus and Nielsen 1999, [8]Cohen et al. 1990

Species	Observed maximum length (cm)	Reported maximum length (cm)
Spotted wolffish *Anarhichas minor*	135	180[1]
Cusk *Brosme brosme*	104	120[2]
Greenland halibut *Reinhardtius hippoglossoides*	98	130[3]
Golden redfish *Sebastes norvegicus*	80	100[4]
Atlantic wolffish *Anarhichas lupus*	124	150[1]
Beaked redfish *Sebastes mentella*	69	78[5]
Norway redfish *Sebastes viviparus*	40	67[5]
Capelin *Mallotus villosus*	21	25[6]
Daubed shanny *Leptoclinus maculatus*	20	20[7]
Polar cod *Boreogadus saida*	28	40[8]

to deep continental shelf waters (Knutsen et al. 2009). Atlantic wolffish is a demersal, denning species that inhabit high-rugosity habitat in coastal waters, as well as gravelly and boulder field habitats in deeper waters (Novaczek et al. 2017). Spotted wolffish is demersal, and similarly inhabits complex and high-rugosity habitat around or within sheltered dens across the Atlantic Ocean (Baker et al. 2012). Daubed shanny is a demersal, circumpolar, cold-adapted species that inhabits soft bottoms (Meyer Ottesen et al. 2011). Lastly, polar cod is a circumpolar demersal species that is the most abundant Arctic fish to inhabit areas under and around pack ice, although it is also found in ice-free areas (David et al. 2016).

Model fitting

GAMs were employed to investigate the influence of temperature and dissolved oxygen concentration (more precisely, OxyResid) on the maximum length of the ten study species. In addition to these environmental covariates, a tensor product smooth between eastings and northings was included to represent the effects of geographic location. This term represents a proxy for latent environmental or ecological covariates that were otherwise not included in the model (e.g. variation in depth). This tensor product smooth term also accounts for the broad-scale spatial autocorrelation that may be present within the maximum length data (Wood 2006; Grüss et al. 2016, 2018a, 2021). For all ten study species, GAMs were fitted to maximum length data using the 'gam' function from the *mgcv* package in the R environment (Wood 2006; Team R Development Core 2021) as follows,

$$g(L) = te(X, Y) + s(Temperature) + s(OxyResid) \quad (1)$$

where L is the maximum length; g is the log-link function between maximum length and each term on the right side of the equation; $te(X,Y)$ is the tensor product smooth between eastings and northings; and s is the thin plate regression spline with shrinkage (bs = 'ts' specified in the smooth function of 'gam' within the *mgcv* library) fitted to temperature and OxyResid (Grüss et al. 2018a).

The Gamma distribution was identified as the most appropriate distribution for the maximum length data employed in the present study, using diagnostics from the *fitdistrplus* package (Delignette-Muller and Dutang 2015) in R (Team R Development Core 2021). The thin plate regression splines employed in GAMs were limited to four degrees of freedom ($k = 4$) in order to prevent overfitting and to preserve the interpretability of model results (Mannocci et al. 2017; Grüss et al. 2018b; Weijerman et al. 2019). In addition, an extra penalty was applied to model covariates as their smoothing parameter approached zero, which allowed for the complete removal of a covariate when its smoothing parameter equalled zero (Marra and Wood 2011; Grüss et al. 2014).

Model validation

To evaluate the GAMs of the ten study species, we relied on two performance metrics: (1) the adjusted coefficient of determination (adjusted-R^2), which indicates the percentage of the variance explained by the GAMs; and (2) Spearman's rank correlation coefficients (Spearman's *rho*'s) between predicted maximum lengths and observed maximum lengths. Our validation procedure consisted, for each GAM, of the following: (1) the dataset of interest was split into a training dataset which was randomly assigned 70% of the data and a test dataset which was assigned the remaining 30% of the data; (2) this was repeated 10 times, such that 10 training datasets and 10 corresponding test datasets were produced; (3) the GAM was fit to each of the 10 training datasets; and (4) the 10 GAMs fitted using the 10 training datasets were evaluated using the corresponding test datasets and the performance metrics (adjusted-R^2 and Spearman's *rho*'s) (Grüss et al. 2016; Egerton et al. 2021). A given GAM was considered to have passed the evaluation test if, across all 10 replicates, the median adjusted-R^2 was larger than 0.1 (Legendre and Legendre 1998; Grüss et al. 2020) and the median Spearman's *rho*'s was significantly different from zero at the $\alpha = 0.05$ level (Grüss et al. 2014, 2021; Weijerman et al. 2019; Egerton et al. 2021).

Analyses with the fitted and validated models

To determine the relative importance of temperature, OxyResid and geographic location in explaining the maximum length of the ten study species, we implemented the approach of Grüss et al. (2016). This approach consists, for each study species, in comparing the predictions of the final GAM with those of GAMs where the values of a given predictor (temperature, OxyResid, eastings or northings) are randomly permuted within the dataset fitted to the model ('random GAMs') (Thuiller et al. 2012; Grüss et al. 2016). An index of relative importance is obtained for each predictor (temperature, OxyResid, eastings and northings) by computing one minus the Pearson's correlation coefficient between the predictions of the final GAMs and the predictions from the random GAMs (Grüss et al. 2016; Dove et al. 2020; Bolser et al. 2020).

We also used the results from the GAMs to predict the maximum length of study species as a function of temperature using the 'predict.gam' function from the *mgcv* package (Wood 2006; Team R Development Core 2021). Specifically, we predicted maximum lengths over a vector of values ranging between the minimum and maximum values of temperature encountered by the species of interest where it was sampled, whilst (1) setting OxyResid to its mean value from the modelled dataset and (2) setting easting and northings to their values at the barycentre of the study area (Grüss et al. 2018c, 2020).

Examining the potential effects of fishing pressure on the maximum length of study species

In order to acknowledge the potential effects of fishing pressure on the maximum length of our study species, we calculated a 'pseudo-*Z*', or pseudo-total mortality (*Z*) value, for the 9 species included in the present study that are targeted by fisheries (all species except for daubed shanny). This was done by employing our maximum length records to construct a length-converted catch curve (Pauly 1990), using the FiSAT II Fish Stock Assessment Tool (Gayanilo et al. 2005). Catch curves were calculated using two growth parameters included in von Bertalanffy growth functions: asymptotic length (L_∞) and growth coefficient (*K*, see Supplementary Table 1 and Appendix for methods). For each species, pseudo-*Z* values were calculated across 5-year periods. We then compared these values to determine whether trends in fishing mortality (*F*) changed across the 30-year study period. Here, we assume that natural mortality (*M*) for species is constant across time, so that changes in pseudo-*Z* reflect changes in *F* ($Z = M + F$; Beverton and Holt 1956).

Results

The length data included in analyses were generally representative of adult size classes for study species (Table 1). Across the study area, mean sea surface temperature ranged from − 1 in the northern extent to 11.5 °C in the southern extent, whilst mean temperature at bottom depth ranged from − 1 to 8.9 °C (Supplementary Fig. 12). The gradient of dissolved oxygen concentration ranged from 8.45 in the southern extent to 10.9 mg/L in the northern extent of the study area (Supplementary Fig. 13).

For all ten study species, temperature, OxyResid and the interaction between eastings and northings were found to have a significant effect ($p < 0.005$) on their maximum length (Table 2). In estimating the relative importance of model covariates in explaining maximum length, eastings and northings were found to be the most important in explaining maximum length for all ten study species (Supplementary Fig. 14). All GAMs passed the model evaluation test, as (1) median adjusted-R^2 values ranged between 0.124 (spotted wolffish) and 0.331 (Greenland halibut); and (2) Spearman's *rho* values ranged between 0.361 (spotted wolffish) and 0.573 (beaked redfish) and were all significantly different from zero at the $\alpha = 0.05$ level (Supplementary Fig. 15).

Predictions of the maximum length of the study species across their temperature range displayed three patterns (Fig. 3). The two species with the largest predicted maximum lengths, spotted wolffish and cusk, were predicted to decrease in maximum length as temperature increased—this was also the case for Norway redfish (Fig. 3). In contrast, capelin, Greenland halibut, golden redfish, daubed shanny and polar cod were predicted to increase in maximum length as temperature increased in the study area. Atlantic wolffish and beaked redfish were predicted to increase in maximum length until a given temperature, after which maximum length decreased (Fig. 3). Lastly, the fishing mortality proxy pseudo-Z values suggested that no observable positive or negative trends occurred across the 30-year study period (Supplementary Table 1).

Discussion

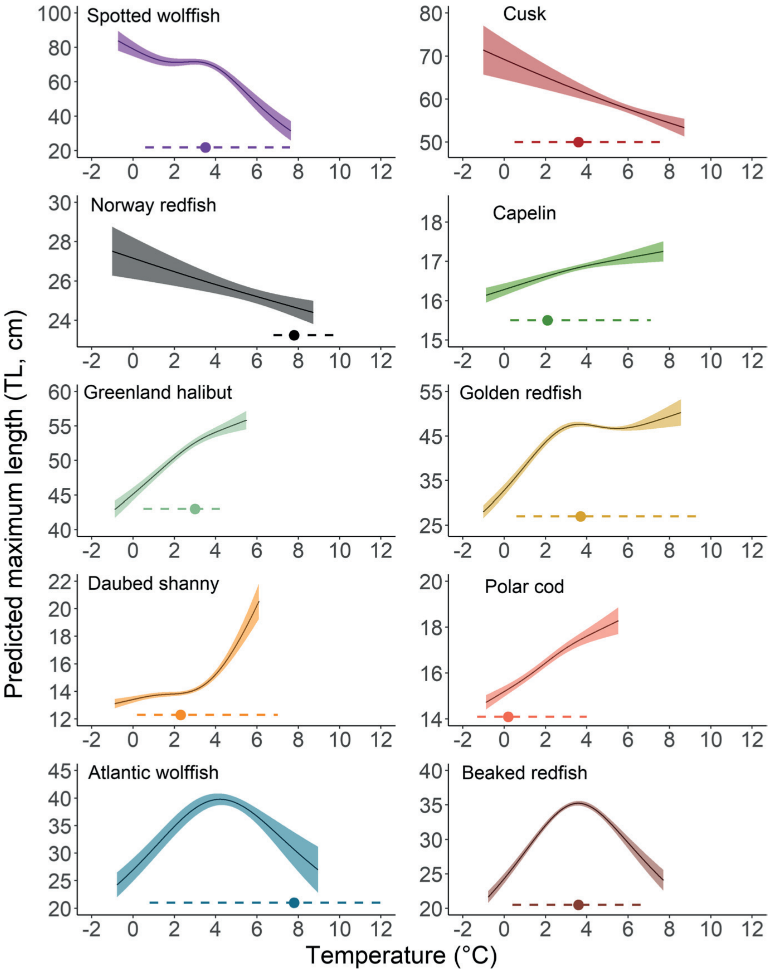
Overall, our results confirm our original hypothesis that large species will exhibit the strongest negative temperature-size response. The two largest species, spotted wolffish and cusk, were predicted to experience the largest relative decrease in maximum body length across their observed temperature range (Fig. 3). These results are consistent with the body of literature that suggests larger species are more likely to experience stronger negative temperature-size responses (Forster et al. 2012; van Rijn et al. 2017). In contrast, the maximum lengths of capelin, Greenland halibut, golden redfish, daubed shanny and polar cod were shown to increase with temperature. Interestingly, all of the aforementioned species display smaller maximum lengths within the coldest extent of their temperature range.

Our results corroborate the temperature-size mechanism that is part of the gill-oxygen limitation theory (GOLT, Pauly 2019, 2021). According to the GOLT, as the 3-dimensional bodies of ectotherms grow towards their asymptotic sizes, their 2-dimensional gills become gradually unable to supply sufficient oxygen (per unit weight) required for the synthesis of body proteins to exceed the rate of spontaneous protein denaturation (Pauly 1979, 1981). As a result, growth ceases when synthesis equals denaturation and, thus, relatively high temperatures for the thermal niche of a species, which promote denaturation, cause ectotherms to remain smaller (Pauly and Cheung 2018; Pauly 2019, 2021), as exhibited here by spotted wolffish, cusk and Norway redfish.

Table 2 Number of data points fitted to the generalised additive models (GAMs) of the ten study species, and the adjusted-R^2 of these GAMs. All GAMs express maximum body length as a function of temperature, the residuals of dissolved oxygen and temperature (OxyResid) and an interaction term (tensor product smooth) between eastings and northings (Eq. 1)

Species	Number of data points	Adjusted-R^2
Spotted wolffish *Anarhichas minor*	4292	0.152
Cusk *Brosme brosme*	3870	0.244
Greenland halibut *Reinhardtius hippoglossoides*	9816	0.345
Golden redfish *Sebastes norvegicus*	8454	0.316
Atlantic wolffish *Anarhichas lupus*	5056	0.164
Beaked redfish *Sebastes mentella*	11,502	0.324
Norway redfish *Sebastes viviparus*	5551	0.173
Capelin *Mallotus villosus*	9887	0.143
Daubed shanny *Leptoclinus maculatus*	3113	0.225
Polar cod *Boreogadus saida*	5334	0.161

Fig. 3 The maximum length (TL, cm) of the ten species as a function of temperature (°C), as predicted by the generalised additive models (GAMs) developed in the present study, with 95% confidence intervals. The dashed line indicates the reported temperature range of species, including the mean (dot) as reported by species-specific mapping parameters in AquaMaps (Kaschner et al. 2019). This figure was created using R Studio (Team R Development Core 2021)



Spontaneous protein denaturation, i.e. the loss of the quaternary structure which give proteins their shapes, and thus enable them to function (e.g. as enzyme), however, is not only accelerated by increasing, but also by decreasing temperature, a process known as 'cold denaturation' (Privalov 1990; Graziano 2014; Sanfelice et al. 2015; Yan et al. 2018). The result has been called 'metabolic cold adaptation', whereby some species have evolved to elevate their metabolic rate to live at cold temperatures (Wohlschlag 1962, 1964; Pauly 1979). Thus, because of the need to replace proteins denatured by the cold temperature they inhabit, some polar fishes display a metabolic rate that is higher than expected given a extrapolation of standard metabolism-temperature relationships (Wohlschlag 1962, 1964; Pauly 1979). Also, Pauly (1980) reported that fishes in water < 4 °C exhibited higher natural mortality rates than expected, other things (i.e. growth parameters) being equal, and body size was significantly negatively correlated with mortality. These results suggest that cold-water fishes are relatively smaller in body size (Pauly 1980).

Cold denaturation has received relatively little attention vis-à-vis the temperature-size relationship for water-breathing ectotherms (Todgham et al. 2007, 2017; Fraser et al. 2007; Peck 2016, 2018). Although it was a constitutive element of the first presentation of the GOLT (Pauly 1979) and was corroborated in Pauly (1980), it was not incorporated into the further development of this theory. In fact, Pauly (2019, pg. 169) sent it into 'profound hibernation'. However, the humped shapes of the temperature-size response for Atlantic wolffish and beaked redfish present evidence for cold denaturation causing a response similar to elevated temperatures, thus justifying reviving the cold denaturation hypothesis as an explanatory mechanism for reduced maximum sizes of fish at very low temperatures. Recent findings from the Antarctic also support the reviving of the cold denaturation hypothesis. Fraser et al. (2022) found that the growth of Antarctic fishes was limited by high 'degradation' rates of proteins relative to temperate species. These and our results add to the growing body of literature highlighting the limitations of growth for marine ectotherms at low temperatures.

As previously mentioned, capelin, Greenland halibut, golden redfish, daubed shanny and polar cod are predicted to increase in maximum length with temperature (Fig. 3). These findings suggest that these species have optimal temperatures which exceed the temperatures at which they were sampled, and beyond, where their maximum length would start to decline, as the data employed in the current study only covers a part of the temperatures our study species experience (Fig. 3). We interpret the parabolic temperature-size response of Atlantic wolffish and beaked redfish, to result from the study area spanning a range of temperatures which include the temperature to which they are best adapted, and thus their maximum length can increase or decrease depending on the local conditions. Overall, we expect that the variable temperature-size responses at both warm and cold extents reflect species-specific growth sensitivities to either warming or cooling temperatures across their geographic range, as well as species traits. We, therefore, recommend applications of our modelling approach that would incorporate further species' traits, including their sensitivities to temperature and dissolved oxygen concentration, to elucidate temperature-size responses at both warm and cold temperatures between species of variable size, milieu, activity and trophic level (van Rijn et al. 2017).

Regarding the relative importance of model covariates, for all study species, geographic location was found to be most important in explaining maximum length. This is to be expected, as these variables were chosen to represent latent environmental and ecological variables in the study region (Grüss et al. 2016, 2018a, 2021; Bolser et al. 2020), and may reflect variation in depth, the availability of resources, ecological competition, size selective predation or mortality, as well as fishing effects (Connolly and Roughgarden 1999; Pauly 2010; Verberk and Bilton 2011; Cheung et al. 2013; Tu et al. 2018; Grüss et al. 2021). Regarding temperature and dissolved oxygen concentration, we recommend that future research compares the temperature-size response between taxonomic groups, as well as the interactive effect between temperature and dissolved oxygen concentration on determining the maximum length of marine ectotherms. For example, those species that are more vulnerable to low oxygen conditions may experience a stronger negative temperature-size response (Rubalcaba et al. 2020).

The maximum body lengths analysed in the current study approximate adult body sizes for all study species (Table 1). Overall, fishing pressure may truncate the size and/or age distribution of fished populations, and conversely, reductions in fishing pressure relative to historical levels could see the increase of maximum body lengths of targeted populations (Worm et al. 2009). Yet, considering the lack of any trend observed in the pseudo-*Z* values, we assume that fishing pressure was unlikely to confound the predictions of maximum length for the study species that are fished within the area (Supplementary Table 1). Nonetheless, the interaction of further ocean warming and fishing pressure may affect the maximum body length of targeted populations (Tu et al. 2018). Therefore, we recommend that the future studies that will utilise our modelling framework to investigate the relationship between maximum length, temperature and dissolved oxygen concentration also consider fishing pressure (e.g. trawl footprint).

In conclusion, by predicting the maximum length of various species across Norwegian waters, our results confirm our hypothesis that the largest species experience the strongest negative temperature-size responses. Furthermore, we have observed limitations to the maximum body length of several species within the coldest extent of their observed temperature range. These results support the temperature-size mechanism as described by the GOLT, and offer evidence to revive the cold denaturation hypothesis as a mechanism that limits the maximum body size of marine ectotherms at very low temperatures.

Acknowledgements We would like to thank very much Daniel Pauly for his advice and communication within the present study, as well as the two reviewers for their comments which have dramatically improved our manuscript.

Author contribution All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Charles P. Lavin, Cesc Gordó-Vilaseca, Fabrice Stephenson and Arnaud Grüss. The first draft of the manuscript was written by Charles P. Lavin and all authors contributed to writing of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by Nord University

Data availability Species' length data analysed during the current study are available on GitHub at https://github.com/charles-patrick-lavin/Norway-maximum-length-EBFI-2022-.git.

Code availability The code used for analysis in the current study is available on GitHub at https://github.com/charles-patrick-lavin/Norway-maximum-length-EBFI-2022-.git. Code for specific functions is available upon request.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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Paper II: Lavin, C. P., Gordó-Vilaseca, C., Stephenson, F., Shi, Z., Costello, M. J. (2022). Warmer temperature decreases the maximum length of six species of marine fishes, crustacean, and squid in New Zealand. Environmental Biology of Fishes, 105: 1431-1446. https://doi.org/10.1007/s10641-022-01251-7

Environ Biol Fish
https://doi.org/10.1007/s10641-022-01251-7

Warmer temperature decreases the maximum length of six species of marine fishes, crustacean, and squid in New Zealand

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Received: 14 July 2021 / Accepted: 30 March 2022

Abstract As global oceans continue to warm and deoxygenate, it is expected that marine ectotherms will reduce in body size resulting from the interactive effects of temperature and dissolved oxygen availability. A temperature-size response describes how wild populations of ectothermic species grow faster and reach a smaller size within warmer temperatures. While temperature-size responses are well observed in marine ectotherms, the mechanisms underpinning such a reduction in body size remain debated. Here, we analyse the relative influence of temperature, dissolved oxygen concentration, and geographic location (which encompasses multiple latent variables), on the maximum body length of four fish, one crustacean, and one squid species, which inhabit shallow to deep sea (1000 m) New Zealand waters across a temperature gradient of 1.5 to 18 °C. We found that all study species displayed a temperature-size response, with the strongest response exhibited by the largest species, hoki (*Macruronus novaezelandiae*). We also found that temperature was more important than dissolved oxygen concentration in determining maximum body length, as dissolved oxygen levels were at or near saturation in the study area. Our results suggest that larger-bodied species may experience the strongest temperature-size responses, and support expectations from the gill-oxygen limitation theory (GOLT) and the oxygen and capacity limited thermal tolerance (OCLTT) concept that increases in oxygen demand may be size- and temperature-dependent, thus driving a reduction in maximum body length of marine ectotherms with warming.

Keywords Temperature-size response · Water-breathing ectotherms · Maximum body length · Gill-oxygen limitation theory (GOLT) · The Oxygen- and Capacity Limited Thermal Tolerance (OCLTT) · Generalised additive models (GAMs)

Introduction

As the majority of marine animals are water-breathing ectotherms, temperature and dissolved oxygen concentration in sea water represent key environmental variables that influence their fitness and geographic distribution (Pauly 2010; Ern 2019). Indeed,

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10641-022-01251-7.

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temperature and oxygen may impact the distribution of marine organisms more so than the availability of food resources (Kramer 1987; Pauly 2021). In turn, if global oceans continue to warm and deoxygenate (e.g., Schmidtko et al. 2017; Breitburg et al. 2018; Bindoff et al. 2019; Laufkötter et al. 2020), water-breathing ectotherms may experience deleterious physiological effects associated with thermal stress and hypoxia (Pörtner 2001, 2002). In general, the response of marine water-breathing ectotherms to warming and deoxygenation consists of shifting their distribution to areas with more suitable environmental conditions (Deutsch et al. 2015; Poloczanska et al. 2016). Increasingly, it is also suggested that a response to warming and deoxygenation is the reduction of body size (Gardner et al. 2011).

Ocean-warming-induced changes in body size are predicted to impact water-breathing ectotherms globally (Cheung et al. 2013). Changes in body size can result from the complex interaction of temperature and dissolved oxygen as warming-induced increases in oxygen demands may not be met by an increase in available dissolved oxygen supply (Pörtner 2001; Pörtner and Knust 2007; Pauly 2010, 2021). While reductions in body size have been widely observed for aquatic ectotherms (Daufresne et al. 2009), the mechanisms behind this response remain debated (Lefevre et al. 2017; Pauly 2021).

The temperature-size rule (TSR) describes how ectothermic species grow faster and mature at a smaller size when reared at warmer temperatures (Atkinson 1994). The TSR refers to the plasticity of individuals throughout ontogeny, and thus can display differing affects to both size at maturity and maximum asymptotic size (Hoefnagel et al. 2018; Verberk et al. 2021). In wild populations, clines in body size across latitudinal gradients, including temperature and dissolved oxygen concentrations, can resemble the body-size responses observed at different laboratory rearing temperatures (Horne et al. 2015), referred to in the present study as a temperature-size response. While temperature-size responses are widely observed, several explanations aim to resolve the mechanisms behind the interaction of environment and growth (Deutsch et al. 2015; Pörtner et al. 2017; Clarke et al. 2021; Pauly 2021; Verberk et al. 2021).

A temperature-size response may depend on the species body size (Rubalcaba et al. 2020), sensitivity to changes in temperature or dissolved oxygen concentration (Forster et al. 2011; Hoefnagel and Verberk 2015), life history (Weber et al. 2015; Audzijonyte et al. 2020), geography (Deutsch et al. 2020; Clarke et al. 2021), environmental niche (Rypel 2014), feeding strategy and behaviour (van Rijn et al. 2017), and physiology (Atkinson et al. 2006). In order to elucidate further the mechanisms behind a temperature-size response, it is useful to compare the degree to which responses differ between species, rather than testing if a species displays a response at all (Verberk et al. 2021).

In the present study, we compare the strength of the temperature-size response of species of fishes, crustacean, and squid in New Zealand waters. Our study relies on generalised additive models (GAMs) fitted to trawl research data. The four fish species included in this study are hoki, *Macruronus novaezelandiae* Hector 1871, Australasian snapper, *Pagrus auratus* Forster 1801, southern blue whiting, *Micromesistius australis* Norman 1937, and orange roughy, *Hoplostethus atlanticus* Collett 1889, while the two invertebrate species are New Zealand arrow squid, *Nototodarus sloanii* Gray 1849, and New Zealand scampi, *Metanephrops challengeri* Balss 1914. Hereafter, the species are called hoki, snapper, blue whiting, orange roughy, arrow squid, and scampi. Species nomenclature follows the World Register of Marine Species (Horton et al. 2021).

The inclusion of two invertebrate species in the present study enabled the comparison of variable temperature-size responses between taxonomic groups, which has traditionally been based on studies of fishes (Pauly 2021). Further, as the bulk of research focuses on body size at maturation and warming, we investigated the influence of temperature and dissolved oxygen concentration on maximum body length, as the mechanisms between these responses may be different (Hoefnagel et al. 2018). Moreover, considering the complex interaction of temperature and dissolved oxygen within a temperature-size response, we assessed the relative importance of model covariates in order to parse between temperature, dissolved oxygen concentration and geographic location (representing other, latent environmental variables) in determining maximum body length of the study species. Doing so may reveal the relative influence of temperature and oxygen in eliciting a temperature-size response in water-breathing ectotherms. Overall, results from related research have found that a negative temperature-size response (e.g., smaller in warmer temperatures) was strongest in larger or more active species (Forster et al. 2012; van Rijn et al. 2017); therefore, we hypothesise that larger study species will exhibit a relatively stronger temperature-size response than smaller species.

Methods

Study area

Our study area was the exclusive economic zone (EEZ) of New Zealand, which spans latitudes 30 to 55°S (Fig. 1). The region is characterised by the influence of several fronts, which result in a broad temperature gradient, as summer sea surface temperatures reach over 21 °C in the north and 13 °C in the south, while winter sea surface temperatures can be as low as 5 °C in the north and 2 °C in the south (Garner 1969). From the north north-west, the Tasman Front and the Subtropical Front direct warm water across both islands and most of the EEZ, while colder and more nutrient-rich water is brought by the Subantarctic Front from the south (Leathwick et al. 2006a) (Fig. 1).

Trawl surveys

The length data employed in analyses were derived from bottom trawl research surveys carried out between 1979 and 2021 (NIWA 2014; SWPRON 2017). These surveys cover the continental shelf surrounding New Zealand, as well as the extensive submarine plateaus throughout the area (Leathwick et al. 2006a). In order to minimise variation between gear and sampling techniques, data were filtered to only include samples gathered by bottom trawl from trawling events that were conducted over a maximum of 3.5 nautical miles. Since the objective of the long-term bottom trawl research surveys is to assess changes in fished stocks, the geographical distribution of sampling effort is biased towards the most productive areas, including the Chatham Rise, the Campbell

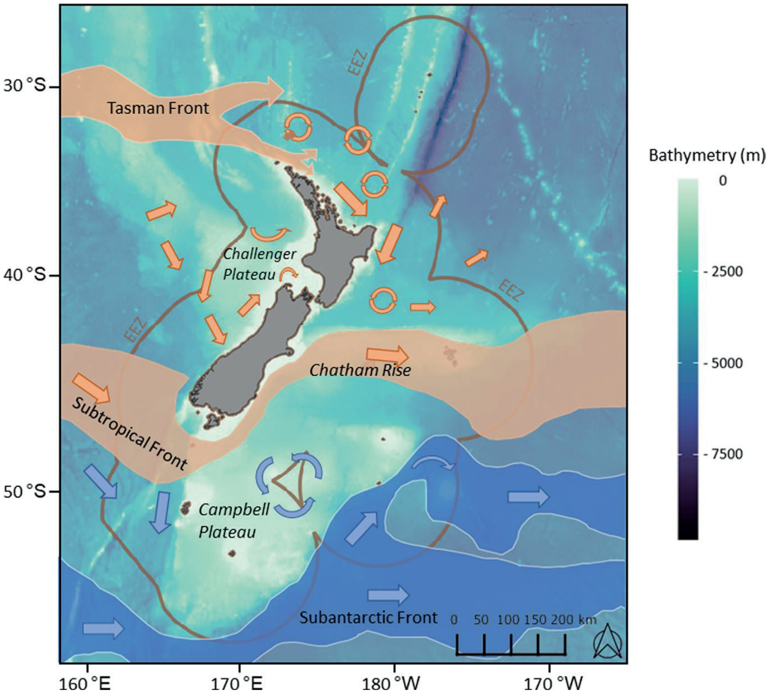


Fig. 1 Map of the study area, indicating notable areas mentioned in the text, plus bathymetry, cold (violet arrows), and warm (ochre arrows) ocean currents, fronts (brown and violet shade), and the Exclusive Economic Zone (EEZ) of New Zealand (red line). This figure has been modified from Stephenson et al. (2018), and was created using QGIS (QGIS 2022)

Plateau, and the Challenger Plateau (Figs. 1 and 2; Francis et al. 2002).

Study species

From all species present in the bottom trawl research survey database ($n = 253$), we selected the six most abundant fish and invertebrate species in terms of the number of individuals and frequency of encounter per sampling event. Hoki is a relatively long-lived, bentho-pelagic fish that is most abundant between 200–800 m depth (Papa et al. 2021). Snapper is a coastal fish species found around rocky reef ecosystems at depths down to 200 m, but is most commonly encountered between 10–50 m (Papa et al. 2021). Blue whiting is a mesopelagic fish found along the outer shelf and slope of New Zealand waters, between 130–800 m depth (Niklitschek et al. 2010). Orange roughy is a slow-growing, long-lived, bathypelagic fish that is found along continental slope margins, seamounts and ridges, between 700–1500 m depth (Papa et al. 2021). Arrow squid is a large pelagic squid that can be found as deep as 600 m depth, although it is primarily found shallower than 300 m (Jackson et al. 2000). Lastly, scampi burrows in soft sediments around the continental shelf and slope between 140–500 m depth (Smith 1999; Yaldwyn and Webber 2011). In the present dataset, the mean depth of species recorded ranged from 58 m (snapper) to 947 m (orange roughy) (Fig. 3a), mean temperatures from 4 °C (orange roughy) to 16 °C (snapper) (Fig. 3b), and mean dissolved oxygen concentrations ranged from 6 mg/L (orange roughy) to 8 mg/L (blue whiting) (Fig. 3c).

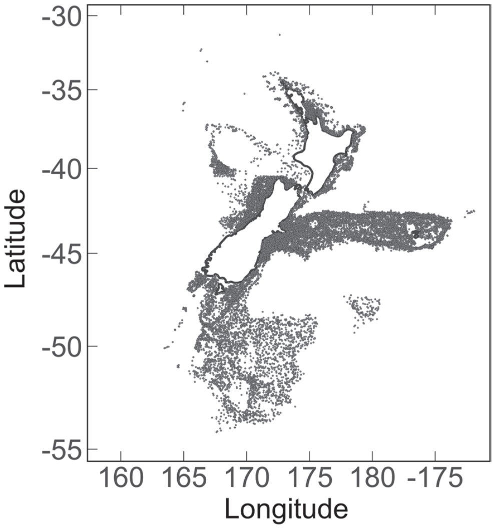


Fig. 2 Location of all trawling events included in the trawl research survey database between 1979 and 2021 in New Zealand waters (NIWA 2014; SWPRON 2017). This figure was created using QGIS (QGIS 2022)

Data and initial exploratory analyses

The total number of length observations for all six study species in the trawl research survey database was 22,661. We defined the maximum length for each species' record as the 95th quantile value of length measurements (cm) taken at each sampling station (i.e., trawling event). All fish species are reported as standard length (SL), arrow squid as mantle length (ML), and scampi as carapace length (CL) (Fig. 3d). Hoki standard lengths were converted from total length (Kloser et al. 2011), snapper from fork length (Ferrell and Sumpton 1997), and blue whiting from fork length (Cohen et al. 1990) using reported length-length linear relationships. Body length was considered the most robust response variable to estimate maximum body size, rather than weight. Related to feeding, energy storage, or reproduction, weight in marine ectotherms is known to fluctuate seasonally (Craig et al. 2000; Mello and Rose 2005), as well, length–weight relationships vary between species based on body shape and other physiological factors (Jisr et al. 2018).

We identified the Gamma distribution as the best distribution model for maximum length data using diagnostics from the *fitdistrplus* package (Delignette-Muller and Dutang 2015) in R (Team R Development Core 2021). Other information gathered from the bottom trawl research survey database included latitude and longitude, expressed in Universal Transverse Mercator (UTM) coordinates (i.e., eastings and northings) in the models, as well as mean depth (m) of trawl. Data for mean temperature and dissolved oxygen concentration at maximum depth layer were extracted from the online database Bio-Oracle (Assis et al. 2018) and associated with the latitude and longitude of samples. These data layers are produced using monthly averages of climate data from 2000 to 2014 (Assis et al. 2018). Dissolved oxygen concentration

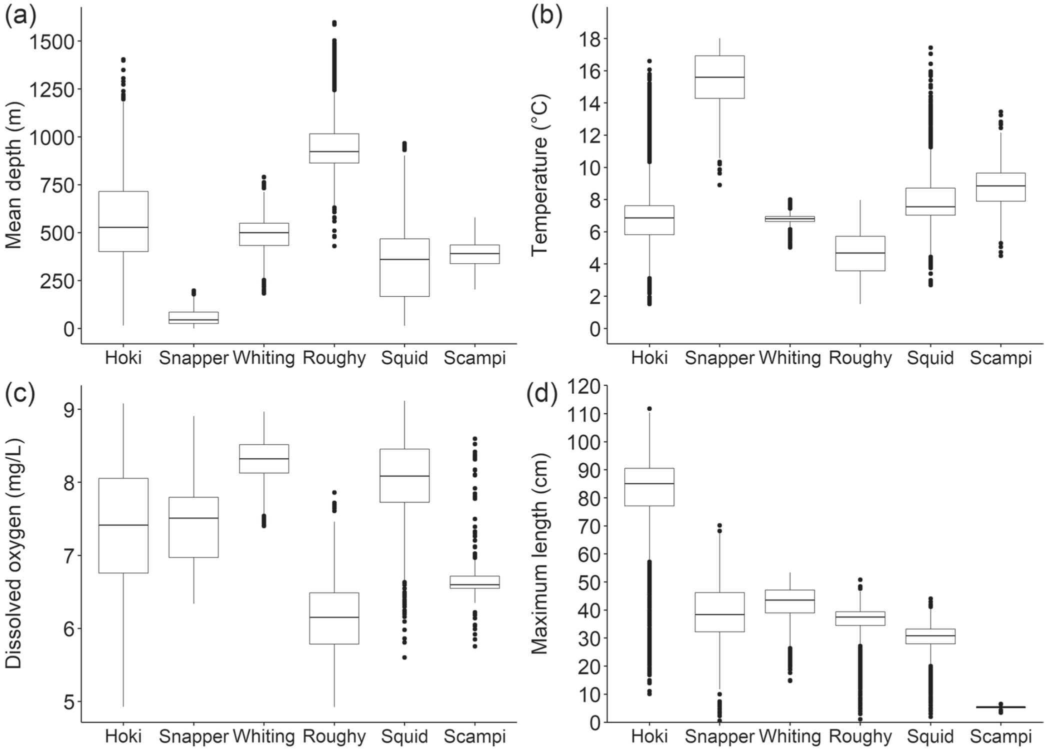
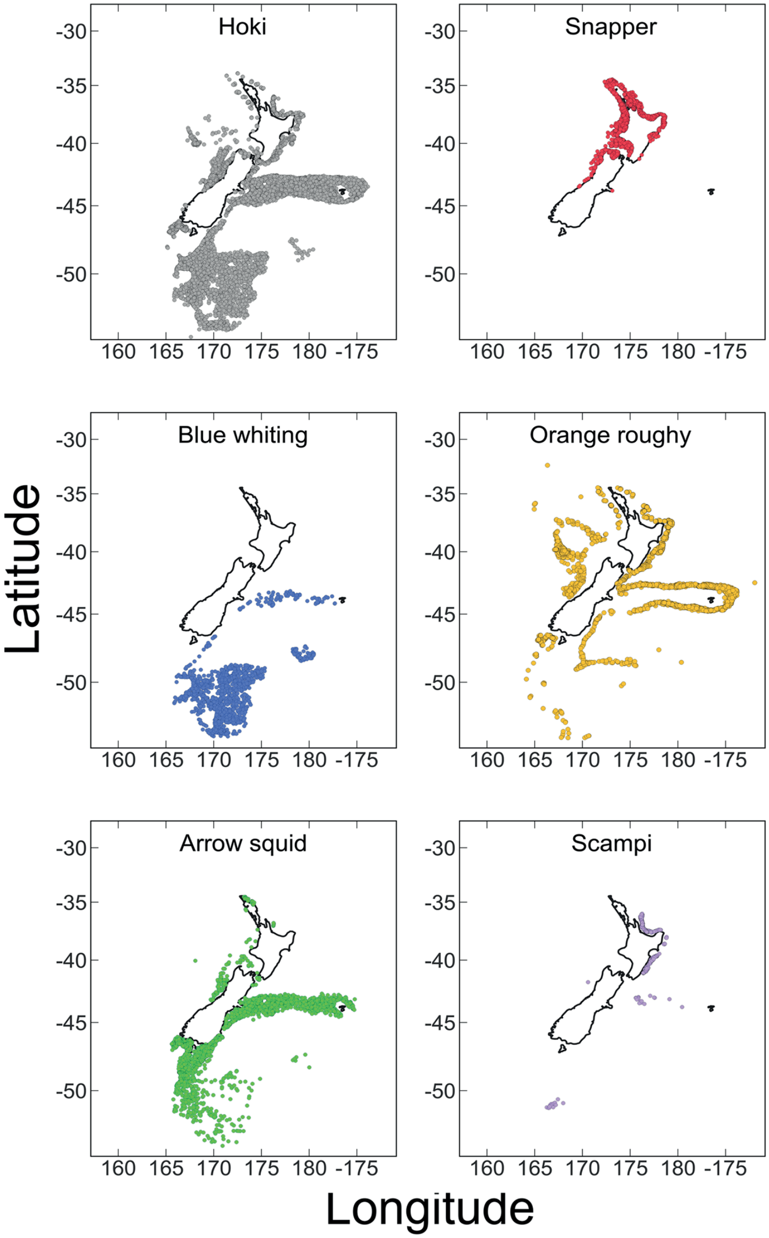


Fig. 3 Boxplot summary of sampling and environmental information, including the interquartile range, minimum and maximum values (lines), plus outliers (dots, 1.5 times the interquartile range from quartiles), for hoki, snapper, blue whiting, orange roughy, arrow squid and scampi. Summary information includes **a** mean depth (m), **b** temperature at maximum depth (°C) from Bio-Oracle, **c** dissolved oxygen concentration at maximum depth (mg/L) from Bio-Oracle, and **d** maximum length (cm) records (NIWA 2014; SWPRON 2017; Assis et al. 2018). This figure was created using R Studio (Team R Development Core 2021)

data from Bio-Oracle were converted from mols/m^{-3} to mg/L in line with unit conversions provided by the International Council for the Exploration of the Sea (ICES n.d.). In situ temperature was recorded during trawling events, but long-term mean temperature and dissolved oxygen concentration derived from Bio-Oracle are likely to better reflect prevailing climatology, and were, therefore, considered to be more relevant for our analyses.

Before model fitting, we explored the distribution of the response variable (maximum length) and explanatory covariates to identify potential outliers and subsequently removed them (Zuur et al. 2010). Following this data trimming, the total number of observations for the six study species was reduced from 22,661 to 22,631 (Fig. 4). We then explored the range of maximum length (cm), depth (m), and environmental covariates of the study species, as well as the relationship between environmental covariates and location. Thereafter, we evaluated the degree of collinearity between temperature, dissolved oxygen concentration, depth, eastings, and northings for each species (Supplementary Fig. 1). A Pearson's correlation coefficient greater than 0.7 in absolute value was considered indicative of collinearity (Leathwick et al. 2006b; Dormann et al. 2013). This collinearity analysis was warranted as GAMs (and other regression methods) are sensitive to correlated continuous covariate variables (Guisan et al. 2002; Dormann et al. 2013). For comparison

Fig. 4 Observed distribution of the data used in the present study for the six study species, including hoki ($n=9420$), snapper ($n=1673$), blue whiting ($n=1308$), orange roughy ($n=6763$), arrow squid ($n=2912$), and scampi ($n=555$) (NIWA 2014; SWPRON 2017). Each record indicates a trawl sample station, where the 95th quantile length measurement was extracted. This figure was created using QGIS (QGIS 2022)



purposes, depth was omitted from GAMs as it was found to be collinear with temperature and dissolved oxygen concentration for hoki and snapper respectively (Supplementary Fig. 1). This allowed the same full factorial model for all species to be undertaken, whilst preserving the model form that incorporates these key environmental variables central to our hypotheses. Moreover, we expect variation in depth to be contained within the effect of geographic location as a model covariate.

Model fitting and evaluation

We utilised GAMs to investigate the influence of temperature and dissolved oxygen concentration on the species' maximum lengths. A tensor product smooth between eastings and northings (the effect of geographic position) was included to serve as a proxy for latent environmental covariates that were otherwise not included in the model (e.g., depth) and account for broad-scale spatial autocorrelation in the length data (Wood 2006; Grüss et al. 2016, 2018a, 2021).

To facilitate equivalent comparisons between species, we initially fitted the same "full" Gamma GAM to maximum length data for each species using the "gam" function from the *mgcv* package in the R environment (Wood 2006; Team R Development Core 2021) following the equation,

$$g(L) = te(X, Y) + s(\text{Temperature}) + s(\text{Oxygen}) \qquad (1)$$

where L is maximum length of the species under consideration, g is the log-link function between maximum length and each term on the right side of the equation, $te(X,Y)$ is the tensor product smooth between eastings and northings, and s is the thin plate regression spline with shrinkage (bs = "ts" specified in the smooth function of "gam" within the *mgcv* library) fitted to temperature and dissolved oxygen concentration (Grüss et al. 2018a). Each thin plate regression spline was limited to four degrees of freedom ($k = 4$) to prevent overfitting and to preserve the interpretability of GAM results (Mannocci et al. 2017; Grüss et al. 2018a; Weijerman et al. 2019).

After running all GAMs using the same form ("full model"; Eq. 1) for all species, collinear or non-significant covariates were removed, including oxygen for snapper and arrow squid (non-significant), and northings for scampi (collinear with oxygen); then, models were re-run. We refer to the re-run models as the "final models." The adjusted final models were compared to full models via Akaike's information criterion (AIC) via the "logLik" function of the *mgcv* package in R (Wood 2006; Team R Development Core 2021). When running the final models, an extra penalty was applied to temperature and dissolved oxygen concentration as their smoothing parameter approached zero, which allowed for the complete removal of temperature or dissolved oxygen concentration from the model when its smoothing was equal to zero (Marra and Wood 2011; Grüss et al. 2014). Ultimately, using the results from final GAMs, we predicted the maximum length of each study species in light of its observed temperature range.

In order to acknowledge the potential effects of fishing pressure on reducing the maximum lengths of our study species, all final models were re-run twice, using records split into two periods based on their collection dates. These periods include a "past" fishing period (1979–1998) and a "recent" fishing period (1999–2021). Here, we assume that the past fishing period, and fishing effort preceding this period ("early" commercial fishing), were more likely to remove the largest individuals from stocks. In turn, we assume that there will no longer be a strong effect of fishing reflected in the predicted maximum body length of species across their temperature range within the recent period relative to the previous period. These assumptions are based on the observation that fished stocks are able to recover in maximum length following a reduction in exploitation rate (Worm et al. 2009).

An evaluation procedure similar to the leave group out cross validation (LGOCV) procedure was employed to validate full and final GAMs (Kuhn and Johnson 2013; Grüss et al. 2016) using two performance metrics: (1) the adjusted coefficient of determination (adjusted R^2), which is indicative of the proportion of the variance in maximum length explained by GAMs (Grüss et al. 2018b), and Spearman's rank correlation coefficients (Spearman's rho's) between the predicted and observed maximum length values. Briefly, our evaluation procedure for each model consisted of (1) splitting randomly the dataset of interest into a training dataset, which receives 70% of the data, and a test dataset, which receives 30% of the data; (2) repeating this ten times so that 10 training datasets and 10 test datasets are generated; (3) fitting a model to each of the 10 training datasets; and (4) performing an evaluation of the 10 fitted models with the test datasets using performance metrics (adjusted R^2 and Spearman's rho's in our case) (Grüss et al. 2016, 2020; Egerton et al. 2021). We considered that a given model passed the evaluation test if the median adjusted R^2 across all 10 replicates were greater than 0.1 (Legendre and Legendre 1998; Grüss et al. 2016) and if the median Spearman's rho's across the 10 replicates was significantly different from zero (Grüss et al. 2014, 2021; Weijerman et al. 2019; Egerton et al. 2021).

In order to estimate the relative importance of temperature and dissolved oxygen concentration in our final GAMs, we followed the same approach as Grüss et al. (2016). For each species, this approach compares the predictions of the final model with the predictions of models after random permutation of the values of a given predictor (temperature, dissolved oxygen concentration, eastings, or northings) within the complete dataset fed into the GAM ("random GAMs") (Thuiller et al. 2012; Grüss et al. 2016). Thereafter, the index of relative importance of the predictors (temperature, dissolved oxygen concentration, eastings, or northings) in explaining maximum length is obtained as one minus the Pearson's correlation coefficient between the predictions of the final model and the predictions from the random models (Grüss et al. 2016; Dove et al. 2020; Bolser et al. 2020).

Table 1 Observed and reported maximum length (cm) for hoki (standard length, SL), snapper (SL), blue whiting (SL), orange roughy (SL), arrow squid (mantle length, ML), and scampi (carapace length, CL). Reported maximum lengths: 1. Cohen et al. 1990 2. Randall et al. 1998, 3. Thomsen 1998, 4. Roper et al. 1984, 5. Cryer et al. 2005. Note: for comparison purposes, the reported maximum lengths for hoki, snapper, and blue whiting were converted to SL using published length-length linear relationships (see methods)

Species	Observed maximum length (cm)	Reported maximum length (cm)
Hoki	111.7 SL	112.3[1]
Snapper	70.1 SL	101.9[2]
Blue whiting	53.4 SL	84.6[1]
Orange roughy	50.8 SL	59.9[3]
Arrow squid	44 ML	42.0[4]
Scampi	6.5 CL	6.0[5]

Results

The length data employed in our models were found to be representative of those observed for the study species, including adult size classes, for all species (Table 1). The temperature data employed in models were found to represent a portion of the reported temperature ranges of species (Supplementary Table 1). Across the study area, there was a north to south latitudinal gradient of temperature and dissolved oxygen concentrations from approximately 19 °C and 7.5 mg/L to 7.5 °C and 9.5 mg/L. In deeper water layers, these gradients were still evident, although with higher variability (18 °C and 4.9 mg/L to 1.5 °C and 9 mg/L; Supplementary Fig. 2).

Temperature was found to have a significant effect on the maximum length of all six study species, while dissolved oxygen was found to be significant for three species: hoki, blue whiting, and orange roughy (Table 2). Following removal of collinear or non-significant covariates, the final GAMs for snapper, arrow squid and scampi differed from their original full models, while the final models for hoki, blue whiting, and orange roughy were identical to the original full models. Overall, the adjusted final models for snapper, arrow squid, and scampi provided little to no

Table 2 Results for the full generalised additive models (GAMs) of all study species. Models express maximum length as a function of temperature, dissolved oxygen concentration, and an interaction term (tensor product smooth) between eastings and northings (Eq. 1)

		Temperature			Dissolved oxygen concentration			Interaction between eastings and northings			
Species	n	*edf*	*F*	*p*	*edf*	*F*	*p*	*edf*	*F*	*p*	Adj. R^2
Hoki	9420	2.98	1378.92	< 0.001	2.82	32.59	< 0.001	21.47	74.75	< 0.001	0.46
Snapper	1673	1.10	9.90	< 0.001	< 0.001	0	0.76	11.59	18.96	< 0.001	0.28
Blue whiting	1308	1.85	4.49	< 0.001	2.83	21.46	< 0.001	15.11	14.53	< 0.001	0.22
Orange roughy	6763	2.67	34.98	< 0.001	2.82	23.02	< 0.001	18.34	35.13	< 0.001	0.13
Arrow squid	2912	2.60	16.97	< 0.001	0.05	0.02	0.24	14.64	34.94	< 0.001	0.20
Scampi	555	1.52	28.89	< 0.001	0.40	0.23	0.10	11.35	6.48	< 0.001	0.27

improvements to the performance of GAMs, as was confirmed by AIC comparison (Table 3), but the final model for scampi passed the evaluation tests while its original full model did not. Further, dissolved oxygen concentration was significant for New Zealand scampi following removal of northings as they were collinear with oxygen (Table 3). Thus, dissolved oxygen concentration was significant for four species within final models. As such, all final GAMs passed the evaluation tests, with the median adjusted R^2 values ranging between 0.104 (orange roughy) and 0.44 (hoki), while median Spearman's rho values ranged from 0.29 (arrow squid) to 0.55 (hoki) (Supplementary Fig. 3).

The species differed in their thermal ranges and temperature-size responses, but all showed decreasing maximum length with temperature (Fig. 5). Temperature was generally a more important covariate than dissolved oxygen concentration in explaining maximum length in the final models, while eastings and northings were the most important covariates for all species except for hoki and scampi (Fig. 6). Finally, the predicted maximum lengths across the past fishing period (1979–1998) and those from the

Table 3 Results for the final generalised additive models (GAMs) for snapper, arrow squid, and scampi; final GAMs result from the removal of collinear or non-significant covariates from the full GAMs (given by Eq. 1). Also listed is the Akaike's information criterion (AIC) for final and full GAMs. Note that the final GAM for scampi included the smooth effect of eastings instead of an interaction term between eastings and northings, as northings were found to be collinear with dissolved oxygen concentration and were, therefore, removed from the scampi GAM

	Temperature			Dissolved oxygen concentration			Interaction between eastings and northings					
Species	*edf*	*F*	*p*	*edf*	*F*	*p*	*edf*	*F*	*p*	Adj. R^2	Final model AIC	Full model AIC
Snapper	1.12	10.03	<0.001				11.61	17.13	<0.001	0.27	−6228.72	−6228.72
Arrow squid	2.63	19.01	<0.001				14.57	35.52	<0.001	0.20	−8856.58	−8856.53
Scampi	1.53	32.45	<0.001	0.83	1.50	0.01	6.31	7.75	<0.001	0.25	−324.23	−313.04

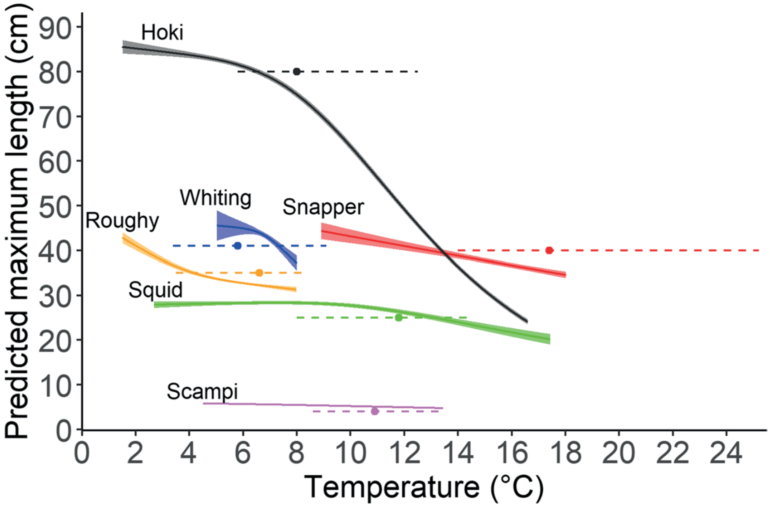


Fig. 5 Maximum lengths predicted by final GAMs (solid line) with 95% confidence interval bands, as a function of temperature (°C) for hoki, snapper, blue whiting, orange roughy, arrow squid, and scampi. The dashed lines of matching colour represent the reported preferred temperature range for each species, including mean preferred temperature (point), as reported by FishBase (for fishes) (Froese & Pauly 2021; www.fishbase.org) and SeaLifeBase (for invertebrates) (Palomares & Pauly 2021; www.sealifebase.org). This figure was created using R Studio (Team R Development Core 2021)

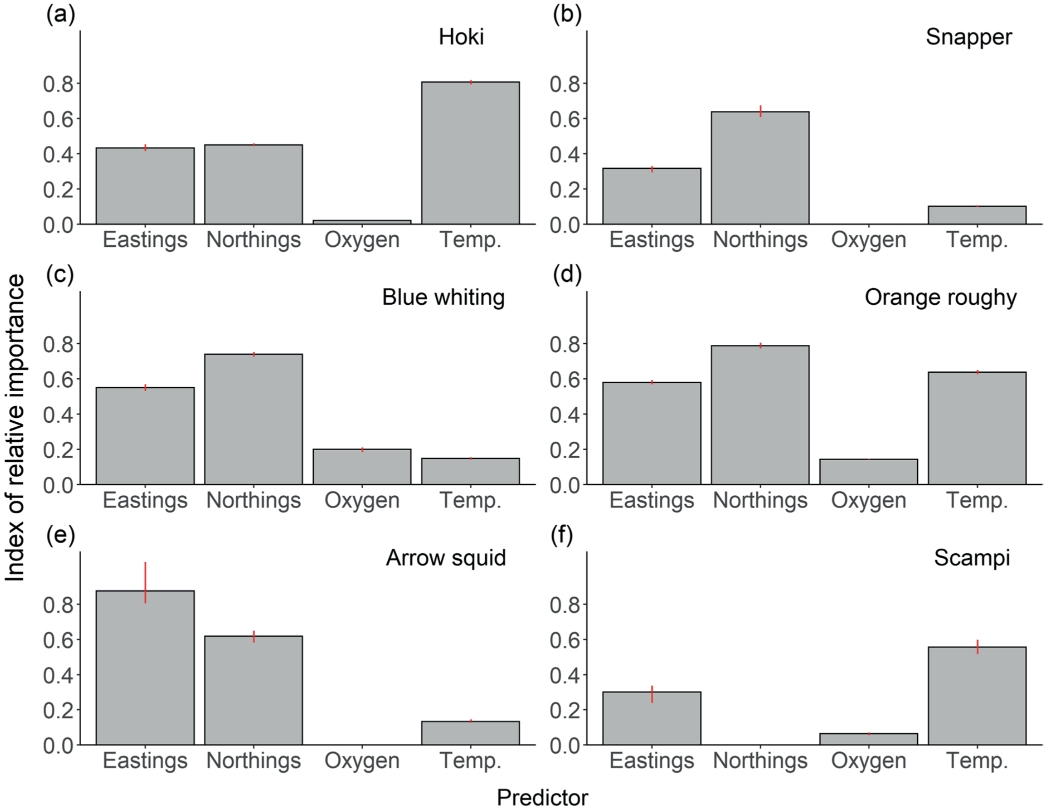


Fig. 6 Estimated relative importance of eastings, northings, dissolved oxygen concentration, and temperature (with 95% confidence intervals), in explaining maximum length predicted by the generalised additive models of **a** hoki, **b** snapper, **c** blue whiting, **d** orange roughy, **e** arrow squid, and **f** scampi. See the main text for a description of the calculation of indices of relative importance. This figure was created using R Studio (Team R Development Core 2021)

recent period (1999–2021) generally displayed the same relationship between maximum body length and temperature, with hoki the only species predicted to be smaller across the warmer extent of its distribution within the recent time period (Supplementary Fig. 4).

Discussion

We found that the maximum body length of all six study species displayed an inverse relationship with temperature. The largest species, hoki, displayed the strongest temperature-size response, with maximum length predicted to decrease by approximately 72% (from 85.5 cm to 24.1 cm SL) across the sampled temperature range (Fig. 5). The predicted decrease in maximum body length was similar for the remaining species, ranging between 30% for arrow squid and 18% for blue whiting (Fig. 5). Overall, the strength of the temperature-size response for the study species was likely underestimated, as our data covered only part of the study species' known temperature and dissolved oxygen concentration ranges (Supplementary Table 1; Fig. 5). The two species with the widest observed temperature ranges, hoki and arrow squid, displayed the strongest reductions in maximum body length. Conversely, blue whiting maintained the narrowest observed temperature range, resulting in the smallest predicted reduction in maximum body length (Fig. 5).

Our results support our initial hypothesis that the largest species display the strongest temperature-size response. Despite a similar temperature range extent, hoki's relative reduction in maximum body length was two times stronger than that of arrow squid. Experimental results from Forster et al. (2012) found that the strength of a temperature-size response in water-breathing ectotherms increased with their maximum body lengths. Further, when investigating the temperature-size responses of 74 fish species across the Mediterranean Sea, van Rijn et al. (2017) concluded that active large species were those that displayed the largest reductions in maximum body size with temperature. While species' traits were not considered in the models developed in the present study, hoki is by far the largest of our study species. Species' traits, life histories and geographic variables may influence the strength of temperature-size responses, and, thus, should be considered in future models.

According to the gill-oxygen limitation theory (*GOLT*), marine ectotherms reach an asymptotic body size due to the limitations of gill surface area to body weight ratio, when the two-dimensional respiratory surface (gill) area is unable to provide sufficient oxygen required for the growth and function of three-dimensional bodies (Pauly 2010, 2021; Pauly and Cheung 2018). Therefore, one mechanism under the GOLT would see species reduce their maximum body length (i.e., limit growth) with increasing temperatures, in order to increase the gill surface area to body weight ratio and, thus, service temperature-dependent oxygen demands (Pauly and Cheung 2018). Another mechanism, the oxygen- and capacity-limited thermal tolerance (*OCLTT*) concept, states that species have upper thermal limits, whereby an animal's capacity to adequately supply oxygen to maintain performance diminishes as it approaches this limit (Pörtner 2001, 2002). According to the OCLTT, an animal's ability to supply oxygen does not scale sufficiently with body size relative to oxygen demand, whilst increasing temperatures and oxygen demand will compound oxygen limitation (Pörtner et al. 2017; Audzijonyte et al. 2019).

While we were unable to mechanistically investigate the variable temperature-size responses between species, our results suggest that large-bodied species' temperature- and size-dependent growth efficiencies were constrained under increasing temperatures (Pörtner 2001; Kozłowski et al. 2004; Pauly 2010; Verberk et al. 2011; Hoefnagel et al. 2018; Rubalcaba et al. 2020), as the assumed increases in oxygen demand (with temperature) were not met despite dissolved oxygen concentration being above known critical levels for marine organisms (Cook and Herbert 2012; Brennan et al. 2016; Shi et al. 2021).

We found that temperature was a more important covariate than oxygen for five of the six study species, with blue whiting the exception (Fig. 6). Across the study area, dissolved oxygen levels were at or near saturation (Supplementary Fig. 2). Therefore, limitations of available dissolved oxygen were unlikely to drive a temperature-size response in species. This conclusion adheres to the proposed mechanisms including the GOLT, and the OCLTT, in that relative reductions in maximum size (i.e., limited growth) are likely required in order to meet the oxygen demands brought about by temperature-induced increases in metabolic activity of water-breathing ectotherms (Pörtner and Peck 2010; Pauly 2021)**.** Furthermore, the inclusion of two invertebrate species in the present study allows for further generalisation of temperature-size responses in marine ectotherms, which has been primarily developed with regard to fishes (Pauly 2010, 2021). As crustaceans and cephalopods generally have a higher tolerance of hypoxia (Shi et al. 2021), future research should continue to compare temperature-size responses between taxonomic groups, and the interactive effect of temperature and dissolved oxygen concentration on the metabolic scope of water-breathing ectotherms. As such, it may be that species that are less tolerant of low oxygen levels may experience a stronger temperature-size response with warming, even if dissolved oxygen levels remain at or near saturation.

Unsurprisingly, the most important variable in explaining maximum body length in our models was generally geographic position (eastings and northings), as this represents latent ecological and environmental variables (Wood 2006; Grüss et al. 2016, 2018a, 2021; Bolser et al. 2020; Egerton et al. 2021). These variables could relate to variation in depth, the availability of suitable habitat, ecological competition, prey availability, size selective predation or mortality, and/or fishery effects (Connolly and Roughgarden 1999; Tu et al. 2018; Penn et al. 2018; Deutsch et al. 2020; Kulatska et al. 2021). These factors associated with a species' distribution may influence the temperature-size response. By including the interaction term between eastings and northings in our models, we were able to compare the importance of temperature and dissolved oxygen concentration in explaining maximum length relative to that of other, unmeasured variables.

It is important to note that all of the species included in the present study are targeted by fisheries in New Zealand waters. The present study uses only survey data, and we did not include fishing pressure in our models. Overall, the maximum body lengths of our study species may have been truncated, as fisheries preferentially target the largest individuals in a population, such that our ability to display the extent of a temperature-size relationship may be confounded by fishing pressure (Cheung et al. 2013; Tu et al. 2018). Yet, the maximum body length ranges for all of our study species approximate adult sizes (Table 1; Fig. 3d). Further, by comparing more recent survey data (1999–2021) to past survey data (1979–1998; Supplementary Fig. 4), we assume that the influence of fishing on removing large individuals from the population no longer influences the maximum length of species across our study area (i.e., beyond previous, higher intensity fishing era). Given that we found few differences in our predicted trends between time periods, we conclude that our results are not severely confounded by fishing effort in our study, but most likely due to the wide environmental and temporal gradient of the study.

In conclusion, our results support the hypothesis that larger-bodied aquatic ectotherms experience the strongest temperature-size responses. They also support expectations from the GOLT and OCLTT theories that increase in oxygen demand may be size- and temperature-dependent. Climate change has already resulted in measurable impacts on marine organisms and ecosystems. This includes the poleward shift in distribution of thousands of species as they track their thermal affinity (Chaudhary et al. 2021), to the increasing number and spatial coverage of marine areas experiencing episodic or chronic hypoxia throughout the last century (Limburg et al. 2020). The observed and projected changes to ocean temperature and dissolved oxygen concentration will likely tax the metabolic demands of water-breathing ectotherms across depths and latitudes (Oschlies 2021), but to varying degrees between species, size-classes or functional groups (Audzijonyte et al. 2020; Rubalcaba et al. 2020). Thus, our results extend the findings of previous studies proposing that larger-bodied species may experience the most significant temperature-size responses with future ocean warming.

Acknowledgements We would like to thank Arnaud Grüss, Daniel Pauly, Donna Dimarchopoulou, Richard O’Driscoll, and Owen Anderson for their help and/or advice at different stages of the present study, as well as journal editors and reviewers for their constructive comments throughout the review process. We thank Fisheries New Zealand for providing the species’ length data used in this analysis.

Author contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Charles P. Lavin, Cesc Gordó-Vilaseca, and Fabrice Stephenson. The first draft of the manuscript was written by Charles P. Lavin, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by Nord University. CPL, CGV, ZS, and MJC were supported by Nord University. FS was partially funded by National Institute of Water and Atmospheric Research (NIWA), Coasts and Oceans Research Programmes 5 (SCI 2021/22).

Data availability Species’ length data are available upon request to the Ministry for Primary Industries, New Zealand.

Code availability The code used for analysis in the current study is available on GitHub at https://github.com/charles-patrick-lavin/New-Zealand-maximum-length-EBFI-2022.git.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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Paper III: Lavin, C. P., Pauly, D., Dimarchopoulou, D., Liang, C., Costello, M. J. (2023). Fishery catch is affected by geographic expansion, fishing down food webs and climate change in Aotearoa, New Zealand. PeerJ, 11:e16070. https://doi.org/10.7717/peerj.16070

Fishery catch is affected by geographic expansion, fishing down food webs and climate change in Aotearoa, New Zealand

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ABSTRACT

Historical fishing effort has resulted, in many parts of the ocean, in increasing catches of smaller, lower trophic level species once larger higher trophic level species have been depleted. Concurrently, changes in the geographic distribution of marine species have been observed as species track their thermal affinity in line with ocean warming. However, geographic shifts in fisheries, including to deeper waters, may conceal the phenomenon of fishing down the food web and effects of climate warming on fish stocks. Fisheries-catch weighted metrics such as the Mean Trophic Level (MTL) and Mean Temperature of the Catch (MTC) are used to investigate these phenomena, although apparent trends of these metrics can be masked by the aforementioned geographic expansion and deepening of fisheries catch across large areas and time periods. We investigated instances of both fishing down trophic levels and climate-driven changes in the geographic distribution of fished species in New Zealand waters from 1950–2019, using the MTL and MTC. Thereafter, we corrected for the masking effect of the geographic expansion of fisheries within these indices by using the Fishing-in-Balance (FiB) index and the adapted Mean Trophic Level (aMTL) index. Our results document the offshore expansion of fisheries across the New Zealand Exclusive Economic Zone (EEZ) from 1950–2019, as well as the pervasiveness of fishing down within nearshore fishing stock assemblages. We also revealed the warming of the MTC for pelagic-associated fisheries, trends that were otherwise masked by the depth- and geographic expansion of New Zealand fisheries across the study period.

Subjects Aquaculture, Fisheries and Fish Science, Marine Biology
Keywords New Zealand, Fisheries, Ocean warming, Mean trophic level, Mean temperature of the catch, Fishing down marine food webs, Fishing-in-Balance index

INTRODUCTION

Shifts in marine species' geographic distribution with ocean warming are increasingly well documented (*Cheung, Watson & Pauly, 2013*; *Pinsky, Selden & Kitchel, 2020*;

Submitted 8 May 2023
Accepted 20 August 2023
Published 21 September 2023

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Academic editor
Alfonso Aguilar-Perera

Additional Information and Declarations can be found on page 23

DOI **10.7717/peerj.16070**

How to cite this article Lavin CP, Pauly D, Dimarchopoulou D, Liang C, Costello MJ. 2023. Fishery catch is affected by geographic expansion, fishing down food webs and climate change in Aotearoa, New Zealand. **PeerJ 11:e16070 DOI 10.7717/peerj.16070**

Chaudhary et al., 2021). Further shifts may alter community structure (García Molinos et al., 2016; Poloczanska et al., 2016), food web interactions (Tekwa, Watson & Pinsky, 2022), and fisheries catch (Cheung et al., 2010; Cheung, Watson & Pauly, 2013). Ocean warming can also impact the fitness of marine ectotherms, particularly large, active predatory species (Forster, Hirst & Atkinson, 2012; van Rijn et al., 2017; Lavin et al., 2022). Concurrently, historical fishing pressure has resulted in deleterious impacts on marine communities and ecosystems (Howarth et al., 2014). Prolonged, intensive fishing results in reductions of population biomass (Worm et al., 2009), as well as the maximum size of harvested species, as fisheries preferentially target the largest species and individuals within a population (Jackson et al., 2001) due to their higher market price (Tsikliras & Polymeros, 2014). Once the largest species, often of the highest trophic levels and long-lived, have been depleted, fishing pressure has been observed to shift to smaller, shorter-lived species of lower trophic levels—termed 'fishing down marine food webs' (Pauly et al., 1998; Pauly & Palomares, 2005). The occurrence of fishing down can have deleterious consequences to the transfer of energy through marine food webs, thus impacting marine biodiversity and ecosystem function though the depletion of high trophic level predators (Pauly et al., 1998; Baum & Worm, 2009; Boyce et al., 2015). Thus, both fishing impacts and climate-change related outcomes to marine populations should be considered in concert in order to inform fisheries and conservation management (Lynam et al., 2017).

One method to infer changes in the geographic distribution of marine fish and invertebrate populations includes the Mean Temperature of the Catch index (MTC, Cheung, Watson & Pauly, 2013). This index represents the catch-weighted mean temperature preference of species in the fisheries catch in an area, and has been applied to a variety of marine ecosystems globally (see Leitão et al., 2018 and Dimarchopoulou et al., 2021b and references therein). Overall, an increase in MTC over time indicates an ocean-warming induced increase in the proportion of species of warmer thermal affinity relatively to those of colder thermal affinity recorded in the catch (Cheung, Watson & Pauly, 2013; Tsikliras & Stergiou, 2014; Liang, Xian & Pauly, 2018). Similarly, one method to infer the occurrence of fishing down includes the Mean Trophic Level index (MTL, also known as the Marine Trophic Index) (Pauly et al., 1998; Pauly & Watson, 2005), *i.e*., the catch-weighted mean trophic level of fisheries within an area. Also utilized extensively (see Liang & Pauly, 2017, and references therein), a decrease in MTL indicates the transition of catch from large, long-lived, higher trophic level species to smaller, short-lived, lower trophic level species, as a result of overexploitation and thus fishing down (Pauly et al., 1998). Conversely, increasing trends in MTL indicate the increasing catch of higher trophic level species, as has been observed during the historical expansion of fisheries (Leitão, 2015).

Yet, for both of these well-utilized indices, apparent trends in catch-weighted values can be masked by a variety of factors. One masking factor includes the 'skipper effect,' in that skippers will continuously and preferentially target certain species, usually of high trophic levels, within a multispecies catch (Pinnegar et al., 2002; Liang & Pauly, 2020). This may also arise when catch quotas prevent shifting catch from one species to another. Another masking effect includes the taxonomic resolution at which analyses are performed, as trends in catch-weighted values may not be apparent when analyzed at coarse taxonomic resolutions (*Pauly & Palomares, 2005*; *Liang & Pauly, 2017*). Lastly, when such indices are calculated across large geographic areas (*e.g.*, exclusive economic zones, EEZs) and time scales, the gradual geographic and depth expansion of fisheries to include new habitats and species (*i.e.*, deep-water species of colder thermal affinity, or higher trophic level species) can mask trends of fishing down or MTC warming (*Bhathal & Pauly, 2008*; *Kleisner, Mansour & Pauly, 2014*).

Fisheries in Aotearoa (henceforth referred to as New Zealand) waters have experienced a significant transformation within the 20th century through technological proliferation and government incentives. Following the establishment of their EEZ in 1978, New Zealand became the first country to implement a Quota Management System (QMS) in 1986, in recognition of declining stocks of important coastal fisheries (*Johnson & Haworth, 2004*). Since then, New Zealand has prioritized the transition towards ecosystem-based fisheries management in line with the targets outlined in the Convention on Biological Diversity (*Cryer, Mace & Sullivan, 2016*; *Durante, Beentjes & Wing, 2020*). Overall, the transition towards an ecosystem-based, multi-species management scheme requires in-depth understanding of the historical effects of fisheries (*Pauly, 1995*), as well as those effects presented by trends in ocean warming (*Free et al., 2019*) in order to inform management under multiple and interacting stressors in a changing ocean.

To investigate the historical impacts of fisheries expansion in New Zealand waters, *Durante, Beentjes & Wing (2020)* calculated the MTL using New Zealand fisheries catch data from 1930–2014. The authors found a positive trend in MTL coinciding with a period of geographic expansion of the fisheries, followed by a negative trend in MTL, thus displaying signals of fishing down. Yet, the authors did not correct the MTL trend for the masking effects of geographic expansion of fisheries across the time series (*Durante, Beentjes & Wing, 2020*). In the present study, we do so by applying the Fishing-in-Balance (FiB) index (*Pauly et al., 1998*; *Pauly, Christensen & Walters, 2000*; *Pauly & Watson, 2005*; *Bhathal & Pauly, 2008*), and the adapted Mean Trophic Level index (aMTL, also known as the region-based Marine Trophic Index, *Kleisner, Mansour & Pauly, 2014*; *Liang & Pauly, 2017*) to New Zealand fisheries catch data from 1950–2019. By accounting for the geographic expansion of fisheries in New Zealand waters, we investigated whether fishing down occurred concurrent with fishery expansion. Further, by separating catch data between species' habitat and gear used, we also investigated whether signals of warming in the MTC were apparent across the study period in line with trends in ocean warming.

MATERIALS AND METHODS

The study area was the New Zealand EEZ (Fig. 1). To quantify the rate of ocean warming, we extracted Sea Surface Temperature Anomaly (SSTA) data from NOAA's Kaplan Extended SST V2 database (*Kaplan et al., 1998*). At 5° latitude by 5° longitude resolution, monthly values were averaged across years from 1950–2019. These SSTA data are relative to temperatures during the period from 1951–1980 (*Kaplan et al., 1998*), and SSTA was chosen as temperature anomalies are considered to present a more consistent indicator of climate-change related ocean warming across large areas relative to absolute Sea Surface

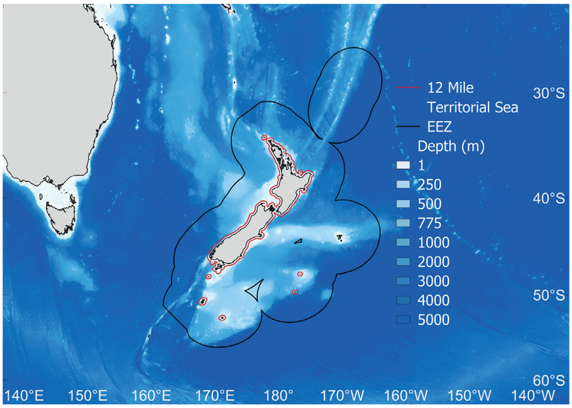

Figure 1 The study area. Fisheries catch data were extracted for the New Zealand Exclusive Economic Zone (EEZ, black line). Also shown is the 12 nautical mile Territorial Sea border (red), as well as depth (m). Map source credit: GADM. Full-size DOI: 10.7717/peerj.16070/fig-1

Temperatures (*Tsikliras & Stergiou, 2014*; *Tsikliras et al., 2015*; *Dimarchopoulou et al., 2021b*). We then performed simple linear regression and segmented linear regression of SSTA on time (Years). Segmented linear regressions were performed in order to test whether trends were better explained by multiple regression lines (*Dimarchopoulou et al., 2021b*), as indicated by the presence of a significant breakpoint (*Muggeo, 2016*). Breakpoints were identified using the *segmented* package in R (*Muggeo, 2008*; *Team R Development Core, 2022*), whereby a non-zero difference in slope on either side of the breakpoint was tested using a p-score test from the *segmented* package (*Muggeo, 2008*).

Primary analyses were completed using fisheries catch data for the New Zealand EEZ extracted from the Sea Around Us database (*Pauly, Zeller & Palomares, 2020*). This database includes reconstructed catches of officially reported statistics from the Food and Agriculture Organization of the United Nations (FAO), plus estimated unreported catch, discards and by-catch from all fishing sectors operating in the area, from 1950–2019 (*Simmons et al., 2016*; *Pauly, Zeller & Palomares, 2020*, Fig. 2A). In order to complete MTC and MTL analyses, species traits', including mean preferred temperature and trophic level were gathered from FishBase (*Froese & Pauly, 2021*) *via* the *rfishbase* package in R (*Boettiger, Lang & Wainwright, 2012*; *Team R Development Core, 2022*). The mean preferred temperature (°C) for each species is based on a compilation of modelled species' distributions informed by occurrence data, and also adjusted for appropriate depth ranges (*Cheung, Watson & Pauly, 2013*; *Froese & Pauly, 2021*). A species' trophic level (TL) is estimated *via* diet information in FishBase (*Froese & Pauly, 2021*), and is represented by a discrete value usually between 2.0 and 5.0 (*Liang & Pauly, 2017*). The trophic level represents the number of trophic links a species maintains from primary production (TL = 1), *i.e.*, herbivorous fish have a trophic level = 2, piscivorous fish have a trophic

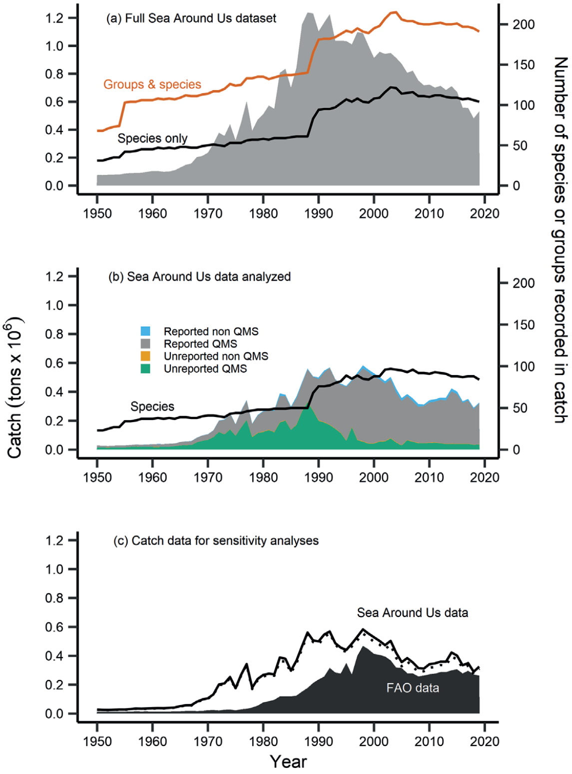

Figure 2 **Fisheries catch data analyzed.** Fisheries catch (solid areas, tons × 10^6, left axis) including (A) the full catch dataset extracted from the Sea Around Us database, (B) the restricted Sea Around Us catch dataset that was analyzed in the present study, and (C) catch data analyzed in sensitivity analyses. The full dataset (A) included catch information at the species level (black line, right axis) and also for groups at higher taxonomic resolution (red line, right axis), while the catch data analyzed (B) was restricted to the species level (black line, right axis), composed of catch from species both included and not included in New Zealand's Quota Management System (QMS), from reported and non-reported sources (*i.e.*, reconstructed). (C) FAO catch data of $n = 42$ species analyzed in sensitivity analyses (black area, left axis), compared to the analyzed Sea Around Us catch data ($n = 102$, solid black line, left axis), and the further reduced Sea Around Us catch data ($n = 42$, dashed line, left axis) also contained in sensitivity analyses.

Full-size DOI: 10.7717/peerj.16070/fig-2

level = 3, and so on, with the maximum trophic levels in marine systems exceeding a value of five (*i.e.*, top predators) (*Stergiou & Karpouzi, 2002*; *Dimarchopoulou et al., 2021a*; *Eddy et al., 2021*).

The number of species with available trait information contained in the catch data was 110. After identifying these species, we compared their Sea Around Us catch trends to officially reported statistics from the FAO (*FAO, 2020*). For several taxonomically-similar species, or species that were historically mislabeled, catch statistics have been reported under a group code or at higher taxonomic resolution (ex. *Allocyttus niger* and *Pseudocyttus maculatus* combined as 'Oreo species,' *Simmons et al., 2016*). In the present study, we restricted analyses to the species-level, as applications of the MTC and MTL at higher taxonomic coarseness have been demonstrated to mask the effects of fishing down trophic levels (*Pauly & Palomares, 2005*; *Liang & Pauly, 2017*). We therefore removed from analyses species that were previously reported in higher taxonomic groups ($n = 7$), were without available trait information ($n = 19$), and records labelled at a higher or an unidentified taxonomic resolution ($n = 103$) (Table S1).

Following this data treatment 102 species were included in analyses (Table 1). They represented 80% of the total species recorded and 48% of the total raw catch data contained in New Zealand's Sea Around Us dataset (Fig. 2B). The majority of this analyzed catch data is of QMS species (96% of data), 67% of which is reported catch and 29% of which is unreported catch (*i.e.*, reconstructed, Fig. 2B). We retained several 'rare' species (of low catch quantities) or bycatch-related species in our analyses. This was done as fish community composition can change over time, such as due to climate warming and shifts in species' geographic distribution to new areas (*Gordó-Vilaseca et al., 2023*). We then calculated the MTC of New Zealand's catch using the formula:

$$MTC_{yr} = \frac{\sum_i^n T_i C_{i,\,yr}}{\sum_i^n C_{i,\,yr}} \tag{1}$$

where T_i is the preferred mean temperature of species i, $C_{i,yr}$ is the catch of species i in year yr, and n equals to total number of species recorded (*Cheung, Watson & Pauly, 2013*). We then calculated the MTL of the same catch data, using the formula:

$$MTL_{yr} = \frac{\sum_i^m TL_i Y_{ik}}{\sum_i^m Y_{ik}} \tag{2}$$

where TL_i is the trophic level of species i, Y_{ik} is the catch of species i in year k, and m is the number of species recorded (*Pauly et al., 1998*). For both MTC and MTL trends, we calculated simple and segmented linear regressions of each index on time (Year) across the study period. In order to relate MTC trends to trends in ocean warming, we computed Kendall's τ correlation between MTC and SSTA using the *stats* package in R (*Team R Development Core, 2022*); with the null hypothesis that there is no correlation between the two variables. Thereafter, in order to first address the geographic expansion of fisheries and thus the masking of MTC and MTL trends, we calculated the Fishing-in-Balance (FiB) index. The FiB index is designed to identify surplus fisheries catch (*i.e.*, from adjacent areas or stock assemblages) based on assumptions of energy transfer between trophic levels. The FiB was calculated using the formula:

$$FiB_k = log_{10}\left[Y_k\left(\frac{1}{TE}\right)^{MTL_k}\right] - log_{10}\left[Y_0\left(\frac{1}{TE}\right)^{MTL_0}\right] \tag{3}$$

Table 1 **Study species information.**

Species	Milieu	Mean pref. temp. (°C)	Trophic level	Mean annual catch (tons) ± SE	(log) Fisheries catch slope across time series	QMS species	FAO species
Beryx decadactylus	Bathydemersal	11.2	4.13	0.3 ± 0.3	0.50	Yes	
Capromimus abbreviatus	Bathydemersal	13	3.45	11.9 ± 3.4	0.13		
Centriscops humerosus	Bathydemersal	7.3	3.57	26.7 ± 3.1	0.08		
Centrophorus squamosus	Bathydemersal	7	4.47	8.8 ± 1.7	0.09		
Centroselachus crepidater	Bathydemersal	7.8	4.16	1.7 ± 0.7	0.03		
Cyttus traversi	Bathydemersal	8.3	3.93	505.4 ± 36.2	0.03	Yes	Yes
Dalatias licha	Bathydemersal	5.3	4.23	315.7 ± 23.6	−0.03		
Diastobranchus capensis	Bathydemersal	7	4.50	6.0 ± 2.0	0.20		
Epigonus telescopus	Bathydemersal	8.9	3.59	2,106.4 ± 243.9	−0.02	Yes	Yes
Eptatretus cirrhatus	Bathydemersal	12.3	5.00	166.4 ± 48.8	0.33		
Genypterus blacodes	Bathydemersal	7.2	4.18	10,674.8 ± 1,074.9	0.07	Yes	Yes
Harriotta raleighana	Bathydemersal	5.2	3.55	78.3 ± 10.9	0.20		
Hydrolagus novaezealandiae	Bathydemersal	10.8	3.52	1,831.3 ± 117.4	0.04	Yes	Yes
Macrourus carinatus	Bathydemersal	6.7	3.70	19.1 ± 6.4	0.61		
Pentaceros decacanthus	Bathydemersal	11.4	3.42	1.7 ± 1.4	0.13		
Plagiogeneion rubiginosum	Bathydemersal	14.2	3.40	449.1 ± 36.1	0.04	Yes	Yes
Tripterophycis gilchristi	Bathydemersal	10.3	3.03	6.5 ± 6.5	−0.10		
Alepisaurus ferox	Bathypelagic	8.9	4.03	0.2 ± NA	NA		
Antimora rostrata	Bathypelagic	2.9	3.58	5.4 ± 1.0	0.14		
Centrolophus niger	Bathypelagic	7	3.92	46.4 ± 5.9	0.02		
Halargyreus johnsonii	Bathypelagic	3.7	3.38	4.3 ± 1.0	0.09		
Hoplostethus atlanticus	Bathypelagic	6.6	4.25	30,114.6 ± 3,679.4	−0.03	Yes	Yes
Lampris guttatus	Bathypelagic	12.1	4.22	133.6 ± 19.8	0.01	Yes	Yes
Lepidorhynchus denticulatus	Bathypelagic	9.2	3.67	3,054.8 ± 337.5	0.09		
Magnisudis prionosa	Bathypelagic	6.8	4.50	0.7 ± 0.3	−0.08		
Mora moro	Bathypelagic	5	3.75	840.5 ± 79.3	0.06	Yes	Yes
Neocyttus rhomboidalis	Bathypelagic	7.8	3.58	121.9 ± 9.5	0.13	Yes	Yes
Paratrachichthys trailli	Bathypelagic	13.3	3.50	7.8 ± 1.1	0.13		
Trachipterus trachypterus	Bathypelagic	13.5	2.88	46.3 ± 10.9	−0.08		

(Continued)

Table 1 (continued)

Species	Milieu	Mean pref. temp. (°C)	Trophic level	Mean annual catch (tons) ± SE	(log) Fisheries catch slope across time series	QMS species	FAO species
Beryx splendens	Benthopelagic	9.2	4.27	2,652.6 ± 109.4	0.02	Yes	
Centroberyx affinis	Benthopelagic	15.9	3.81	80.2 ± 8.1	0.02	Yes	Yes
Galeocerdo cuvier	Benthopelagic	26.4	4.56	0.3 ± 0.1	0.06		
Galeorhinus galeus	Benthopelagic	12.3	4.34	2,364.7 ± 203.4	0.04	Yes	Yes
Girella tricuspidata	Benthopelagic	16.6	2.09	77.4 ± 4.3	0.01	Yes	Yes
Hyperoglyphe antarctica	Benthopelagic	7.5	3.95	1,708.8 ± 161.9	0.11	Yes	Yes
Lepidocybium flavobrunneum	Benthopelagic	9.9	4.34	31.3 ± 4.9	0.10		
Lepidopus caudatus	Benthopelagic	12.1	3.82	2,474.8 ± 186.0	0.07	Yes	Yes
Macruronus novaezelandiae	Benthopelagic	8	4.53	115,806.5 ± 12,799.5	0.13	Yes	Yes
Merluccius australis	Benthopelagic	8.6	4.28	7,110.5 ± 854.3	0.16	Yes	Yes
Micromesistius australis	Benthopelagic	5.8	3.66	38,893.7 ± 3,142.3	−0.01	Yes	Yes
Mugil cephalus	Benthopelagic	23.2	2.48	773.6 ± 40.5	0.02	Yes	
Odontaspis ferox	Benthopelagic	17.3	4.16	0.3 ± 0.1	−0.23		
Ruvettus pretiosus	Benthopelagic	12.9	4.18	41.0 ± 6.6	−0.05		
Scorpis violacea	Benthopelagic	17.9	3.44	19.2 ± 7.3	0.02		
Seriola lalandi	Benthopelagic	14.9	4.16	913.9 ± 27.5	0.01	Yes	
Seriolella brama	Benthopelagic	14.4	3.73	2,505.5 ± 240.8	0.06	Yes	Yes
Seriolella punctata	Benthopelagic	13	3.53	10,172.2 ± 397.1	0.00	Yes	Yes
Sphoeroides pachygaster	Benthopelagic	19.4	4.20	0.5 ± 0.2	−0.28		
Squalus acanthias	Benthopelagic	9.9	4.37	6,191.8 ± 422.2	0.04	Yes	Yes
Squalus mitsukurii	Benthopelagic	14.1	4.37	76.1 ± 6.6	−0.04		
Thyrsites atun	Benthopelagic	11.2	3.63	23,589.3 ± 1,776.3	0.07	Yes	Yes
Zenopsis nebulosa	Benthopelagic	14.5	4.39	77.4 ± 9.9	0.16		
Aldrichetta forsteri	Demersal	17.1	2.51	39.8 ± 2.7	−0.01	Yes	Yes
Argentina elongata	Demersal	11.2	3.40	70.4 ± 9.7	0.03		
Callorhinchus milii	Demersal	15.2	3.60	1,428.2 ± 63.3	0.00	Yes	Yes
Chelidonichthys kumu	Demersal	19.3	3.68	4,532.9 ± 144.8	0.00	Yes	Yes
Cyttus novaezealandiae	Demersal	13.1	3.67	242.3 ± 47.4	−0.02		
Genyagnus monopterygius	Demersal	16.6	4.50	42.1 ± 2.0	−0.02		
Kathetostoma giganteum	Demersal	11.2	4.21	1,950.4 ± 189.4	0.09	Yes	Yes
Meuschenia scaber	Demersal	15.1	2.83	383.3 ± 41.1	0.07	Yes	
Mustelus lenticulatus	Demersal	13.7	3.51	2,051.1 ± 148.3	0.01	Yes	Yes
Notopogon lilliei	Demersal	11.7	3.52	6.3 ± 2.0	−0.04		

Table 1 (continued)

Species	Milieu	Mean pref. temp. (°C)	Trophic level	Mean annual catch (tons) ± SE	(log) Fisheries catch slope across time series	QMS species	FAO species
Notorynchus cepedianus	Demersal	14.2	4.68	9.1 ± 1.7	0.06		
Parapercis colias	Demersal	12.6	3.89	2,452.1 ± 97.0	0.00	Yes	Yes
Paristiopterus labiosus	Demersal	15.9	3.33	18.1 ± 4.5	−0.03		
Pseudophycis bachus	Demersal	11	3.93	7,111.3 ± 742.2	0.04	Yes	Yes
Arripis trutta	Pelagic-neritic	17.4	4.07	987.5 ± 19.7	0.00	Yes	Yes
Brama brama	Pelagic-neritic	11.8	4.08	364.6 ± 44.9	0.00	Yes	Yes
Coryphaena hippurus	Pelagic-neritic	27.4	4.21	82.5 ± 13.4	0.02		
Sardinops sagax	Pelagic-neritic	17.9	2.84	318.8 ± 54.9	0.08	Yes	Yes
Scomber australasicus	Pelagic-neritic	18.7	4.23	8,201.8 ± 790.6	0.09	Yes	Yes
Seriolella caerulea	Pelagic-neritic	9.2	3.20	1,582.1 ± 151.3	0.06	Yes	Yes
Allothunnus fallai	Pelagic-oceanic	18.4	3.70	16.3 ± 2.6	0.07		
Alopias superciliosus	Pelagic-oceanic	27.1	4.46	0.5 ± 0.2	−0.34		
Alopias vulpinus	Pelagic-oceanic	23.3	4.50	18.9 ± 1.8	0.03		
Carcharhinus longimanus	Pelagic-oceanic	26.8	4.16	9.9 ± 1.0	−0.03		
Carcharodon carcharias	Pelagic-oceanic	18.1	4.53	1.1 ± 0.4	0.02		
Cetorhinus maximus	Pelagic-oceanic	11.4	3.20	960.1 ± 92.6	0.05		
Dissostichus eleginoides	Pelagic-oceanic	4.5	4.49	11.7 ± 2.5	0.23	Yes	
Istiompax indica	Pelagic-oceanic	25.4	4.50	1.5 ± 0.2	0.02		
Istiophorus platypterus	Pelagic-oceanic	25.6	4.50	0.1 ± 0.1	−0.26		
Isurus oxyrinchus	Pelagic-oceanic	17.4	4.52	54.7 ± 7.6	0.04	Yes	Yes
Kajikia audax	Pelagic-oceanic	25.9	4.50	95.9 ± 11.5	0.02		
Katsuwonus pelamis	Pelagic-oceanic	26.2	4.43	4,919.9 ± 644.4	0.09		
Lamna nasus	Pelagic-oceanic	7.8	4.46	80.0 ± 11.6	0.08	Yes	Yes
Makaira Mazara	Pelagic-oceanic	19.3	4.46	0.1 ± 0.0	−0.01		
Mola mola	Pelagic-oceanic	10.2	3.28	1.2 ± 0.2	0.00		

(Continued)

Table 1 (continued)

Species	Milieu	Mean pref. temp. (°C)	Trophic level	Mean annual catch (tons) ± SE	(log) Fisheries catch slope across time series	QMS species	FAO species
Prionace glauca	Pelagic-oceanic	14.8	4.35	886.8 ± 76.4	0.07	Yes	Yes
Regalecus glesne	Pelagic-oceanic	23.9	3.20	9.5 ± 4.6	−0.33		
Sphyrna zygaena	Pelagic-oceanic	26.5	4.94	12.2 ± 0.6	0.00		
Tetrapturus angustirostris	Pelagic-oceanic	26.2	4.50	0.2 ± 0.2	0.01		
Thunnus alalunga	Pelagic-oceanic	15.1	4.30	1,729.0 ± 147.0	0.03		
Thunnus albacares	Pelagic-oceanic	26.7	4.41	197.4 ± 29.2	−0.03	Yes	Yes
Thunnus maccoyii	Pelagic-oceanic	5	3.93	1,959.7 ± 318.8	0.00	Yes	Yes
Thunnus obesus	Pelagic-oceanic	26.6	4.42	384.9 ± 35.9	0.01	Yes	Yes
Thunnus orientalis	Pelagic-oceanic	24.3	4.50	107.8 ± 14.4	0.07	Yes	Yes
Xiphias gladius	Pelagic-oceanic	22.7	4.53	532.3 ± 49.0	0.05	Yes	Yes
Carcharhinus brachyurus	Reef-associated	17.4	4.33	23.1 ± 2.0	−0.03		
Carcharhinus falciformis	Reef-associated	26.7	4.35	70.2 ± 7.1	−0.01		
Carcharhinus galapagensis	Reef-associated	23.8	4.23	0.1 ± NA	NA		
Latris lineata	Reef-associated	14.9	3.41	45.3 ± 5.4	0.05	Yes	
Pagrus auratus	Reef-associated	17.4	3.59	16,163.0 ± 930.4	−0.01	Yes	Yes

Note:
Species trait information included in mean temperature of the catch (MTC) and mean trophic level (MTL) calculations (n = 102). Included are the species milieu (*i.e.*, habitat association), species' mean preferred temperature (°C), trophic level, mean annual catch (tons ± SE), and the slope of (log) catch values across the time series. Species' milieu classifications were gathered directly from the FishBase online database (*Froese & Pauly, 2021*), while mean temperature preference and trophic level were accessed *via* the *rfishbase* package in R (*Boettiger, Lang & Wainwright, 2012*; *Team R Development Core, 2022*). Fisheries catch data were extracted for the New Zealand EEZ from the Sea Around Us (*Pauly, Zeller & Palomares, 2020*). We also list which species are included in New Zealand's Quota Management System (QMS), as well, which species are contained within the FAO dataset (n = 42) analyzed for sensitivity analyses (*FAO, 2020*). The same FAO species are also included within the reduced Sea Around Us dataset (n = 42) contained in further sensitivity analyses.

where Y is the catch and MTL is the mean trophic index value for year k, while Y_0 and MTL_0 are the catch and MTL value for the first year of data, and TE is the transfer efficiency between trophic levels (TE = 0.1), as estimated and assumed constant by *Pauly & Christensen (1995)* and used in *Bhathal & Pauly (2008)*. Under this assumption of trophic transfer efficiency, a decrease in TL of 1 should yield a 10-fold increase in catch, or conversely, an increase in TL of 1 should yield a 10-fold decrease in catch (*Kleisner, Mansour & Pauly, 2014*; *Liang & Pauly, 2017*). As such, fisheries are considered to be "fishing in balance" (FiB = 0) when a decline in MTL value corresponds to the expected increase in catch, or vice versa, in line with assumptions of constant TE (*Kleisner, Mansour & Pauly, 2014*). However, when catch increases more than what is expected from decreases in MTL (FiB > 0), this implies that excess catch came from adjacent stocks and thus indicates the geographic expansion of fisheries (*Kleisner, Mansour & Pauly, 2014*; *Liang & Pauly, 2017*; *Dimarchopoulou et al., 2021a*). We also applied linear and segmented regression to the trend of FiB across the study period (*Muggeo, 2008*).

In order to quantify the geographic expansion of fisheries across the time series, we then computed the adapted Mean Trophic Level (aMTL) in line with *Kleisner, Mansour & Pauly (2014)* and *Liang & Pauly (2017)*. The aMTL was developed under the assumption that geographic expansion occurs once a certain fished area or stock shows signs of depletion. Considering costs of fuel and equipment, it is assumed that most fishing activities are first concentrated within nearshore waters. Once the nearshore fisheries become overexploited, fishing effort then expands further away from shore and/or deeper (*Kleisner, Mansour & Pauly, 2014*; *Liang & Pauly, 2017*). Based on the FiB index (Eq. (3)), if fishing occurs "in balance", where FiB = 0, with initial catch Y_0 and MTL_0, catch Y_k of year k can be computed:

$$Y_k = Y_0 \times \left(\frac{1}{TE}\right)^{MTL_0 - MTL_k} \tag{4}$$

As such, if $Y_k > \; Y_0 \times \left(\frac{1}{TE}\right)^{MTL_0 - MTL_k}$, this indicates that a geographic expansion of the fisheries has occurred (*Liang & Pauly, 2017*), *i.e.*, accessing previously unexploited assemblage of fish stocks in adjacent areas, habitats or depths (*Kleisner, Mansour & Pauly, 2014*). Upon identification of an expansion, a 'node' marks the year of occurrence, after which new aMTL values can be calculated for those newly identified stock assemblages (*Kleisner, Mansour & Pauly, 2014*). This identification of expansion operates on two main assumptions: that fishing does not cease in the original stock assemblages, and that fishing in the original stock assemblage is in balance (*i.e.*, FiB = 0), or in decline (*Kleisner, Mansour & Pauly, 2014*).

Since the initial mean trophic level (MTL_0) in Eq. (4) may not be fully representative of all trophic levels present within the ecosystem, we corrected for this by assigning a range of possible trophic levels between the lowest TL (TL_{lower}) and highest TL (TL_{upper}) within the catch data (*Liang & Pauly, 2017*). Amongst J trophic levels, within the range [TL_{lower}, TL_{upper}], at each trophic level j, the catch potential pY_{kj} was calculated:

$$pY_{kj} = Y_0 \times \left(\frac{1}{TE}\right)^{TL_j - MTL_k} \tag{5}$$

while the corresponding maximum catch potential for year k is calculated:

$$pY_{kj} = \sum\nolimits_{j=1}^{J} \left(pY_{kj} \times \Pr(TL_j)\right) \tag{6}$$

with $\Pr(TL_j)$ equal to the probability that $MTL_0 = TL_j$ (*Liang & Pauly, 2017*). By calculating pY_{kj}, which is independent of MTL_0, we are able to estimate the maximum catch value that fisheries could achieve within a distinct stock assemblage, under the assumption of TE. When a reported catch $Y_k > pY_k$, this indicates a geographic expansion has occurred, whereby year k is assigned node n_r, and r indicates the newly identified stock assemblage (*Liang & Pauly, 2017*). For any year and stock assemblage that follows n_r, catch and aMTL was calculated amongst distinct assemblages, with the maximum number of assemblages computed = 3, in line with the assumptions and caveats presented by *Kleisner, Mansour & Pauly (2014)*. For a conceptual diagram of the workflow and calculations of the aMTL, see *Liang & Pauly (2017)*.

To unmask the potential effects of the geographic expansion of fisheries on the MTC, we separated the fisheries catch based on species' habitat classification (*i.e.*, milieu) and also by the fishing gear used in order to re-calculate MTC trends for each group and gear type (*Leitão et al., 2018*). Since the overall MTC trend can be masked by the dominance of few (deep, cold-water) species, we separated catch by habitat associations and gear used, in an attempt to reduce the overall effect of dominant species on possible MTC trends of warming within different sectors of New Zealand fisheries. Species' specific milieu identifications were done according to FishBase (*Froese & Pauly, 2021*, Table 1), while 23 distinct fishing gear classifications included in the catch data were aggregated into 12 general groups (Table S2). For the complete list of species caught by each gear type, see Table S3. We then calculate the MTC by gear, as the type of gear utilized will vary by the habitat exploited and thus determine the species composition of catch (*Leitão et al., 2018*). Similarly, we calculated MTC by milieu classification in order to group species based on similar environmental conditions and habitats utilized (*Stephenson et al., 2020*), and thus, distinguish between different habitats, geographic areas and species assemblages exploited throughout the period of fisheries expansion in the area. We also computed Kendall's τ correlation between MTC values for each gear and milieu group and SSTA as well as the "full" MTC trend calculated for all analyzed species ($n = 102$).

Sensitivity analyses were completed in order to address the validity of the calculated metrics using the reconstructed Sea Around Us catch dataset. First, we computed the MTC, MTL, FiB and aMTL metrics using officially reported catch data from the *FAO (2020)*. This dataset was composed of 42 species that were: both present in our calculations and also those of *Durante, Beentjes & Wing (2020)*, had available trait information, and whose catch was reported at the species level (Table 1, Fig. 2C). Since gear information was not available in the FAO metadata, we thereafter calculated MTC by species' milieu only. All species contained in this subset were QMS species, and represent 30% of the full catch data and 19% of all species/groups present in the FAO catch dataset. Second, we reduced the Sea Around Us dataset to those species contained in the FAO dataset ($n = 42$) and re-ran analyses. These 42 species represented 95% of the total analyzed Sea Around Us catch data (Fig. 2C).

RESULTS

Across the study area and period, SSTA displayed a weak positive trend, increasing 0.04 °C per decade from 1950–2019 (Fig. 3A), with no significant breakpoint detected from segmented regression. When calculating the MTC of fisheries catch data, a segmented

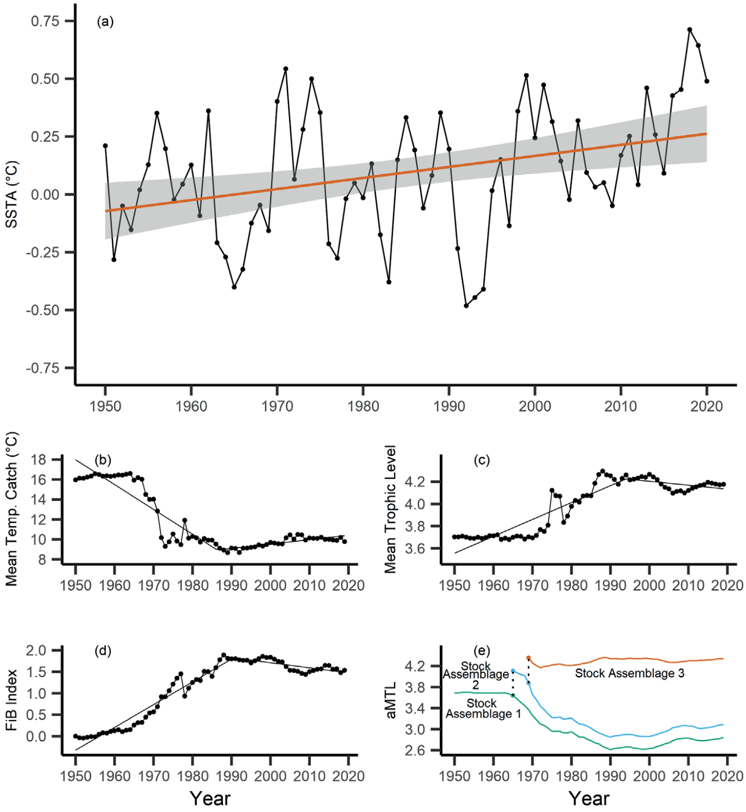

Figure 3 **Results of calculated indices.** Trends for the various indices calculated across the New Zealand Exclusive Economic Zone (EEZ) and for fisheries catch from 1950–2019, including: (A) sea surface temperature anomaly (SSTA, °C), and its linear regression slope (red) and 95% confidence interval (grey band) (regression slope equation: $y = -9.3 + 0.004x$, Adj. $R^2 = 0.11$, p-value = 0.002), (B) the mean temperature of the catch (MTC, °C), (C) the mean trophic level (MTL), and (D) the Fishing-in-Balance (FiB) index, including their segmented regression slopes. (E) Results from calculating the adapted Mean Trophic Level (aMTL), including the three identified stock assemblages (green, blue and red lines), as well as the years identified for node expansions (points) to include new stock assemblages (dashed lines).

Full-size DOI: 10.7717/peerj.16070/fig-3

regression identified a significant breakpoint at 1986–whereby the MTC decreased 2.49 °C per decade from 1950–1986, while the MTC increased 0.44 °C per decade thereafter, *i.e.*, from 1986–2019 (Table 2, Fig. 3B). Trends in MTL displayed a significant breakpoint at 1994, with the MTL increasing 0.15 per decade from 1950–1994, and decreasing from 1994–2019 (second slope = −0.03 per decade, Table 2, Fig. 3C). Results from the FiB index also reveal an overall positive trend, as the index increased 0.52 per decade until a detected

Table 2 Results from simple linear regression and segmented linear regression for analyses of New Zealand's fisheries catch data.

Index	Years	Decadal rate of change	Adj. R^2	*p*-value	Breakpoint ± SE
MTC	1950–2019	−1.14	0.62	<0.01	
	1950–1986	−2.49	0.88	<0.01	1986 ± 1.7
	1986–2019	0.44			
MTL	1950–2019	0.09	0.74	<0.01	
	1950–1994	0.15	0.86	<0.01	1994 ± 2.8
	1994–2019	−0.03			
FiB	1950–2019	0.29	0.74	<0.01	
	1950–1999	0.52	0.96	<0.01	1999 ± 1.9
	1999–2019	−0.11			

Note:

Results from simple linear regression and segmented linear regression for the Mean Temperature of the Catch (MTC, °C), the Mean Trophic Level (MTL), and the Fishing-in-Balance Index (FiB) for New Zealand fisheries catch data from 1950–2019. For each index is listed the time period to which the regression applies, the decadal rate of change of the given index, the Adjusted R^2 value, the *p*-value, as well as the year (±standard error SE) of a segmented regression breakpoint.

breakpoint in 1999, while the subsequent slope decreased 0.11 per decade from 1999–2019 (Table 2, Fig. 3D). Thus, with modest levels of ocean warming across the study area, the MTC decreased sharply from 1950–1986, and has since gradually increased, whilst both the MTL and FiB indices increased sharply until the 1990s, and thereafter decreased gradually.

When calculating the aMTL, three distinct stock assemblages were identified when correcting for the geographic expansion of fisheries across New Zealand's EEZ. In line with assumptions of the aMTL (*Kleisner, Mansour & Pauly, 2014*), the first stock assemblage includes the nearshore fisheries (Fig. 3E, green line), which maintained a stable aMTL from 1950–1964, thereafter decreasing until the 1990s. A second stock assemblage was identified in 1965 (Fig. 3E, blue line), indicating the first major geographic expansion of fisheries. In this case, fisheries started catching higher trophic level species compared to the initial nearshore assemblage, and aMTL also subsequently declined until the 1990s (Fig. 3E, blue line). The third stock assemblage was identified in 1969, which has since caught the highest trophic levels in New Zealand fisheries (aMTL values > 4) from 1969–2019 (Fig. 3E, red line).

Results from the aMTL confirmed the geographic expansion of New Zealand fisheries offshore throughout the study period. In turn, we separated fisheries catch data between species' milieu and between fishing gear groups to re-calculate MTC trends. Results reveal a general pattern of MTC cooling for both bottom-associated species and fishing gears, with few groups displaying little to no MTC trend across the study period (Tables 3, 4, Figs. 4, 5). We do not report results for fishing gear groups 'pots or traps', 'mixed gear', 'pelagic trawl' or 'pole and line' as there was insufficient data to produce linear regression trends. The MTC for benthopelagic and demersal species displays strong reductions until 1979 and 1995, respectively (Table 3, Figs. 4C, 4D), with similar negative trends for bottom trawl (breakpoint: 1987), gillnet (breakpoint: 1999), longline (breakpoint: 1969), small scale

Table 3 Regression and correlation results for the MTC between species milieu.

Milieu	Years	Decadal rate of change	Adj. R^2	p-value	Breakpoint ± SE	Kendall's τ corr. with SSTA (p-val)	Kendall's τ corr. with MTC (p-val)
Bathydemersal	1950–2019	0.14	0.78	<0.01		0.07 (p = 0.41)	−0.43 (p =< 0.01)
Bathypelagic	1975–2019	0.32	0.58	<0.01		0.35 (p =< 0.01)	0.14 (p = 0.17)
	1975–1980	3.14	0.85	<0.01	1980 ± 0.59		
	1980–2019	0.19					
Benthopelagic	1950–2019	−0.98	0.60	<0.01		−0.11 (p = 0.18)	0.70 (p =< 0.01)
	1950–1979	−2.54	0.84	<0.01	1979 ± 1.97		
	1979–2019	−0.01					
Demersal	1950–2019	−0.43	0.50	<0.01		−0.04 (p = 0.64)	0.57 (p =< 0.01)
	1950–1995	−0.82	0.73	<0.01	1995 ± 2.31		
	1995–2019	0.55					
Pelagic-neritic	1950–2019	−0.04	<0.01	0.30		0.01 (p = 0.86)	0.19 (p = 0.02)
	1950–1980	−0.39	0.22	<0.01	1980 ± 4.28		
	1980–2019	0.20					
Pelagic-oceanic	1950–2019	1.46	0.45	<0.01		0.12 (p = 0.13)	−0.17 (p = 0.04)
	1950–1965	−4.01	0.62	<0.01	1965 ± 2.39		
	1965–2019	2.24					
Reef-associated	1950–2019	<0.01	<0.01	0.58		0.03 (p = 0.74)	−0.33 (p =< 0.01)

Note:

Results from simple linear regression and segmented linear regression for the Mean Temperature of the Catch (MTC, °C) of New Zealand fisheries data, from 1950–2019, separated by species' milieu. Included is the time period to which the regression applies to, the decadal rate of change, the Adjusted R^2 value, the p-value, as well as the location of a segmented regression breakpoint (±standard error SE). Also listed is each MTC's Kendall's τ correlation value (and p-value) with Sea Surface Temperature Anomaly (SSTA) and the full Sea Around Us MTC trend.

(breakpoint: 1989) and unknown (breakpoint: 1979) fishing gear groups (Table 4, Fig. 5). Conversely, strong positive trends in MTC were observed for pelagic-oceanic species following 1965 (Table 3, Fig. 4F) and for purse seine fisheries (Fig. 5F) across the study period, as well as the 'other' fishing gear group after 1964 (Table 4, Fig. 5E). Overall, these results reflect the general trend of MTC cooling for bottom-associated species and fisheries, but also reveal warming MTC trends for pelagic and oceanic species across the study area.

Results from Kendall's τ correlation found only the bathypelagic MTC trend to be significantly positively correlated with SSTA trends (Table 3), while the rest of the milieu and fishing gear MTCs were not correlated, including the primary MTC trend. Correlations with the primary dataset (n = 102) MTC trend were strongest for those milieu and gears that had strong MTC reductions, including benthopelagic and demersal species, as well as bottom trawl and small-scale gears (Table 4). These results show that milieu- or gear-specific MTC trends were not strongly associated with low levels of ocean warming across New Zealand waters, while the primary MTC trend is correlated with bottom associated species- and fishing gear trends of MTC cooling.

Sensitivity analyses calculating all of the aforementioned metrics using FAO catch data (n = 42) and a reduced Sea Around Us dataset (n = 42) reveal similar results from the

Table 4 **Regression and correlation results for the MTC between fishing gear used.**

Fishing gear	Years	Decadal rate of change	Adj. R^2	p-value	Breakpoint ± SE	Kendall's τ corr. with SSTA (p-val)	Kendall's τ corr. with MTC (p-val)
Bottom trawl	1951–2019	−1.42	0.71	<0.01		−0.13 (p = 0.12)	0.75 (p =< 0.01)
	1951–1987	−2.87	0.92	<0.01	1987 ± 1.44		
	1987–2019	0.24					
Gillnet	1951–2019	−0.92	0.78	<0.01		−0.16 (p = 0.06)	0.49 (p =< 0.01)
	1951–1999	−1.19	0.84	<0.01	1999 ± 3.44		
	1999–2019	0.12					
Hand lines	1951–2019	−0.20	0.01	0.20		0.04 (p = 0.65)	0.32 (p =< 0.01)
Longline	1950–2019	−0.33	0.11	<0.01		0.02 (p = 0.80)	0.15 (p = 0.06)
	1950–1969	−3.05	0.51	<0.01	1969 ± 2.10		
	1969–2019	0.30					
Other	1955–2018	0.93	0.36	<0.01		0.04 (p = 0.63)	−0.15 (p = 0.09)
	1955–1964	8.49	0.58	<0.01	1964 ± 1.78		
	1964–2018	0.45					
Purse seine	1951–2019	0.86	0.12	<0.01		−0.02 (p = 0.80)	−0.01 (p = 0.95)
Small scale	1950–2019	−1.11	0.66	<0.01		−0.12 (p = 0.13)	0.84 (p =< 0.01)
	1950–1989	−2.17	0.87	<0.01	1989 ± 1.88		
	1989–2019	0.39					
Unknown	1951–2019	−0.64	0.26	<0.01		0.01 (p = 0.88)	0.49 (p =< 0.01)
	1951–1979	−3.07	0.81	<0.01	1979 ± 1.38		
	1979–2019	0.79					

Note:

Results from simple linear regression and segmented linear regression for the Mean Temperature of the Catch (MTC, °C) of New Zealand fisheries data, from 1950–2019, separated by fishing gear. Included is the time period to which the regression applies to, the decadal rate of change, the Adjusted R^2 value, the p-value, as well as the location of a segmented regression breakpoint (±standard error SE). Also listed is each MTC's Kendall's τ correlation value (and p-value) with Sea Surface Temperature Anomaly (SSTA) and the full Sea Around Us MTC trend.

primary Sea Around Us dataset (n = 102) analyzed (Tables S4, S5, Figs. S1–S4). This includes the identification of three stock assemblages *via* the aMTL, with the first two assemblages displaying fishing down trends, although the years of identified expansion into new stock assemblages are 6 and 8 years later, respectively, within the FAO dataset (Fig. S1D). Milieu- and gear-specific MTCs also reveal similar trends, with negative slopes in bottom-associated fisheries and species. For the pelagic-oceanic milieu MTC, FAO data displayed strong warming until 2009, thereafter decreasing (Fig. S2F), while the Sea Around Us data subset displayed a consistent positive slope (Fig. S4F). Although for purse seine fisheries, strong trends of MTC warming were not present within the Sea Around Us subset (Fig. S4L). Overall, sensitivity analyses support the validity of our findings from the primary Sea Around Us dataset.

DISCUSSION

Our results have identified and unmasked aspects of MTC warming during the geographic expansion of New Zealand fisheries catch into offshore waters from 1950–2019.

By separating fisheries catch between species' habitat and by fishing gear, we observed warming trends of pelagic-oceanic species across the study period. Results from sensitivity

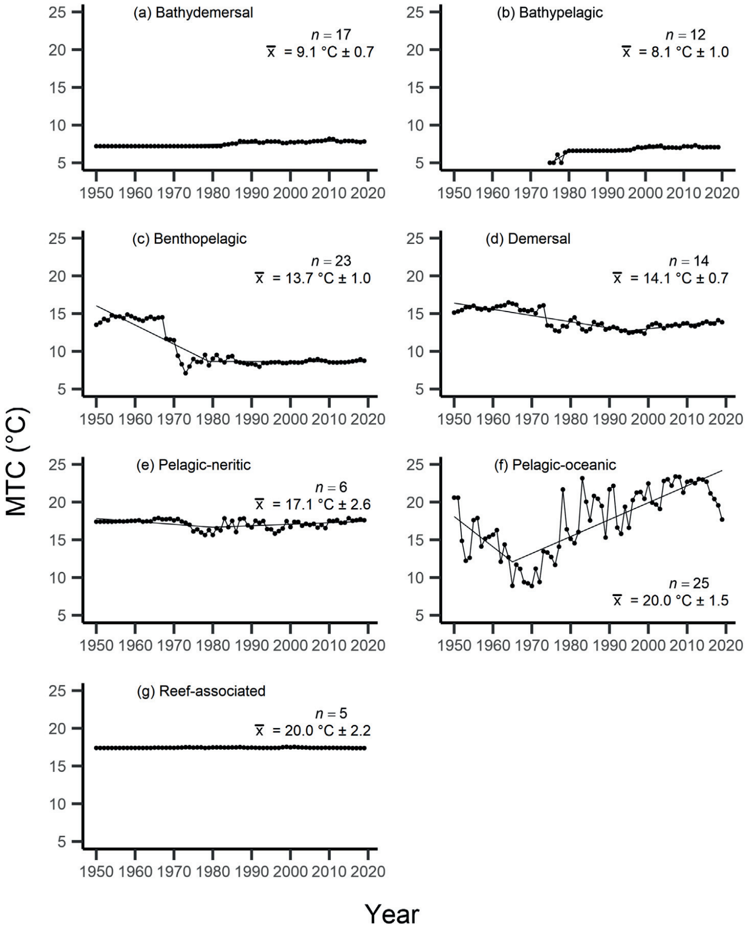

Figure 4 MTC results per species' milieu. The mean temperature of the catch (MTC, °C), of New Zealand's fisheries from 1950–2019, and their regression lines, separated by species' milieu, including: (A) bathydemersal, (B) bathypelagic, (C) benthopelagic, (D) demersal, (E) pelagic-neritic, (F) pelagic-oceanic and (G) reef-associated. Listed in panels is the number of species included in each milieu (*n*), as well as the mean temperature preference (°C ± SE) of all included species.

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analyses confirmed a warming trend of pelagic-oceanic species, although FAO data showed this trend to occur from 1950–2009, thereafter reversing (Fig. S2F). As well, sensitivity analyses using the reduced Sea Around Us dataset removed strong trends of warming in purse seine fisheries (Fig. S4L), and thus, must be considered when

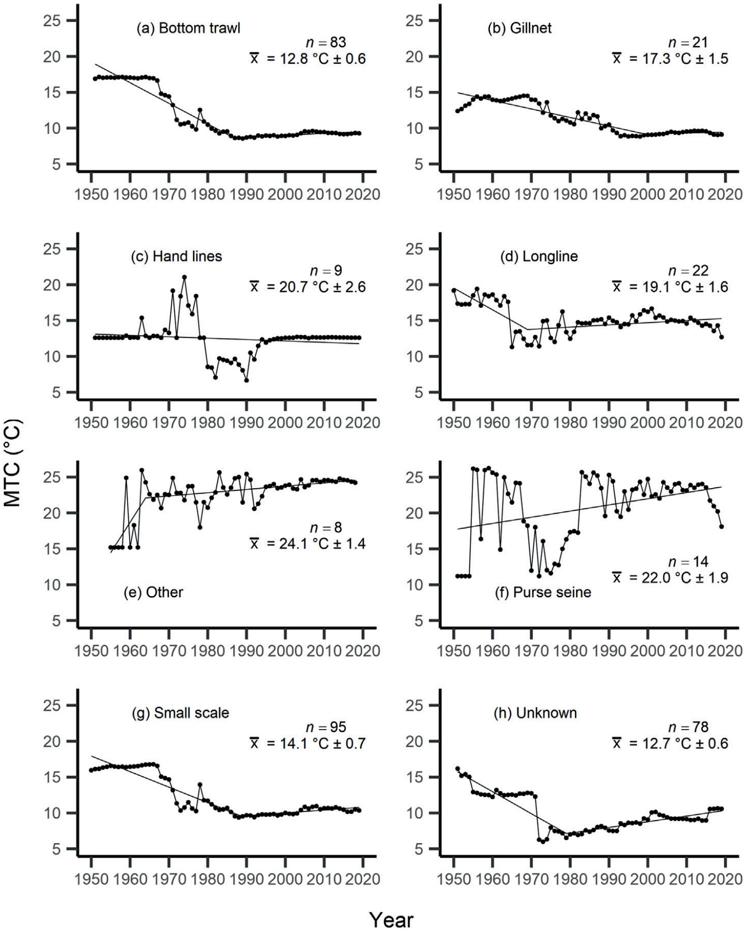

Figure 5 MTC results per fishing gear group. The mean temperature of the catch (MTC, °C), of New Zealand's fisheries from 1950–2019, and their regression lines, separated by fishing gear, including: (A) bottom trawl, (B) gillnet, (C) hand lines, (D) longline, (E) other, (F) purse seine, (G) small scale and (H) unknown. Each panel lists the number of species included in each fishing gear's catch (*n*), as well as the mean temperature preference (°C ± SE) of all included species in that gear group.

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interpreting the primary results of purse seine MTC warming. Nonetheless, overall results reflect the increasing proportion of pelagic-oceanic species of warmer thermal affinity caught in New Zealand from 1950 until at least 2009. This trend was otherwise masked in the full MTC by the geographic expansion and deepening of fishing operations (Fig. 3B).

Strong correlations between bottom-associated habitat- and gear-specific MTC trends and the full, primary MTC suggests that cooling resulted from deepening of New Zealand's catch. This similarly masked result in New Zealand waters was reported by *Cheung, Watson & Pauly (2013)* during the initial application of the MTC.

Following the calculation of the primary, masked MTC, in a step-wise process we calculated the MTL of the same catch data. These results were in line with those reported by *Durante, Beentjes & Wing (2020)* who also analyzed New Zealand fisheries, displaying a strong positive trend of MTL values until the early 2000s, and thereafter decreasing. This increasing trend of MTL, that indicated harvesting of higher trophic level species, corresponds to the period of geographic expansion and deepening of fisheries into colder waters in the area (*Leitão, 2015*), as new habitats and species (*i.e.*, of higher trophic levels) were gradually included into New Zealand fisheries (*Durante, Beentjes & Wing, 2020*). Thereafter, incorporating the MTL into FiB and aMTL indices, we identified two discrete periods of fisheries expansion, with the first occurring in 1965, and the second in 1969.

The geographic expansion of New Zealand's fisheries tracks the modernization of the country's fisheries technology as well as policy. By the 1950s and 1960s, technologically-accessible nearshore fisheries were approaching saturation, and began to show signs of overexploitation (Stock Assemblage 1, Fig. 3E), coinciding with widescale deregulation measures for nearshore fisheries in 1963 (*Clark, Major & Mollett, 1988*; *Pinkerton, 2017*; *Durante, Beentjes & Wing, 2020*). Deregulation facilitated the rapid development of a domestic fisheries industry within the newly established 12 nautical mile Territorial Sea in 1965 (*Bradstock, 1979*; *Clark, Major & Mollett, 1988*; Fig. 1). This led to an expansion of fishing effort in shelf waters (*Jackson et al., 2001*; *Kleisner, Mansour & Pauly, 2014*), and coincided with our identification of the geographic expansion to include the second stock assemblage in 1965 (Fig. 3E). As we assume that this expansion occurred within shelf waters (*sensu Kleisner, Mansour & Pauly, 2014*), these two stock assemblages are parallel geographically (along New Zealand's shelf) and thus maintain similar species assemblages (in contrast to the offshore Stock Assemblage 3). In turn, our results show similar trends of fishing down to have occurred in Stock Assemblages 1 and 2, which represents the full exploitation of species and thus the range of trophic levels available to fisheries within shelf waters during this period of fisheries expansion in New Zealand. A similar trend was observed between the first and second stock assemblage identified during the analysis of geographic expansion of fisheries in Indian waters (*Kleisner, Mansour & Pauly, 2014*).

As shelf-water fisheries continued to develop throughout the 1960s, high trophic level species were being depleted, thus Stock Assemblages 1 and 2 began to show signs of fishing down (Fig. 3E). This trend was revealed by the application of the FiB and aMTL indices, and was otherwise masked by the calculation of MTL of fisheries catch across the New Zealand EEZ (Fig. 3C, *Durante, Beentjes & Wing, 2020*). Similar results from *Leitão (2015)* reported signals of overfishing in nearshore stocks during a period of fisheries expansion, and thus support our results, as well as the assumptions of aMTL analyses, in that persistent fishing down in nearshore and shelf stock assemblages (*i.e.*, Stock Assemblage 1 and 2) incentivizes expansion into previously unexploited stock assemblages (*i.e.*, Stock Assemblage 3) (*Kleisner, Mansour & Pauly, 2014*). Concurrently, through further economic incentives including subsidies for new vessels, new processing plants, and an expanded list of exploitable species, New Zealand's fisheries fleets expanded further offshore (*Johnson & Haworth, 2004*; *Durante, Beentjes & Wing, 2020*), coinciding with the expansion of fisheries into the third identified stock assemblage in 1969 (Fig. 3E). This third stock assemblage has maintained the highest mean trophic levels of catch across the time series (Fig. 3E), likely due to consistently high catches of the commercially-important hoki (*Macruronus novaezelandiae*, TL = 4.5, Table 1) since the early 1970s.

By completing sensitivity analyses with the reduced Sea Around Us catch data ($n = 42$) and the FAO catch data ($n = 42$), our results of fishing down within nearshore stock assemblages was confirmed throughout the period of fisheries expansion in New Zealand waters. The identification of node expansion into new stock assemblages occurred later within the aMTL from FAO data. This is expected, as FAO reported catch quantities are lower than those for the reconstructed Sea Around Us catch, including but not limited to the period from the 1950s to 1970s (Fig. 2C). Moreover, it is documented that the identification of node expansion can occur later if catch increases more gradually (*Kleisner, Mansour & Pauly, 2014*), as is the case for the analyzed FAO catch data.

By separating and re-calculating the MTC between species' milieu and fishing gear type, MTC trends are in line with results reported *via* the aMTL. Several fisheries with bottom-associated gear or species, including deep-water species, displayed negative MTC trends from the mid- to late 1960s until the 1980s and 1990s (Figs. 4, 5). This cooling of the MTC coincides with the expansion of fishing operations to include Stock Assemblage 3 from 1969 onwards. As gear development promoted further expansion into deeper and cooler waters, new catches of barracouta (*Thyrsites atun*), southern blue whiting (*Micromesistius australis*) and hoki drove down MTC trends (Figs. 6A, 6B). By the 1980s, catches of hoki dominated not only gear- and habitat-specific fisheries catch, but also overall catch in New Zealand waters. This led to the levelling off of both hoki-dominated gear- and habitat-specific MTCs (*e.g.*, Figs. 4C, 5A) and also the general trend of New Zealand's MTC (Fig. 3B).

For pelagic-oceanic species and pelagic purse seine fisheries, trends of MTC warming were driven by the increasing catch of the subtropical skipjack tuna (*Katsuwonus pelamis*) and blue mackerel (*Scomber australasicus*), paired with the decreasing catch of the temperate southern bluefin tuna (*Thunnus maccoyii*, Figs. 6C, 6D). These results are in line with observations of pelagic species undergoing relatively rapid shifts in geographic distribution with oceanographic changes (*Champion, Brodie & Coleman, 2021*), albeit the changes in SSTA of the present study area are modest. Such changes in the composition of pelagic-oceanic species present in fisheries catch may be driven by the adult fishes' ability to shift synchronously with their pelagic habitat to track local climate velocities (*Pinsky, Selden & Kitchel, 2020*; *García Molinos et al., 2022*). Moreover, these results suggest that the observed levels of ocean warming may favor the increased abundance of subtropical, smaller-bodied skipjack tuna and blue mackerel *vs* the temperate and larger-bodied southern bluefin tuna. In line with these results, and in recognition of the complexities of variable shifts in geographic distribution between different species (*Dunn et al., 2022*), we

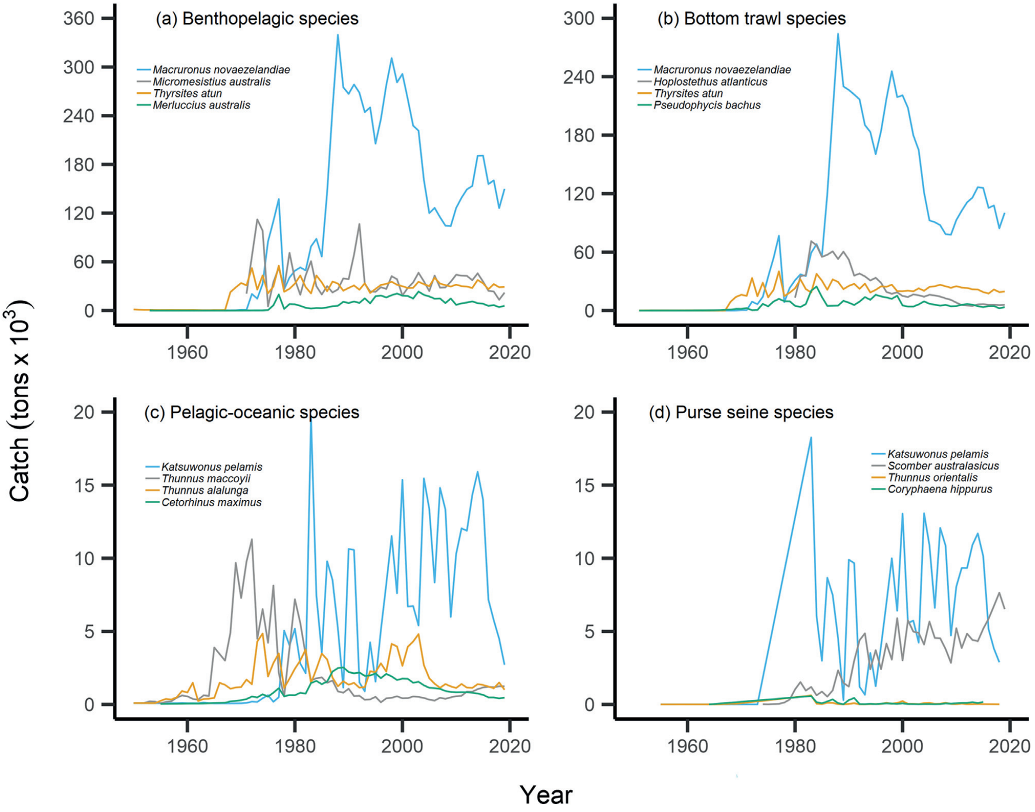

Figure 6 **Catch trends for most abundant bottom-associated and pelagic-associated species.** Species with the highest overall catches (tons × 10^3) across the study period for: (A) benthopelagic species, (B) species caught in bottom trawl fisheries, (C) pelagic-oceanic species and (D) species caught in purse seine fisheries.

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recommend that further research investigates the variability of shifts in geographic distribution of teleost fish species in line with ocean warming across New Zealand waters.

Our results of the positive trend in SSTA are in line with observations of the gradual warming of New Zealand waters. Overall, ocean warming within New Zealand's EEZ has exhibited relatively weak trends and significant interannual variability due to the dynamic influences of the warm Subtropical Front (STF) from the north, north-west and the cold Subantarctic Front (SAF) from the south (*Shears & Bowen, 2017*; *Sutton & Bowen, 2019*). Management must consider the additive or synergistic effects of both fishing pressure as well as ocean-warming-induced changes in productivity and geographic distribution of fish populations. For example, fishing effort may be reduced on stocks that are overexploited and/or are shifting the trailing edge of their geographic distribution away from historically fished areas as they track their thermal affinity (*Szuwalski & Hollowed, 2016*; *Gaines et al., 2018*; *Lamine et al., 2022*). In the present study, this may apply to the cold-water southern bluefin tuna, which displays strong reductions in overall catch from the 1970s onward (Fig. 6C). This may also be relevant as other commercially-important species such as hoki are predicted to shift their geographic distribution polewards with future ocean warming (*Dunn et al., 2022*). Conversely, the leading edge of pelagic, warm-water skipjack tuna and blue mackerel may be penetrating deeper into New Zealand's EEZ, thus facilitating higher catches. The joint application of the present indices can help inform such management decisions.

Interpretation of trends in the MTC should also consider historical fishing pressure and management within this particular system. Demersal or reef-associated species like the Australasian snapper *Pagrus auratus* were already displaying signs of overexploitation by the 1970s (*Durante, Beentjes & Wing, 2020*), as confirmed by our calculation of the nearshore and shelf aMTLs (Stock Assemblage 1 and 2, Fig. 3E). As a result, New Zealand implemented their quota management system (QMS) in 1986 (*Clark, Major & Mollett, 1988*), and since then, overall fisheries catches have decreased (Fig. 2A), and that of Australasian snapper has remained steady but well-below its maximum catch values seen in the 1960s and 1970s (Supplemental Files). Conversely, since the 1980s, skipjack tuna and blue mackerel have displayed oscillating but gradually increasing catches (Figs. 6C, 6D). This may be a result of the then newly-implemented QMS, the technological and geographic expansion of fisheries in New Zealand waters, as well as trends in ocean warming and the increased abundance of pelagic, warm-water fishes in the area.
We therefore recommend that interpretation of the present MTC warming trend considers both the thermal affinity tracking of pelagic species with ocean warming, as well as fisheries management in New Zealand adapting to stock changes.

CONCLUSIONS

Overall, our results build on previous research of the MTL to correct for the geographic expansion of fisheries within the New Zealand EEZ from the 1950s onward. Using the FiB and aMTL indices, we identified trends of fishing down trophic levels in nearshore fishing stocks, a trend that was otherwise masked within the full calculation of New Zealand's MTL (*Durante, Beentjes & Wing, 2020*). Thereafter, by separating catch between species' milieu and fishing gear groups, increasing catches of subtropical skipjack tuna and blue mackerel revealed positive MTC trends for pelagic species and fishing gear. These trends were also otherwise masked by the offshore expansion and deepening (into colder depths) of fishing operations and catch, as species such as hoki came to dominate overall catches across the same time period. These results highlight the pervasiveness of fishing down food webs in New Zealand fisheries throughout a period of technological development and fisheries geographic expansion. These results also reveal how fisheries catch composition may change due to the responsiveness of pelagic, mobile species to track local climate velocities with ocean warming.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding
The authors received no funding for this work.

Competing Interests
Mark John Costello is an Academic Editor for PeerJ.

Author Contributions
- Charles Patrick Lavin conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Daniel Pauly conceived and designed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Donna Dimarchopoulou conceived and designed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Cui Liang conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Mark John Costello conceived and designed the experiments, authored or reviewed drafts of the article, and approved the final draft.

Data Availability
The following information was supplied regarding data availability:

The data utilized in the present study, as well as code to perform analyses, is available from Zenodo: Charles P. Lavin. (2023). Code and data for: Fishery catch is affected by geographic expansion, fishing down food webs and climate change in Aotearoa, New Zealand. Zenodo. https://doi.org/10.5281/zenodo.8207722

Supplemental Information
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.16070#supplemental-information.

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Marine water-breathing ectotherms can be negatively impacted by ocean warming and deoxygenation in line with anthropogenic climate change. These environmental changes induce universal responses of marine ectotherms including reductions in body size as well as shifts in geographic distribution. Such responses are required in order for these animals to remain within their evolved thermal niche, as well, obtain sufficient dissolved oxygen from sea water to maintain aerobic metabolism. Yet, such changes will not occur uniformly between species or across biogeographic regions, and thus, the stability of marine communities and food webs can be stressed. Concurrently, persistent fishing pressure can further stress marine community stability, especially through the preferential harvesting of high trophic level species. This thesis investigated instances of changing body size and geographic shifts of marine ectotherm populations, plus instances of overfishing top predators, between two unique ecoregions, Norway and New Zealand. Novel insight provided in the present thesis into these individual stressors can inform a more wholistic understanding of how cumulative stressors will interact within future scenarios of ocean warming and fishing. Such insight is necessary in order to inform conservation and fisheries management.

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