Persistence and trophic interactions of range-expanding tropical herbivores in southwestern Australia: implications for the functioning of temperate ecosystems

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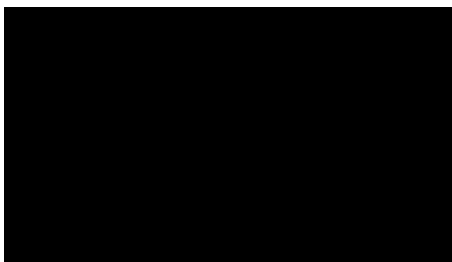
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General Abstract

Climate change is modifying species distributions around the world, forcing some tropical species poleward, where they can alter trophic interactions in their receptive ecosystems. Some tropical herbivorous fishes have expanded into temperate ecosystems in Japan, The Mediterranean Sea, Gulf of Mexico and eastern and western Australia, where their long term persistence is expected to affect the functioning of the ecosystems by increasing herbivory rates. However, many aspects about their biological performance, along with the magnitude and variability of their impacts remain unknown. My thesis evaluates the changes that tropical herbivores can experience on their life-histories due to range expansions (Chapter 2), the spatial and temporal variability of their interactions with temperate foundation species and competitor herbivores (Chapters 3 & 4) and their capacity to persist and contribute to the maintenance of canopy-free ecosystems states in tropicalized temperate reefs (Chapter 5).

A key aspect for the understanding of the capacity of tropical herbivorous fish to expand into and persist within temperate regions are the possible life-history trade-offs that they can experience in their new environments. In Chapter 2, I reviewed this for the range-shifting rabbitfish *Siganus fuscescens* and *Siganus rivulatus* in their temperate and tropical environments around the globe (Western Australia, Philippines, Korea, Japan, India, Saudi Arabia, Emirates, Oman, Egypt, Israel, Lebanon, Syria, Turkey, and Libya). I described their fecundity, spawning periods, growth rate, maximum size attained and longevity across climates. I found strong plasticity in the life-history characteristics of populations at the leading edge of the range-extension that can maximize their fitness according to stronger seasonal fluctuations of temperature. Rabbitfish at higher latitudes had shortened reproductive periods and reduced growth rates, taking longer to reach sexual maturity and maximum sizes, but compensated for this with higher absolute fecundity per length class and longer lifespans than populations in warmer environments. *S. rivulatus* in temperate environments had lower length at maturity and lower maximum body sizes than expected when compared to subtropical populations, possibly due to the added effect of lower primary productivity (*i.e.*, a common proxy for nutrition) and low temperatures; however, given their reduced growth rates this maximized their life-time reproductive output. These results suggest that the range-shifting to temperate environments will carry species-specific trade-offs in some life-history traits. The plasticity in fecundity and longevity of these species of rabbitfish could support their persistence in temperate environments and possible further expansions.

Winter temperatures at higher latitudes can be challenging for tropical species, affecting their survival and impact on the ecosystem. In Chapter 3, I assessed the seasonal variation in abundances, macrophyte consumption and detritus production of the range-extending tropical rabbitfish *Siganus fuscescens* and the temperate silver drummer *Kyphosus sydneyanus* and herring cale *Olisthops cyanomelas* in south-western Australia. Rabbitfish overwintered in temperate reefs, consumed more kelp and other macrophytes in all feeding modes and defecated more during both summer and winter than the temperate herbivores. Herbivory and defecation were dependent on temperature, with higher rates attained during summer and lower rates in winter. This led to a five-fold acceleration in the transformation of macrophyte standing stock to detritus, a function usually attributed to sea urchins in kelp forests.

The overall ecological impact that range-shifting herbivorous species can have in the receptive ecosystem can be determined by biotic interactions. In Chapter 4, I assessed the spatial overlap and habitat associations of native temperate and range-expanding tropical herbivorous fishes in south-western Australia to determine how incursions of tropical species may have affected the diversity, redundancy, spatial extent and intensity of specific herbivory functions. Overlap between tropical and temperate herbivores was highest in the northern subregions, with no apparent displacements of temperate species. The addition of tropical species increased functional diversity and uniqueness (the complement of redundancy). Seagrass browsing increased in spatial extent (27%) and intensity (15×), while seaweed browsing, and grazing increased in intensity by up to 2.5× in regions with high abundances of tropical herbivores. These results suggest that the addition of tropical species with different habitat affinities, behaviors and diets will introduce novel herbivory functions to many locations because the diversity of herbivory functions is relatively low in temperate marine ecosystems.

Understanding the mechanisms that support the resilience of alternative ecosystem states is important to predict potential regime-shifts and reversals to the baseline state of the ecosystem. In Chapter 5, I evaluated the mechanisms that support turf-dominated states (recruitment of tropical herbivores, browsing and grazing rates, and turf cover) and those that resist it (kelp recruitment, survival, and reproduction) in temperate reefs which experienced a complete loss of their kelp forests and an influx of tropical herbivores following a marine heatwave in 2011. I found that the reefs remained tropicalized with high cover of turf and high abundance of tropical herbivores after nine years from the regime shift. The most important herbivores, the rabbitfish *Siganus fuscescens* and the chub *Kyphosus bigibbus*, persisted with high abundances, supported by the adjacent reef lagoon, where seagrass meadows and the backreef habitats hosted juveniles of both species. Tropical herbivores exerted a strong control on turf seaweed, possibly microscopic kelp sporophytes, and adult

kelps during herbivory assays, reducing kelp recruitment and recovery in open areas. However, in topographical refuges in the reefs, herbivory was low and we found some kelp individuals in crevices having reproductive tissue, which could provide local sources of propagules to recolonize open spaces in the future.

Overall, my research showed that certain range-expanding herbivores can have strong plasticity in their life-history traits in relation to changes in climate, which can benefit their persistence and further expansions at higher latitudes. The importance of nursery grounds for their persistence was demonstrated, providing feedback towards a long-term increase in top-down control over foundation species in temperate ecosystems. Tropical herbivores accelerated the rates of macrophyte consumption and detritus production throughout the year, with potential consequences for the energy and nutrient flow across trophic levels. Further warming and expansions of tropical species could cause additional increases in intensity of different herbivory functions, reducing canopy cover and hindering kelp recovery in synergy with environmental disturbances, but this will be highly heterogenous in space. My thesis provides evidence about the ecological impacts of the tropicalization of herbivorous communities of temperate coastal ecosystems of western Australia, a phenomenon affecting several regions of the world, and its implications for their conservation and its potential transformation into novel ecosystems in the future.

Table of Contents

Acknowledgements

Authorship declaration

This thesis contains work that has been published and prepared for publication.

Details of the work:
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Student contribution to work: S.Z.P. conceived the study; S.Z.P. acquired the funding; D. F., C. D. and J.D. provided fish specimens; S.Z.P. dissected fish otoliths, R.A. mounted fish otoliths, S.Z.P. and B.T. aged fish otoliths; S.Z.P. conducted the literature review, the meta-analyzes, and wrote the first draft of the paper and all co-authors commented on the manuscript and gave final approval for publication.
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S.Z.P. conceived the study; S.Z.P. acquired the funding; S.Z.P. collected the field data; S.Z.P. and G.C. analyzed the data; S.Z.P. wrote the paper and all authors contributed to drafting the manuscript and gave final approval for publication.

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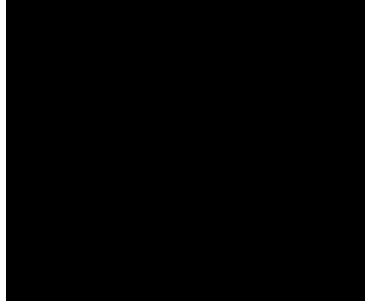
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I, Professor Thomas Wernberg, certify that the student's statements regarding their contribution to each of the works listed above are correct.

As all co-authors' signatures could not be obtained, I hereby authorize inclusion of the co-authored work in the thesis.

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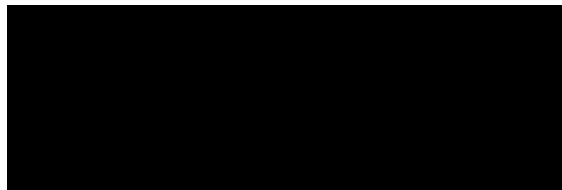
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The following is a list of additional publications not included in this thesis but published and submitted with national and international collaborations during this Doctor of Philosophy program.

Zarco-Perello, **S.**, & Enríquez, S. (2019). Remote underwater video reveals higher fish diversity and abundance in seagrass meadows, and habitat differences in trophic interactions. *Scientific Reports*, *9*, 6596. https://doi.org/10.1038/s41598-019-43037-5

Barrientos S., **Zarco-Perello S.**, Piñeiro-Corbeira C, Barreiro R. and Wernberg T. Feeding choice of tropical herbivores amid novel species interactions with temperate species. *Marine Environmental Research*, 172, 105508. https://doi.org/10.1016/j.marenvres.2021.105508

Mulders Y., Filbee-Dexter K., Bell S., Bosch NE., Pessarrodona A., Sahin D., Vranken S., **Zarco-Perello S.** & Wernberg T. Intergrading reef communities across discrete seaweed habitats in a temperate - tropical transition zone: lessons for species reshuffling in a warming ocean. *Accepted for publication in Ecology and Evolution (10/12/2021).*

Bosch N.E., McLean M., **Zarco-Perello S.,** Vergés A., Stuart-Smith R.D., Bennett S., Pessarrodona A., Tuya F., Langlois T., Spencer C., Bell S., and Wernberg T. A persistent thermally-driven functional reorganization of herbivorous fish impairs the recovery of seaweed forests in tropicalised temperate reefs. S*ubmitted to Global Change Biology Accepted for publication (19/12/2021).*

Chapter 1. General Background

1.1. Direct and indirect effects of climate change on marine ecosystems.

Anthropogenic climate change is advancing, and it has been estimated that global warming is now irreversible in the foreseeable future (IPCC 2021). While local and regional variation is significant, atmospheric temperature has increased by 0.9-1.2◦C worldwide and forecasts indicate that warming is likely to reach +1.5◦C by 2030, and +4◦C by 2090 in the worst case scenario of greenhouse emissions (IPCC 2021). Oceanic systems are absorbing as much as 90% of the excess heat from the atmosphere and its rate of warming has doubled since 1993, with average future projections of +1◦C by 2040, and +3◦C by 2090 (IPCC 2021; Ruela *et al.* 2020). Some temperate regions are warming 2-3 times faster than the global average due to the intensification of heat transport from equatorial regions to higher latitudes (Wu *et al.* 2012; Hobday & Pecl 2014). In addition, marine heatwaves (anomalous increases of temperature over a discrete period of time) have increased in frequency by 34% and duration by 17% during the last century, and this trend is predicted to continue in the future (Oliver *et al.* 2018; IPCC 2019; Laufkötter *et al*. 2020), with important consequences for the community structure of marine ecosystems around the world (Wernberg *et al.* 2016; Sanford *et al.* 2019; Smale *et al.* 2019; Lonhart *et al.* 2019; Strydom *et al.* 2020; Bernal *et al.* 2020).

Changes in climate are having significant direct and indirect effects on natural ecosystems (Walther *et al.* 2002; Stenseth *et al.* 2002; Blowes *et al.* 2019). Ectothermic organisms are the most vulnerable to global warming, since their metabolic rate and biological processes are directly dependent on environmental temperature, such as reproduction, recruitment and growth (Brander 1995; Roessig *et al.* 2004). Living organisms have a range of thermal tolerance, where the performance for specific biological processes (*e.g.* reproduction or growth) is maximum at specific thermal conditions and falls as temperatures increase or decrease. Beyond minimum and maximum thermal thresholds, physiological stress increases until a critical level, where biological processes such as respiration cease and organisms cannot survive (Angilletta *et al.* 2002; Pörtner & Peck 2010). Global increases in temperature are forcing natural populations to respond in various ways to avoid extinction (Maclean & Wilson 2011). The possible responses can be broadly classified in (i) genetic adaptation or phenotypic plasticity under the new environmental conditions in their current distribution (Merilä & Hendry 2014), (ii) behavioral changes in phenology of reproduction or migration within local habitats according to daily and seasonal fluctuations in temperature (Root *et al.* 2003; Pörtner & Peck 2010) or

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(iii) geographic changes in distribution towards higher latitudes where temperatures are within their range of tolerance (Tsuchida 1995; Eme & Bennett 2009; Rijnsdorp *et al.* 2009).

Increasing global temperatures will cause changes in species composition, richness and abundance in space and time (Stenseth *et al.* 2002). Sessile organisms are some of the most vulnerable to global warming due to their inability to move and avoid disturbances (Smale *et al.* 2019). Scleractinian corals (Anthozoa, Scleractinia) in tropical reefs, seagrass meadows (Angiosperms, Monocotyledons) in coastal lagoons and kelp forests (Phaeophyta, Laminariales) in temperate reefs around the world have suffered mass mortality events due to warming (Hughes *et al.* 2007; Thomson *et al.* 2015; Stuart-Smith *et al.* 2018; Wernberg *et al.* 2019; Smale *et al.* 2019). Their decline has caused bottom-up trophic cascades in many locations, with an overall reduction in habitat complexity and associated biodiversity, because they act as foundation species, providing shelter and trophic resources to many other species (Steneck *et al.* 2002; Boström *et al.* 2006; Pratchett *et al.* 2011; Zarco-Perello & Enríquez 2019; Lamy *et al.* 2020). The survival of some species in warmer oceans is dependent on their ability to increase their thermotolerance (Reusch 2014; Coleman *et al.* 2020; Kleypas *et al.* 2021) or shift their distribution to higher latitudes where temperatures are more optimal, the latter being particularly important for tropical species (Yamano*et al.* 2011; Kumagai *et al.* 2018).

Mobile organisms also can suffer severe adverse effects as a result of warming but some may be more able to respond based on the three general categories described earlier (Pörtner & Peck 2010). Fishes are highly mobile and perform a range of essential ecosystem services in coastal marine habitats. As such, their responses to climate change have been some of the most evident because changes in their community structure can have significant cascading effects on the ecosystems they reside (Burkepile & Hay 2008; Hamilton & Caselle 2015; Eger & Baum 2020). Evidence of their possible adaptation and phenotypic plasticity in response to global warming has increased during recent decades, including evidence that tolerance to higher temperatures could be possible (Munday *et al.* 2017). A high amount of evidence exists of phenological and morphological changes that help maintain maximum fitness in warmer environments (Crozier & Hutchings 2014). Generally, populations living in warm environments have higher growth rates, earlier sexual maturity, lower fecundity, smaller maximum body sizes and shorter life-spans in comparison to conspecific individuals in cooler environments, a pattern referred as the Temperature-Size-Rule (Vila-Gispert *et al.* 2002; Angilletta & Dunham 2003). Thus, it is predicted that future warming will affect the life-history traits of many organisms in combination with other factors, such as predation and food availability (Angilletta *et al.* 2004; Audzijonyte *et al.* 2020). Adaptations in phenology in several places of the world have been documented extensively (Parmesan 2006). In regions experiencing significant warming, species have

shifted the start and duration of annual reproduction to earlier months as temperatures rise sooner and winters are shorter in the year (Fincham *et al.* 2013; Rogers & Dougherty 2019).

Changes in temperature can also affect migration patterns, recruitment success, and shifts in the geographic distribution of marine species. Such effects have been observed in pelagic species in response to decadal temperature fluctuations associated with the North Atlantic Oscillation, El Niño-Southern Oscillation and the Pacific Decadal Oscillation (Dippner 1997; Planque & Frédou 1999; Ottersen *et al.* 2001; Lehodey *et al.* 2006; Rijnsdorp *et al.* 2009). Sustained temperature increases coupled with episodic marine heatwaves are having similar effects (Wu *et al.* 2012; Cetina-Heredia *et al.* 2015; Blowes *et al.* 2019; Burrows *et al.* 2019; Laufkötter *et al.* 2020), causing a redistribution of marine biodiversity around the world by boosting the expansion of warm-water species to higher latitudes at an estimated rate of 6-19.0 km year^{-1} (Cheung *et al.* 2009; Sorte *et al.* 2010; Poloczanska *et al.* 2013). Reports of this process for fish communities have been documented in the eastern and western coasts of the Pacific Ocean (Holbrook *et al.* 1997; Booth *et al.* 2007; Johnson *et al.* 2011; Nakamura *et al.* 2013; Tose *et al.* 2017; Fowler *et al.* 2017; Sanford *et al.* 2019; Lonhart *et al.* 2019), the western and eastern Atlantic ocean (Parker & Dixon 1998; Fodrie *et al.* 2010; Paxton *et al.* 2019; Burrows *et al.* 2019), the North Sea and Barents Sea in the Arctic Ocean (Beare *et al.* 2004; Perry *et al.* 2005; Fossheim *et al.* 2015; Polyakov *et al.* 2020), the Mediterranean Sea (Ben Rais Lasram *et al.* 2008; Raitsos *et al.* 2010; Lejeusne *et al.* 2010; Bianchi *et al.* 2018) and in the Indian Ocean (Lloyd *et al.* 2012; Richards *et al.* 2016; Wernberg *et al.* 2016). As warming increases in the future, this process, referred as tropicalization, is forecast to continue into the coming decades (Cheung *et al.* 2008; Cheung *et al.* 2009; Cheung *et al.* 2016; Morley *et al.* 2018; Pinsky *et al.* 2018).

1.2. Threats to temperate ecosystems by range-expansions

The poleward expansions of species are creating new trophic interactions that have the potential to modify the community structure of receptive ecosystems (Albouy *et al.* 2014). Similarly to invasive species, range-shifts of tropical species induced by climate change can increase competition and modify trophic processes (Sorte *et al.* 2010; Wallingford *et al.* 2020) and change ecosystem functioning (Connell *et al.* 2011; Milazzo *et al.* 2013; Ling *et al.* 2015; Marshak & Heck 2017). Among the functional groups of marine fishes, herbivorous species have some of the highest potential to alter trophic processes in temperate ecosystems (Vergés *et al.* 2014a; Hyndes *et al.* 2016). Herbivores are important ecological engineers that mediate the transfer of energy between trophic levels and help shape the habitat structure of ecosystems (Gruner *et al.* 2008; Steneck *et al.* 2017). Herbivory in tropical reefs is intense due to high abundances, species richness and diversity of feeding modes of

macro-herbivores (*e.g.* fish), which can effectively suppress algal biomass in favor of scleractinian corals and other sessile invertebrates (Hughes *et al.* 2007). In contrast, herbivory in temperate ecosystems is generally lower, due to few species of macro-herbivores and low metabolic rates influenced by cold temperatures (Meekan & Choat 1997; Floeter *et al.* 2005; Steneck *et al.* 2017; Longo *et al.* 2018). This commonly results in a surplus of primary production and dominance of canopy-forming macrophytes (Poore *et al.* 2012; Vergés *et al.* 2018). However, significant removal of seaweed cover can occur under high densities of herbivorous sea urchins, which has caused extensive clearings in kelp forests, creating barren habitats and triggering trophic cascades leading to lower biodiversity and ecosystem services (Filbee-Dexter & Scheibling 2014; Ling *et al.* 2015).

The tropicalization of temperate herbivorous communities could have similar effects by increasing the diversity, abundance and feeding rates of different functional groups of herbivores (Vergés *et al.* 2014a, 2019). Rabbitfishes (Siganidae), surgeonfishes (Acanthuridae), parrotfishes (Scaridae), drummers (Kyphosidae) and damselfishes (Pomacentridae) are important families of tropical herbivorous fish that functionally can be broadly classified as (i) browsers: consumers of foliose and canopy-forming seaweed, or (ii) grazers: consumers of short filamentous algae, sediments and detritus in the substrate (Mantyka & Bellwood 2007; Cvitanovic & Bellwood 2009; Brandl & Bellwood 2014; Streit *et al.* 2019). The expansion of browsers to temperate ecosystems could drive reductions in the abundance of macrophytes, while increases in grazers can prevent recruitment of seaweed, affecting demographic processes of foundation species, the habitat structure and energy and nutrient fluxes in temperate ecosystems, which can contribute to drive regime-shifts to alternative ecosystem states (Vergés *et al.* 2014a; Bennett *et al.* 2015).

1.3. Current evidence of tropicalization of herbivorous fish communities on temperate ecosystems and its impact

Evidence of the poleward expansion of tropical herbivorous fishes to temperate regions of the world is increasing (Vergés *et al.* 2014a). In Japan, the parrotfish *Calotomus japonicus*, the surgeonfish *Prionurus scalprum*, the drummer *Kyphosus bigibbus* and the rabbitfish *Siganus fuscescens* have increased their populations in kelp forests (Nakayama 1999; kiriyama, Fujii & Fujita 2005; Yatsuya *et al.* 2015; Kumagai *et al.* 2018). In the Mediterranean Sea, the expansion of tropical herbivores across the basin has increased in recent decades, such as the rabbitfish *Siganus rivulatus* and *Siganus luridus* (Azzurro & Andaloro 2004; Azzurro *et al.* 2017), the drummers *Kyphosus vaigiensis* (syn. *Kyphosus incisor*) and *Kyphosus sectatrix* (Kiparissis *et al.* 2012; Azzurro *et al.* 2013; Mannino *et al.* 2015; Knudsen & Clements 2016; Goren *et al.* 2016; Kiyağa *et al.* 2019), the damselfishes *Abudefduf saxatilis*

and *Abudefduf hoefleri* (Dragičević *et al.* 2021), the parrotfish *Scarus ghobban* (Goren & Aronov 2002; Bariche & Saad 2008; Erguden *et al.* 2018) and the surgeonfish *Acanthurus monroviae,* which also has new distributional records in Portugal (Vasconcelos *et al.* 2017), like vagrants of *K. sectatrix* and *K. vaigiensis* which have been reported in Galician waters (Bañón 2004; Bañón, Barros-García & De Carlos 2017; Encarnação *et al.* 2019). In the Gulf of Mexico the parrotfish *Nicholsina usta* and *Sparisoma viride* have increased their abundance and distribution in northern regions (Fodrie *et al.* 2010). In southeastern Australia, vagrant tropical herbivores of juvenile surgeonfish or damselfish have been observed over the last decades (Booth *et al.* 2007, 2018; Figueira & Booth 2010; Fowler *et al.* 2017; Monaco *et al.* 2021). In southwestern Australia, the parrotfish *S. ghobban* increased its abundances (Bennett *et al.* 2015; Parker *et al.* 2019), while the rabbitfish *S. fuscescens* expanded its distribution, with signs of forming self-recruiting populations (Lenanton *et al.* 2017).

Assessments of the capacity of tropical herbivores to modify ecological processes in temperate ecosystems indicate that these are driving increases in herbivory rates in different macrophytes. In Japan, tropical herbivores have been documented consuming kelp individuals based on qualitative or descriptive assessments of fish bite marks in field conditions or aquarium experiments (Nakayama 1999; Hasegawa 2010; Tanaka *et al.* 2012) and thwarting kelp restoration efforts by efficiently consuming transplanted kelp individuals (Nimura *et al.* 2007; Hasegawa 2010; Kuwahara 2015). Herbivory assays in the Mediterranean Sea showed that rabbitfish are consumers of the habitat-forming seaweeds *Cystoseira* spp., *Sargassum* spp. and filamentous seaweed based on gut content analyses, correlations of herbivore-seaweed abundances and field herbivory assays (Lundberg *et al.* 2001; Sala *et al.* 2011; Vergés *et al.* 2014b). More recently in southeastern Australia, aquarium feeding experiments showed that vagrant juvenile surgeonfish can be more important consumers of turf seaweed than temperate species (Basford *et al.* 2016) and in southwestern Australia tropical herbivores consumed translocated kelp individuals in tropicalized reefs that lost their kelp populations due to the marine heatwave (Bennett *et al.* 2015) and have caused significant increases in kelp consumption in temperate reefs at higher latitudes (Zarco-Perello *et al.* 2017). Assessments of the interactions of tropical herbivores on seagrass meadows are limited, but gut content analyses and feeding experiments in aquaria have shown that tropical parrotfish in the Gulf of Mexico can consume four times more seagrass biomass *per capita* than temperate species (Heck *et al.* 2015).

1.4. Research Questions

The impact that tropical herbivores can have in temperate ecosystems depends primarily on their ability to expand their distribution and persist in their new environments (Bates *et al.* 2014). The

range-expansion of tropical fishes to higher latitudes is predicted to depend firstly on traits related to their ability to migrate or disperse their propagules, such as their swimming abilities, spawning strategy (pelagic vs benthic), fecundity (egg productivity), and pelagic larval duration. Following this, their settlement would be determined by the presence of adequate nursery grounds for recruitment and food resources for growth until adulthood. Finally, their persistence would be dependent on the ability of adults to reproduce, maintain recruitment, and be successful against new competitors and predators of temperate habitats (Feary *et al.* 2014; Sunday *et al.* 2015; Arndt & Schembri 2015; Tose *et al.* 2017; Monaco *et al.* 2020). While it has been documented that certain tropical herbivorous fishes are present in temperate marine ecosystems and can consume temperate macrophytes, few analyses exist of the spatial and temporal variability of their abundances, habitat associations, recruitment, feeding rates and behaviors, and interactions with temperate competitors. My research aimed to increase our understanding of these aspects through the analyses of datasets collected from the published literature and field surveys on the temperate ecosystems of southwestern Australia (Figure 1.1). This region is a global warming hotspot (Pearce & Feng 2007; Caputi *et al.* 2009; Hobday & Pecl 2014), where tropical herbivorous fishes have increased their abundances and expanded its distribution swiftly following a marine heatwave in 2011 (Bennett *et al.* 2015; Wernberg *et al.* 2016; Zarco-Perello *et al.* 2017) and where it is likely that range-expansions will continue in the future (Cheung *et al.* 2012).

In chapter 2, I ask the general question: are range-expanding herbivorous species experiencing changes in their life history? For this I conducted a global literature review and meta-analysis of changes in phenology and phenotype of the rabbitfish species *Siganus rivulatus* and *Siganus fuscescens* across 67° of latitude. I then discuss how these changes could relate to their fitness and further poleward range expansion.

In chapter 3, I asked the questions: (i) are populations of the tropical herbivore *SIganus fuscescens* able to overwinter in temperate reefs in southwestern Australia and remain with stable abundances across space and time?; (ii) if so, what is their relative importance on transforming the standing stock of macrophytes into detritus over the seasons of the year?; and (iii) how does this change according to the interaction between the number of herbivorous individuals and the environmental temperature? The latter two factors are predicted to increase in the future on temperate reefs and I then discuss its implications for the flux of energy and nutrient cycle in temperate ecosystems.

In chapter 4, I ask the questions: (i) how do tropical herbivores overlap spatially with temperate competitors in different habitats and locations of southwestern Australia? and (ii) how does this affect the diversity, intensity and spatial extent of different herbivory functions? I then discuss its

implications for resource partitioning, species displacements, functional complementarity, and the intensity of herbivory with the advent of new herbivorous species as tropicalization progresses.

In chapter 5, I asked the questions: (i) have populations of tropical herbivores persisted with high abundances in temperate reefs after ten years from their incursion following a marine heatwave?; (ii) are seagrass meadows functioning as nursery grounds for tropical herbivores?; (iii) have kelp populations recovered in these reefs?; and (iv) what is the survival rate of kelp individuals in topographical shelters vs exposed areas in the reefs? I then discuss the interplay between the processes that resist (kelp recruitment, survival and reproduction) and maintain canopy free states (recruitment of tropical herbivores, browsing and grazing rates and turf cover) and its implications for conservation management in the context of global warming and further range-shifts of tropical herbivores.
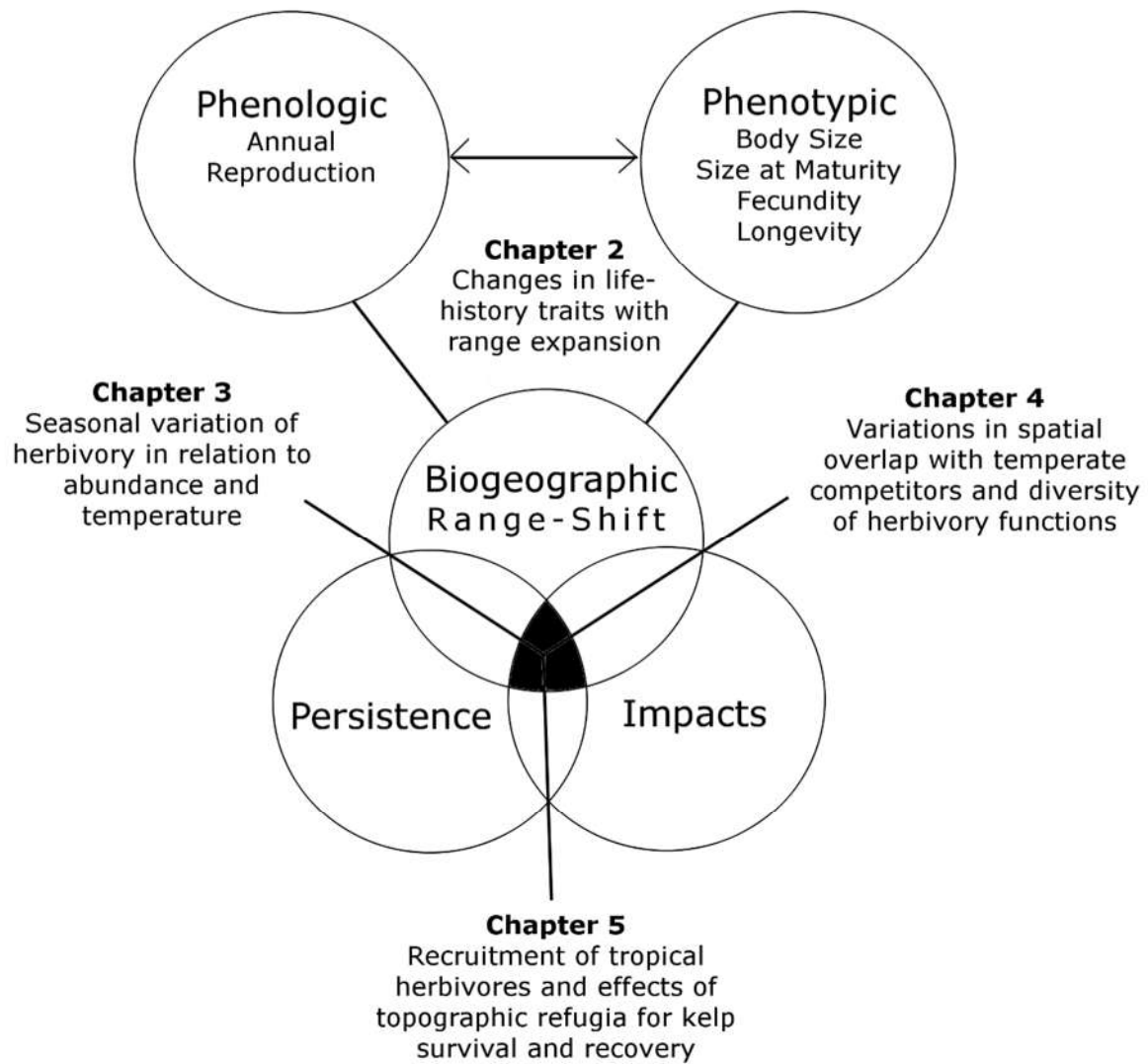
Figure 1.1. Diagram of the research chapters of this thesis and its relationship with the direct impacts of climate change to ectotherms (phenology, phenotype and biogeography) and the indirect impacts that poleward range-shifting tropical herbivores can have on receptive temperate ecosystems.

1.5. References

Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D. & Gravel, D. (2014) From projected species distribution to food-web structure under climate change. *Global Change Biology*, **20**, 730–741.

Angilletta, M.J. & Dunham, A.E. (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *The American Naturalist*, **162**, 332–342.

Angilletta, M.J., Niewiarowski, P.H. & Navas, C.A. (2002) The evolution of thermal physiology in ectotherms. *Journal of thermal biology*, **27**, 249–268.

Angilletta, M.J., Steury, T.D. & Sears, M.W. (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, **44**, 498–509.

Arndt, E. & Schembri, P.J. (2015) Common traits associated with establishment and spread of Lessepsian fishes in the Mediterranean Sea. *Marine Biology*, **162**, 2141–2153.

Audzijonyte, A., Richards, S.A., Stuart-Smith, R.D., Pecl, G., Edgar, G.J., Barrett, N.S., Payne, N. & Blanchard, J.L. (2020) Fish body sizes change with temperature but not all species shrink with warming. *Nature Ecology & Evolution*.

Azzurro, E. & Andaloro, F. (2004) A new settled population of the lessepsian migrant Siganus luridus (Pisces: Siganidae) in Linosa Island—Sicily Strait. *Journal of the Marine Biological Association of the UK*, **84**, 819–821.

Azzurro, E., Franzitta, G., Milazzo, M., Bariche, M. & Fanelli, E. (2017) Abundance patterns at the invasion front: the case of Siganus luridus in Linosa (Strait of Sicily, Central Mediterranean Sea). *Marine and Freshwater Research*, **68**, 697.

Azzurro, E., Peña-Rivas, L., Lloris, D. & Bariche, M. (2013) First documented occurrence of Kyphosus incisor in the Mediterranean Sea. *Marine biodiversity records*, **6**.

Bañón, R., Barros-García, D. & De Carlos, A. (2017) Integrative taxonomy supports the presence of two species of Kyphosus (Perciformes: Kyphosidae) in Atlantic European waters. *Scientia marina*, **81**, 467.

Bañón, R. (2004) New records of two southern fish in Galician waters (NW Spain). *Cybium*, **28**, 367–368.

Bariche, M. & Saad, M. (2008) Settlement of the lessepsian blue-barred parrotfish Scarus ghobban (Teleostei: Scaridae) in the eastern Mediterranean. *Marine biodiversity records*, **1**.

Basford, A.J., Feary, D.A., Truong, G., Steinberg, P.D., Marzinelli, E.M. & Vergés, A. (2016) Feeding habits of range-shifting herbivores: tropical surgeonfishes in a temperate environment. *Marine and Freshwater Research*, **67**, 75.

Bates, A.E., Pecl, G.T., Frusher, S., Hobday, A.J., Wernberg, T., Smale, D.A., Sunday, J.M., Hill, N.A., Dulvy, N.K., Colwell, R.K., Holbrook, N.J., Fulton, E.A., Slawinski, D., Feng, M., Edgar, G.J., Radford, B.T., Thompson, P.A. & Watson, R.A. (2014) Defining and observing stages of climate-mediated range shifts in marine systems. *Global Environmental Change*, **26**, 27–38.

Beare, D.J., Burns, F., Greig, A., Jones, E.G., Peach, K., Kienzle, M., McKenzie, E. & Reid, D.G. (2004) Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. *Marine Ecology Progress Series*.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J. & Saunders, B.J. (2015) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters*, **18**, 714–723.

Ben Rais Lasram, F., Tomasini, J.A., Guilhaumon, F., Romdhane, M.S., Do Chi, T. & Mouillot, D. (2008) Ecological correlates of dispersal success of Lessepsian fishes. *Marine Ecology Progress Series*, **363**, 273–286.

Bernal, M.A., Schunter, C., Lehmann, R., Lightfoot, D.J., Allan, B.J.M., Veilleux, H.D., Rummer, J.L., Munday, P.L. & Ravasi, T. (2020) Species-specific molecular responses of wild coral reef fishes during a marine heatwave. *Science Advances*, **6**, eaay3423.

Bianchi, C.N., Caroli, F., Guidetti, P. & Morri, C. (2018) Seawater warming at the northern reach for southern species: Gulf of Genoa, NW Mediterranean. *Journal of the Marine Biological Association of the UK*, **98**, 1–12.

Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I.H., Winter, M., Bjorkman, A.D., Bowler, D.E., Byrnes, J.E.K., Gonzalez, A., Hines, J., Isbell, F., Jones, H.P., Navarro, L.M., Thompson, P.L. & Dornelas, M. (2019) The geography of biodiversity change in marine and terrestrial assemblages. *Science*, **366**, 339–345.

Booth, D.J., Beretta, G.A., Brown, L. & Figueira, W.F. (2018) Predicting Success of Range-Expanding Coral Reef Fish in Temperate Habitats Using Temperature-Abundance Relationships. *Frontiers in Marine Science*, **5**.

Booth, D.J., Figueira, W.F., Gregson, M.A., Brown, L. & Beretta, G. (2007) Occurrence of tropical fishes in temperate southeastern Australia: Role of the East Australian Current. *Estuarine, Coastal and Shelf Science*, **72**, 102–114.

Boström, C., Jackson, E.L. & Simenstad, C.A. (2006) Seagrass landscapes and their effects on associated fauna: A review. *Estuarine, Coastal and Shelf Science*, **68**, 383–403.

Brander, K. (1995) The effect of temperature on growth of Atlantic cod (Gadus morhua L.). *ICES Journal of Marine Science*, **52**, 1–10.

Brandl, S.J. & Bellwood, D.R. (2014) Individual-based analyses reveal limited functional overlap in a coral reef fish community. *The Journal of Animal Ecology*, **83**, 661–670.

Burkepile, D.E. & Hay, M.E. (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 16201–16206.

Burrows, M.T., Bates, A.E., Costello, M.J., Edwards, M., Edgar, G.J., Fox, C.J., Halpern, B.S., Hiddink, J.G., Pinsky, M.L., Batt, R.D., García Molinos, J., Payne, B.L., Schoeman, D.S., Stuart-Smith, R.D. & Poloczanska, E.S. (2019) Ocean community warming responses explained by thermal affinities and temperature gradients. *Nature Climate Change*.

Caputi, N., de Lestang, S., Feng, M. & Pearce, A. (2009) Seasonal variation in the long-term warming trend in water temperature off the Western Australian coast. *Marine and Freshwater Research*, **60**, 129.

Cetina-Heredia, P., Roughan, M., van Sebille, E., Feng, M. & Coleman, M.A. (2015) Strengthened currents override the effect of warming on lobster larval dispersal and survival. *Global Change Biology*, **21**, 4377–4386.

Cheung, W.W.L., Lam, V.W.Y. & Pauly, D. (2008) *Dynamic Bioclimate Envelope Model to Predict Climate-Unduced Changes in Distributions of Marine Fishes and Invertebrates* (eds C WWL, L VWY, and P D). Campbell, NY.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. & Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. , **10**, 235–251.

Cheung, W.W.L., Meeuwig, J.J., Feng, M., Harvey, E., Lam, V.W.Y., Langlois, T., Slawinski, D., Sun, C. & Pauly, D. (2012) Climate-change induced tropicalisation of marine communities in Western Australia. *Marine and Freshwater Research*, **63**, 415.

Cheung, W.W.L., Reygondeau, G. & Frölicher, T.L. (2016) Large benefits to marine fisheries of meeting the 1.5°C global warming target. *Science*, **354**, 1591–1594.

Coleman, M.A., Wood, G., Filbee-Dexter, K., Minne, A.J.P., Goold, H.D., Vergés, A., Marzinelli, E.M., Steinberg, P.D. & Wernberg, T. (2020) Restore or redefine: future trajectories for restoration. *Frontiers in Marine Science*, **7**.

Connell, S.D., Russell, B.D. & Irving, A.D. (2011) Can strong consumer and producer effects be reconciled to better forecast 'catastrophic' phase-shifts in marine ecosystems? *Journal of Experimental Marine Biology and Ecology*, **400**, 296–301.

Crozier, L.G. & Hutchings, J.A. (2014) Plastic and evolutionary responses to climate change in fish. *Evolutionary applications*, **7**, 68–87.

Cvitanovic, C. & Bellwood, D.R. (2009) Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral reefs (Online)*, **28**, 127–133.

Dippner, J.W. (1997) Recruitment success of different fish stocks in the North Sea in relation to climate variability. *Deutsche Hydrographische Zeitschrift*, **49**, 277–293.

Dragičević, B., Fricke, R., Soussi, J.B., Ugarković, P., Dulčić, J. & Azzurro, E. (2021) On the occurrence of Abudefduf spp.(Pisces: Pomacentridae) in the Mediterranean Sea: a critical review with new records. *Bioinvasions records*, **10**.

Eger, A.M. & Baum, J.K. (2020) Trophic cascades and connectivity in coastal benthic marine ecosystems: a meta-analysis of experimental and observational research. *Marine Ecology Progress Series*, **ITRS**.

Eme, J. & Bennett, W.A. (2009) Critical thermal tolerance polygons of tropical marine fishes from Sulawesi, Indonesia. *Journal of thermal biology*, **34**, 220–225.

Encarnação, Morais, J.;, Baptista, P.;, Cruz, V.;, Teodósio, J.; & Alexandra, M. (2019) New Evidence of Marine Fauna Tropicalization off the Southwestern Iberian Peninsula (Southwest Europe). *Diversity*.

Erguden, D., Bayhan, Y.K., Alagöz Erguden, S. & Altun, A. (2018) Range extension of blue-barred parrotfish Scarus ghobban Forsskal, 1775 along the Mediterranean Coast of Turkey. *Acta Biologica Turcica*, **31**, 82–85.

Feary, D.A., Pratchett, M.S., J Emslie, M., Fowler, A.M., Figueira, W.F., Luiz, O.J., Nakamura, Y. & Booth, D.J. (2014) Latitudinal shifts in coral reef fishes: why some species do and others do not shift. , **15**, 593–615.

Figueira, W.F. & Booth, D.J. (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Global Change Biology*, **16**, 506–516.

Filbee-Dexter, K. & Scheibling, R.E. (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*, **495**, 1–25.

Fincham, J.I., Rijnsdorp, A.D. & Engelhard, G.H. (2013) Shifts in the timing of spawning in sole linked to warming sea temperatures. *Journal of Sea Research*, **75**, 69–76.

Floeter, S.R., Behrens, M.D., Ferreira, C.E.L., Paddack, M.J. & Horn, M.H. (2005) Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology*, **147**, 1435–1447.

Fodrie, F.J., Heck, K.L., Powers, S.P., Graham, W.M. & Robinson, K.L. (2010) Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. *Global Change Biology*, **16**, 48–59.

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M. & Dolgov, A.V. (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature climate change*, **5**, 673–677.

Fowler, A.M., Parkinson, K. & Booth, D.J. (2017) New poleward observations of 30 tropical reef fishes in temperate southeastern Australia. *Marine Biodiversity*, **48**, 1–6.

Goren, M. & Aronov, A. (2002) First record of the Indo-Pacific parrotfish *Scarus ghobban* in the eastern Mediterranean. *Cybium*, **26**, 239–240.

Goren, M., Galil, B.S., Gevili, R. & Stern, N. (2016) First record of the Brassy Chub*Kyphosus vaigiensis* (Quoy & Gaimard, 1825) in the Eastern Mediterranean (Osteichthyes: Perciformes: Kyphosidae). *Zoology in the Middle East*, **62**, 319–322.

Gruner, D.S., Smith, J.E., Seabloom, E.W., Sandin, S.A., Ngai, J.T., Hillebrand, H., Harpole, W.S., Elser, J.J., Cleland, E.E., Bracken, M.E.S., Borer, E.T. & Bolker, B.M. (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecology Letters*, **11**, 740–755.

Hamilton, S.L. & Caselle, J.E. (2015) Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proceedings. Biological Sciences / the Royal Society*, **282**, 20141817.

Hasegawa, M. (2010) Isoyake studies in Shizuoka Prefecture, Japan. *Bull Fish Res Agen*.

Heck, K.L., Fodrie, F.J., Madsen, S., Baillie, C.J. & Byron, D.A. (2015) Seagrass consumption by native and a tropically associated fish species: potential impacts of the tropicalization of the northern Gulf of Mexico. *Marine Ecology Progress Series*, **520**, 165–173.

Hobday, A.J. & Pecl, G.T. (2014) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. *Reviews in fish biology and fisheries*, **24**, 415–425.

Holbrook, S.J., Schmitt, R.J. & Stephens, J.S. (1997) Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications*.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. & Willis, B. (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, **17**, 360–365.

Hyndes, G.A., Heck, K.L., Vergés, A., Harvey, E.S., Kendrick, G.A., Lavery, P.S., McMahon, K., Orth, R.J., Pearce, A., Vanderklift, M., Wernberg, T., Whiting, S. & Wilson, S. (2016) Accelerating tropicalization and the transformation of temperate seagrass meadows. *Bioscience*, **66**, 938–948.

IPCC. (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (eds V Masson-Delmotte, P Zhai, A Pirani, SL Connors, C Péan, S Berger, N Caud, Y Chen, L Goldfarb, MI Gomis, M Huang, K Leitzell, E Lonnoy, JBR Matthews, TK Maycock, T Waterfield, O Yelekçi, R Yu, and B Zhou). Cambridge University Press. Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R., Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R. & Taw, N. (2011) Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology*, **400**, 17–32.

Kiparissis, S., Loukovitis, D. & Batargias, C. (2012) First record of the Bermuda sea chub Kyphosus saltatrix (Pisces: Kyphosidae) in Greek waters. *Marine biodiversity records*, **5**.

kiriyama, T., Fujii, A. & Fujita, Y. (2005) Feeding and Characteristic Bite Marks on Sargassum fusiforme by Several Herbivorous Fishes. *Aquaculture Science*, **53**, 355–365.

Kiyağa, V.B., Mavruk, S., Özyurt, C.E., Akamca, E. & Coşkun, Ç. (2019) Range extension of *Kyphosus vaigiensis* (Quoy & Gaimard, 1825) in the northeastern Mediterranean, İskenderun Bay, Turkey. *TURKISH JOURNAL OF ZOOLOGY*.

Kleypas, J., Allemand, D., Anthony, K., Baker, A.C., Beck, M.W., Hale, L.Z., Hilmi, N., Hoegh-Guldberg, O., Hughes, T., Kaufman, L., Kayanne, H., Magnan, A.K., Mcleod, E., Mumby, P., Palumbi, S., Richmond, R.H., Rinkevich, B., Steneck, R.S., Voolstra, C.R., Wachenfeld, D. & Gattuso, J.-P. (2021) Designing a blueprint for coral reef survival. *Biological Conservation*, **257**, 109107.

Knudsen, S.W. & Clements, K.D. (2016) World-wide species distributions in the family Kyphosidae (Teleostei: Perciformes). *Molecular Phylogenetics and Evolution*, **101**, 252–266.

Kumagai, N.H., García Molinos, J., Yamano, H., Takao, S., Fujii, M. & Yamanaka, Y. (2018) Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **115**, 8990–8995.

Kuwahara, H. (2015) The Evaluation of Current Status for Grazing Control Techniques of Herbivorous Fish. *Fisheries Engineering*, **51**, 253–257.

Lamy, T., Koenigs, C., Holbrook, S.J., Miller, R.J., Stier, A.C. & Reed, D.C. (2020) Foundation species promote community stability by increasing diversity in a giant kelp forest. *Ecology*, e02987.

Laufkötter, C., Zscheischler, J. & Frölicher, T.L. (2020) High-impact marine heatwaves attributable to human-induced global warming. *Science*, **369**, 1621–1625.

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J.M., Hare, S.R., Ottersen, G., Perry, R.I., Roy, C., van der Lingen, C.D. & Werner, F. (2006) Climate variability, fish, and fisheries. *Journal of climate*, **19**, 5009–5030.

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F. & Pérez, T. (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology & Evolution*, **25**, 250–260.

Lenanton, R.C.J., Dowling, C.E., Smith, K.A., Fairclough, D.V. & Jackson, G. (2017) Potential influence of a marine heatwave on range extensions of tropical fishes in the eastern Indian Ocean— Invaluable contributions from amateur observers. *Regional Studies in Marine Science*, **13**, 19–31.

Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon, A.K., Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., Blamey, L.K., Hereu, B., Ballesteros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M., Fujita, D. & Johnson, L.E. (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **370**, 20130269.

Lloyd, P., Plagányi, É.E., Weeks, S.J., Magno-Canto, M. & Plagányi, G. (2012) Ocean warming alters species abundance patterns and increases species diversity in an African sub-tropical reef-fish community. *Fisheries Oceanography*, **21**, 78–94.

Longo, G.O., Hay, M.E., Ferreira, C.E.L. & Floeter, S.R. (2018) Trophic interactions across 61 degrees of latitude in the Western Atlantic. *Global Ecology and Biogeography*.

Lonhart, S.I., Jeppesen, R., Beas-Luna, R., Crooks, J.A. & Lorda, J. (2019) Shifts in the distribution and abundance of coastal marine species along the eastern Pacific Ocean during marine heatwaves from 2013 to 2018. *Marine biodiversity records*, **12**, 13.

Lundberg, B., Ogorek, R., Galil, B.S. & Goren, M. (2001) Dietary choices of siganid fish at shiqmona reef, israel. *Israel journal of zoology*, **50**, 39–53.

Maclean, I.M.D. & Wilson, R.J. (2011) Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 12337–12342.

Mannino, A.M., Balistreri, P., Iaciofano, D., Galil, B.S. & Brutto, S.L. (2015) An additional record of Kyphosus vaigiensis (Quoy & Gaimard, 1825) (Osteichthyes, Kyphosidae) from Sicily clarifies the confused situation of the Mediterranean kyphosids. *Zootaxa*, **3963**, 45–54.

Mantyka, C.S. & Bellwood, D.R. (2007) Macroalgal grazing selectivity among herbivorous coral reef fishes. *Marine Ecology Progress Series*, **352**, 177–185.

Marshak, A.R. & Heck, K.L. (2017) Interactions between range-expanding tropical fishes and the northern Gulf of Mexico red snapper Lutjanus campechanus. *Journal of Fish Biology*, **91**, 1139–1165.

Meekan, M.G. & Choat, J.H. (1997) Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs. *Marine Biology*, **128**, 373–383.

Merilä, J. & Hendry, A.P. (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary applications*, **7**, 1–14.

Milazzo, M., Mirto, S., Domenici, P. & Gristina, M. (2013) Climate change exacerbates interspecific interactions in sympatric coastal fishes. *The Journal of Animal Ecology*, **82**, 468–477.

Monaco, C.J., Booth, D.J., Figueira, W.F., Gillanders, B.M., Schoeman, D.S., Bradshaw, C.J.A. & Nagelkerken, I. (2021) Natural and anthropogenic climate variability shape assemblages of range-extending coral-reef fishes. *Journal of biogeography*.

Monaco, C.J., Bradshaw, C.J.A., Booth, D.J., Gillanders, B.M., Schoeman, D.S. & Nagelkerken, I. (2020) Dietary generalism accelerates arrival and persistence of coral-reef fishes in their novel ranges under climate change. *Global Change Biology*.

Morley, J.W., Selden, R.L., Latour, R.J., Frölicher, T.L., Seagraves, R.J. & Pinsky, M.L. (2018) Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *Plos One*, **13**, e0196127.

Munday, P.L., Donelson, J.M. & Domingos, J.A. (2017) Potential for adaptation to climate change in a coral reef fish. *Global Change Biology*, **23**, 307–317.

Nakamura, Y., Feary, D.A., Kanda, M. & Yamaoka, K. (2013) Tropical fishes dominate temperate reef fish communities within western Japan. *Plos One*, **8**, e81107.

Nakayama, Y. (1999) Grazing of the brown alga Ecklonia cava by three herbivorous fishes on the coast of Nakagi, South Izu, central Japan (tran S Arai). *Japanese Journal of Phycology*, 105–112.

Nimura, K., Takatsuji, H., Masuda, S. & Shimamoto, J. (2007) Growth and maturation of *Ecklonia cava* and Eisenia arborea seedlings transplanted along the coast of Hainan, Shizuoka prefecture and the grazing caused by herbivorous fish *Siganus fuscescens*. *Aquaculture Science*, **55**, 541–546.

Oliver, E.C.J., Donat, M.G., Burrows, M.T., Moore, P.J., Smale, D.A., Alexander, L.V., Benthuysen, J.A., Feng, M., Sen Gupta, A., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Straub, S.C. & Wernberg, T. (2018) Longer and more frequent marine heatwaves over the past century. *Nature Communications*, **9**, 1324.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. & Stenseth, N. (2001) Ecological effects of the North Atlantic Oscillation. *Oecologia*, **128**, 1–14.

Parker, R.O. & Dixon, R.L. (1998) Changes in a North Carolina reef fish community after 15 years of intense fishing—global warming implications. *Transactions of the American Fisheries Society*, **127**, 908–920.

Parker, J.R.C., Saunders, B.J., Bennett, S., DiBattista, J.D., Shalders, T.C. & Harvey, E.S. (2019) Shifts in Labridae geographical distribution along a unique and dynamic coastline. *Diversity & Distributions*.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Paxton, A.B., Peterson, C.H., Taylor, J.C., Adler, A.M., Pickering, E.A. & Silliman, B.R. (2019) Artificial reefs facilitate tropical fish at their range edge. *Communications Biology*, **2**, 168.

Pearce, A. & Feng, M. (2007) Observations of warming on the Western Australian continental shelf. *Marine and Freshwater Research*, **58**, 914.

Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.

Pinsky, M.L., Reygondeau, G., Caddell, R., Palacios-Abrantes, J., Spijkers, J. & Cheung, W.W.L. (2018) Preparing ocean governance for species on the move. *Science*, **360**, 1189–1191.

Planque, B. & Frédou, T. (1999) Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 2069–2077.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A. & Richardson, A.J. (2013) Global imprint of climate change on marine life. *Nature climate change*, **3**, 919–925.

Polyakov, I.V., Alkire, M.B., Bluhm, B.A., Brown, K.A., Carmack, E.C., Chierici, M., Danielson, S.L., Ellingsen, I., Ershova, E.A., Gårdfeldt, K., Ingvaldsen, R.B., Pnyushkov, A.V., Slagstad, D. & Wassmann, P. (2020) Borealization of the Arctic Ocean in Response to Anomalous Advection From Sub-Arctic Seas. *Frontiers in Marine Science*, **7**.

Poore, A.G.B., Campbell, A.H., Coleman, R.A., Edgar, G.J., Jormalainen, V., Reynolds, P.L., Sotka, E.E., Stachowicz, J.J., Taylor, R.B., Vanderklift, M.A. & Duffy, J.E. (2012) Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters*, **15**, 912–922.

Pörtner, H.O. & Peck, M.A. (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*, **77**, 1745–1779.

Pratchett, M.S., Hoey, A.S., Wilson, S.K., Messmer, V. & Graham, N.A.J. (2011) Changes in Biodiversity and Functioning of Reef Fish Assemblages following Coral Bleaching and Coral Loss. *Diversity*, **3**, 424–452.

Raitsos, D.E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulou, A.M., Theocharis, A. & Papathanassiou, E. (2010) Global climate change amplifies the entry of tropical species into the eastern Mediterranean Sea. *Limnology and Oceanography*, **55**, 1478–1484.

Reusch, T.B.H. (2014) Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evolutionary applications*, **7**, 104–122.

Richards, Z., Kirkendale, L., Moore, G., Hosie, A., Huisman, J., Bryce, M., Marsh, L., Bryce, C., Hara, A., Wilson, N., Morrison, S., Gomez, O., Ritchie, J., Whisson, C., Allen, M., Betteridge, L., Wood, C., Morrison, H., Salotti, M., Hansen, G. & Fromont, J. (2016) Marine Biodiversity in Temperate Western Australia: Multi-Taxon Surveys of Minden and Roe Reefs. *Diversity*, **8**, 7.

Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Mollmann, C. & Pinnegar, J.K. (2009) Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*, **66**, 1570–1583.

Roessig, J.M., Woodley, C.M., Cech, J.J. & Hansen, L.J. (2004) Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in fish biology and fisheries*, **14**, 251–275.

Rogers, L.A. & Dougherty, A.B. (2019) Effects of climate and demography on reproductive phenology of a harvested marine fish population. *Global Change Biology*, **25**, 708–720.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Ruela, R., Sousa, M.C., deCastro, M. & Dias, J.M. (2020) Global and regional evolution of sea surface temperature under climate change. *Global and planetary change*, **190**, 103190.

Sala, E., Kizilkaya, Z., Yildirim, D. & Ballesteros, E. (2011) Alien marine fishes deplete algal biomass in the Eastern Mediterranean. *Plos One*, **6**, e17356.

Sanford, E., Sones, J.L., García-Reyes, M., Goddard, J.H.R. & Largier, J.L. (2019) Widespread shifts in the coastal biota of northern California during the 2014-2016 marine heatwaves. *Scientific Reports*, **9**, 4216.

Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C., Burrows, M.T., Alexander, L.V., Benthuysen, J.A., Donat, M.G., Feng, M., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Sen Gupta, A., Payne, B.L. & Moore, P.J. (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature climate change*, **9**, 306–312.

Sorte, C.J.B., Williams, S.L. & Carlton, J.T. (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, **19**, 303–316.

Steneck, R.S., Bellwood, D.R. & Hay, M.E. (2017) Herbivory in the marine realm. *Current Biology*, **27**, R484–R489.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental conservation*, **29**.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.

Streit, R.P., Cumming, G.S. & Bellwood, D.R. (2019) Patchy delivery of functions undermines functional redundancy in a high diversity system. *Functional ecology*.

Strydom, S., Murray, K., Wilson, S., Huntley, B., Rule, M., Heithaus, M., Bessey, C., Kendrick, G.A., Burkholder, D., Holmes, T., Fraser, M.W. & Zdunic, K. (2020) Too hot to handle: unprecedented seagrass death driven by marine heatwave in a World Heritage Area. *Global Change Biology*.

Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M. & Edgar, G.J. (2018) Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature*, **560**, 92–96.

Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., Edgar, G.J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R.A., Smale, D.A., Fulton, E.A., Slawinski, D., Feng, M., Radford, B.T., Thompson, P.A. & Bates, A.E. (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, **18**, 944–953.

Tanaka, K., Taino, S., Haraguchi, H., Prendergast, G. & Hiraoka, M. (2012) Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. *Ecology and Evolution*, **2**, 2854–2865.

Thomson, J.A., Burkholder, D.A., Heithaus, M.R., Fourqurean, J.W., Fraser, M.W., Statton, J. & Kendrick, G.A. (2015) Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Global Change Biology*, **21**, 1463–1474.

Tose, K., Hirata, T., Kotera, Y., Kanda, M. & Nakamura, Y. (2017) Occurrence and reproduction of tropical fishes in ocean warming hotspots of Japanese temperate reefs. *Environmental biology of fishes*, **100**, 617–630.

Tsuchida, S. (1995) The relationship between upper temperature tolerance and final preferendum of Japanese marine fish. *Journal of thermal biology*, **20**, 35–41.

Vasconcelos, P., Carvalho, A.N., Moura, P., Ramos, J. & Gaspar, M.B. (2017) First record of Acanthurus monroviae (Osteichthyes: Perciformes: Acanthuridae) in southern Portugal, with notes on its recent distributional spread in the northeastern Atlantic and Mediterranean. *Marine Biodiversity*, 1–9.

Vergés, A., Doropoulos, C., Czarnik, R., McMahon, K., Llonch, N. & G. B. Poore, A. (2018) Latitudinal variation in seagrass herbivory: Global patterns and explanatory mechanisms. *Global Ecology and Biogeography*.

Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M.A., Wernberg, T., Ainsworth, T. & Steinberg, P.D. (2019) Tropicalisation of temperate reefs: Implications for ecosystem functions and management actions. *Functional ecology*, **33**, 1000–1013.

Vergés, A., Steinberg, P.D., Hay, M.E., Poore, A.G.B., Campbell, A.H., Ballesteros, E., Heck, K.L., Booth, D.J., Coleman, M.A., Feary, D.A., Figueira, W., Langlois, T., Marzinelli, E.M., Mizerek, T., Mumby, P.J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A.S., Smale, D.A. & Wilson, S.K. (2014a) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings. Biological Sciences / the Royal Society*, **281**, 20140846.

Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z., Dendrinos, P., Karamanlidis, A.A., Spiegel, D. & Sala, E. (2014b) Tropical rabbitfish and the deforestation of a warming temperate sea. *The Journal of Ecology*, **102**, 1518–1527.

Vila-Gispert, A., Moreno-Amich, R. & García-Berthou, E. (2002) Gradients of life-history variation: an intercontinental comparison of fishes. *Reviews in Fish Biology and Fisheries*.

Wallingford, P.D., Morelli, T.L., Allen, J.M., Beaury, E.M., Blumenthal, D.M., Bradley, B.A., Dukes, J.S., Early, R., Fusco, E.J., Goldberg, D.E., Ibáñez, I., Laginhas, B.B., Vilà, M. & Sorte, C.J.B. (2020) Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. *Nature Climate Change*.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C.J., Hovey, R.K., Harvey, E.S., Holmes, T.H., Kendrick, G.A., Radford, B., Santana-Garcon, J., Saunders, B.J., Smale, D.A., Thomsen, M.S., Tuckett, C.A., Tuya, F. & Wilson, S. (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science*, **353**, 169–172.

Wernberg, T., Krumhansl, K., Filbee-Dexter, K. & Pedersen, M.F. (2019) Status and trends for the world's kelp forests. *World seas: an environmental evaluation* pp. 57–78. Elsevier.

Wu, L., Cai, W., Zhang, L., Nakamura, H., Timmermann, A., Joyce, T., McPhaden, M.J., Alexander, M., Qiu, B., Visbeck, M., Chang, P. & Giese, B. (2012) Enhanced warming over the global subtropical western boundary currents. *Nature climate change*, **2**, 161–166.

Yamano, H., Sugihara, K. & Nomura, K. (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophysical research letters*, **38**.

Yatsuya, K., Kiyomoto, S. & Yoshimura, T. (2015) Seasonal changes in dietary composition of the herbivorous fish Kyphosus bigibbus in southwestern Japan. *Fisheries science : FS*, **81**, 1025–1033.

Zarco-Perello, S. & Enríquez, S. (2019) Remote underwater video reveals higher fish diversity and abundance in seagrass meadows, and habitat differences in trophic interactions. *Scientific Reports*, **9**, 6596.

Zarco-Perello, S., Wernberg, T., Langlois, T.J. & Vanderklift, M.A. (2017) Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports*, **7**, 820.

Chapter 2. Maximization of fitness by phenological and phenotypic plasticity in range expanding rabbitfish (Siganidae).

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2.1. Abstract

Global warming is modifying the phenology, phenotype and biogeography of species around the world. Evidence of these effects have increased over recent decades; however, we still have a poor understanding of the possible outcomes of their interplay, hindering our ability to accurately predict the consequences of climate change in populations and ecosystems. We examined the effect that changes in biogeography can have on the life-history traits of two of the most successful range-extending fish species in the world: the tropical rabbitfishes *Siganus fuscescens* and *Siganus rivulatus*. Both species have established abundant populations at higher latitudes in the northern and southern hemispheres and have been identified as important ecological engineers with the potential to alter the community structure of seaweed forests (Laminariales and Fucales) in temperate regions. Life-history trait information from across their global distribution was compiled from the published literature and meta-analyses were conducted to assess changes in (i) the onset and duration of reproductive periods, (ii) fecundity, (iii) size at maturity, (iv) growth rates, (v) maximum body sizes and (vi) longevity in populations at the leading edge of range expansion in relation to sea surface temperature and primary productivity (*i.e.*, a common proxy for nutritional resource levels). Results showed that populations at highest latitudes had shortened their reproductive periods and reduced growth rates, taking longer to reach sexual maturity and maximum sizes, but compensated this with higher fecundity per length class and longer lifespans than populations in warmer environments. Conditions of low primary productivity and temperature in the Mediterranean Sea resulted in lower growth rates and body sizes for *S. rivulatus*, but also lower length at maturity, leading to increased life-time reproductive output. The results suggest that plasticity in the phenology and phenotype of range-expanding species would be important to enhance their fitness in environments with greater seasonal fluctuations of temperature, facilitating their persistence at higher latitudes and possible further poleward expansions. Quantifying the magnitude and direction of these responses can improve our understanding and ability to forecast species redistributions and the repercussions in the functioning of temperate ecosystems.

2.2. Introduction

Climate change is affecting all the levels of organization in natural ecosystems (Pecl *et al.* 2017). Temperature is one of the strongest environmental factors triggering phenotypic plasticity in all domains of life, including physiology, morphology and behavior (Brown *et al.* 2004; Sommer 2020). Global warming has continued for decades with forecasts indicating that this trend is likely irreversible and will continue until the end of the century (IPCC 2021). As a consequence, temperatures rising

earlier in the year have triggered advances in the reproductive phenology of many species, with a generally faster pace of change in the ocean (Burrows *et al.* 2011). By shifting phenological patterns, species are allowing their offspring to develop under the best thermal conditions during spring and summer (Burrows *et al.* 2011; Cohen, Lajeunesse & Rohr 2018). Recent evidence also suggests that species are experiencing decreases in their average body sizes as a consequence of environmental warming (Daufresne, Lengfellner & Sommer 2009; Sheridan & Bickford 2011; Baudron *et al.* 2014). These changes align with the pervasive size-temperature patterns for endotherms (Bergmann's Rule) and ectotherms (Temperature-Size-Rule) around the globe, which describe a negative relationship between the body dimensions and temperature (Atkinson & Sibly 1997; Meiri & Dayan 2003). Additionally, warming has facilitated poleward range expansions. Rising temperatures at low latitudes are affecting populations by reaching upper critical thresholds for core biological activities, leading to range contractions. In contrast, higher latitudes are becoming more favorable for warm-affinity species, causing an increase in species richness in temperate regions (Chaudhary *et al.* 2021). Climate-induced changes in distribution are considered important indirect effects of climate change, because as introduced species, they can create novel biotic interactions and modify the trophic chains and ecosystem functioning (Blois *et al.* 2013). Thus, identifying biological traits and processes allowing species to extend their ranges is an important and active field of research (Sunday *et al.* 2015).

Successful range-expanding species must have the flexibility to maximize their fitness through modifications in their life-history according to the new local environment (Atkinson & Sibly 1997). Several evaluations exist about how some biological traits can favor range-shifts, such as migratory capacity, diet breath, or habitat requirements (Sunday *et al.* 2015; McLean, Mouillot & Auber 2018). However, following expansion, the permanent establishment of new populations relies in successful reproduction and offspring survival under novel thermal regimes, largely dependent on the plasticity in life-history strategies of species (Bates *et al.* 2014; Sommer 2020). While increases in mean temperature around the world are important, facilitating range expansions, seasonal fluctuations will remain larger at higher latitudes (Amarasekare & Simon 2020). In particular, winters in temperate regions are more severe and last longer than in the tropics, acting as a strong selective force that dictates developmental rates and survival of early ontogenetic stages (Osland *et al.* 2021). Thus, populations at the leading edge of range expansion may have to retard and shorten their reproductive activities to synchronize the rearing of their offspring with the warmest months in the year (Burrows *et al.* 2011; Cohen *et al.* 2018). Development under lower temperatures would likely result in reductions of growth rates and possibly increase body sizes in the long term (Sheridan & Bickford 2011). In turn, changes in body size can carry trade-offs in other traits; for instance, bigger organisms tend to grow slower and start reproducing later but can have greater fecundity and longer life-spans,

having the advantage of reproducing for more years but only if external sources of mortality, such as predation, are low (Vila-Gispert, Moreno-Amich & García-Berthou 2002; Angilletta, Steury & Sears 2004). The magnitude and direction of change will depend on the combined influence of other environmental factors in addition to temperature. Food availability is particularly important (the resource availability hypothesis), because poor nutrition results in limited somatic development even under the optimal thermal conditions (Geist 1987; Morales-Castilla, Rodríguez & Hawkins 2012).

Knowledge of these responses is important because a better understanding of the drivers of species' persistence at higher latitudes could improve the accuracy of forecasts of changes in geographic distribution and ecosystem impacts (Valladares *et al.* 2014). This has been recognized in modelling frameworks and conceptual models by acknowledging the importance of phenotypic plasticity, but empirical evidence remains scarce (Donelson *et al.* 2019). The present study aimed to assess the magnitude and direction of life-history trait variation for range-shifting species by compiling information spanning 67° of latitude and conducting a meta-analysis of the phenological and phenotypic changes of two of the most successful range-expanding species of fish in the northern and southern hemispheres of the world: the rabbitfish (Siganidae) *Siganus fuscescens* and *Siganus rivulatus* (Bariche, Harmelin-Vivien & Quignard 2003; Akiyama, Naganuma & Katayama 2009; Lenanton *et al.* 2017). Specifically, we assessed how distributional shifts can affect (i) reproductive phenology: the start, peak and duration of their annual spawning period, (ii) fecundity (eggs per individual), (iii) minimum size at maturity, (iv) growth rates, (v) maximum body sizes and (vi) longevity. We hypothesized that range-expanding populations will experience (1) shorter spawning periods with onsets later in the year, (2) increases in fecundity factored by fish size, (3) increases in size at maturity and (4) decreases in growth rates that will lead to (5) increases in maximum sizes and longevity, in comparison with populations in warmer regions.

2.3. Materials and Methods

Species of study

Species of the family Siganidae are considered important herbivores and ecological engineers which can mediate the community structure of marine ecosystems through high consumption rates of macrophytes (Fox & Bellwood 2008). Their range-expansion has been identified as a potential threat to the biodiversity levels and services of temperate ecosystems because they can contribute to overgrazing of the canopy-forming seaweed that constitute the foundation species (Sala *et al.* 2011; Bennett *et al.* 2015; Kumagai *et al.* 2018; Zarco-Perello *et al.* 2021). This study focused on two successful range-extending rabbitfish species. (1) *Siganus fuscescens* has expanded its distribution to

temperate western Australia following an unprecedented intensification of the Leeuwin Current during a marine heatwave in 2011 (Zarco-Perello *et al.* 2017, 2019) and to northern Japan following a gradual warming of the Kuroshio Current (Kumagai *et al.* 2018). (2) *Siganus rivulatus* expanded its distribution from the Red Sea into the Mediterranean Sea following the opening of the Suez Canal, and continues to expand further as waters keep warming due to climate change (Azzurro *et al.* 2017).

Data collection

Quantitative information was obtained from the literature using the following two independent search criteria in the Web of Science: {*Siganus OR rabbitfish* AND *reproduction OR fecundity OR spawning*} and {*Siganus OR rabbitfish* AND *size OR length OR growth OR Age OR abundance*}. Publications with useful information were then selected, and the references cited within, as well as the publications that had cited each of these works, were reviewed in turn to obtain more publications that were not detected by the initial online searches. *Siganus fuscescens* (Houttuyn 1782) and *Siganus canaliculatus* were considered synonyms (from here on referred to as *S. fuscescens*) and data from studies of these were pooled (Hsu et al. 2011). In total we obtained 46 studies related to reproduction, 14 studies related to growth and 91 studies related to body size (including studies that included both reproduction and growth). Data collected for *S. fuscescens* spanned tropical, subtropical and temperate environments across the Indian and Pacific Oceans, whereas data for *Siganus rivulatus* (Forsskål & Niebuhr 1775) spanned subtropical and temperate environments across the Red Sea and Mediterranean Sea (Fig. 1 and Table S1 in Supporting Information). Data were extracted from tables and scatterplot figures using the software DataThief (Flower et al. 2016). In all cases, length was standardized to fork length (FL) using the length-length equations reported in FishBase for *S. fuscesens* (Froese and Pauly 2019), and by Shakman et al. (2008) for *S. rivulatus*.
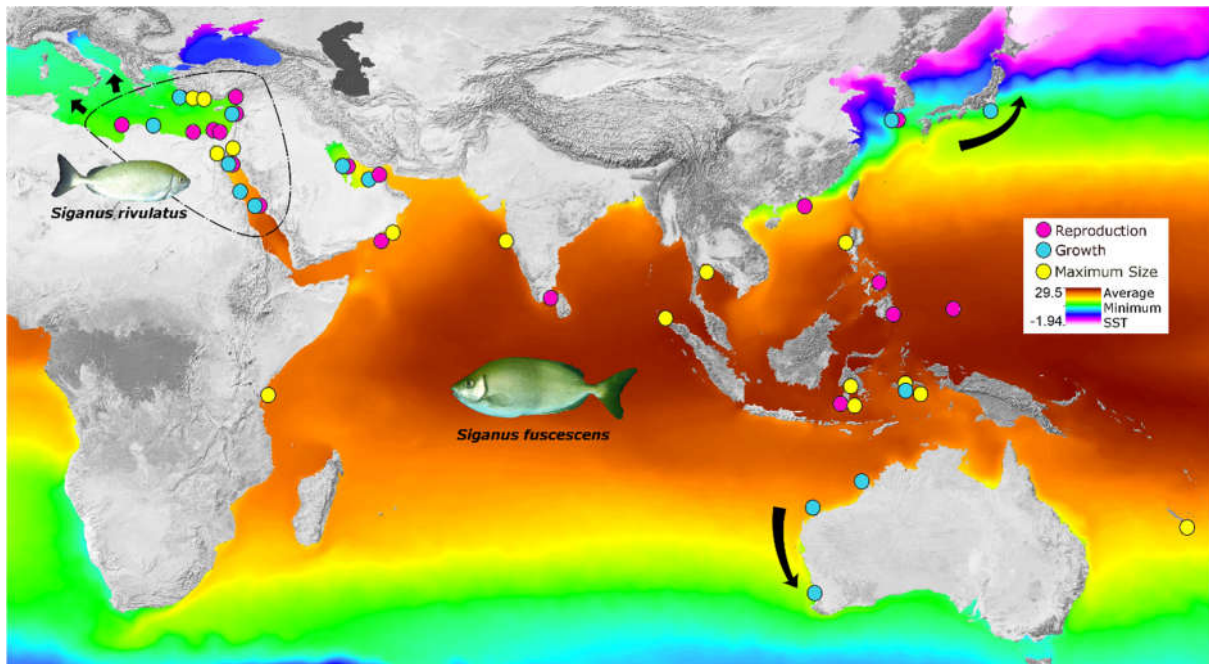
Figure 1. Sampling locations of information collected from the literature on reproduction (spawning and fecundity), growth rates, longevity and maximum length of *Siganus rivulatus* and *Siganus fuscescens*. Maximum body size information was also obtained from studies that included both reproduction and growth. Arrows indicate the direction of range expansion towards temperate environments for each species of rabbitfish.

Reproduction

Information about the annual period and peak of spawning (specific months and duration), its relationship with the moon cycle, minimum length at maturity (mm) and fecundity was extracted only from studies with consistent monthly sampling across the year (n=18), which determined reproductive stages by examination of gonads, gonadosomatic index (GSI = [Gonad Weight/Body Weight] x 100) and fecundity (gravimetric total number of ripe eggs per individual = Eggs in Gonad Subsample x Total Gonad Weight/Gonad Subsample Weight) across multiple length classes of female fish (Table S1).

Growth and Longevity

Information on growth and longevity for both species of rabbitfish was only extracted from studies that reported growth curves based on length-at-age information produced from the analysis of sagittal otoliths of females and males. In addition, we estimated length-at-age information for populations of *S. fuscescens* from temperate (Perth) and tropical environments (Pilbara and Kimberley) of Western Australia (WA). Temperate WA specimens (n=387) were collected from 2012 to 2017 by hand seine net (Department of Primary Industries and Regional Development; DPIRD), purse-seine (donated by commercial fishermen) and spearfishing (collected by DiBattista J.), while tropical WA specimens from

the Pilbara (n=62) and Kimberley (n= 109) were caught between 2014 to 2017 with trawl nets by DPIRD vessels (Table S2). The total length and fork lengths of all specimens were measured (mm) and their sagittal otoliths extracted, dried, mounted on a microscope glass slide with thermoplastic resin (Crystal Bond) and grinded transversally with lapping film (30 µm) to the nucleus to expose its opaque and translucent bands (Taylor et al. 2017). The opaque bands in each otolith were counted under low-power magnification with reflected light against a black background (Fig. S1). The final count was determined by a third independent reading of the otoliths and only values that matched any of the two previous readings were retained. The spawning period was determined based on the temperature-spawning patterns found in the global literature review about reproduction (see previous section). These were set as January-February for Perth, December-January for Pilbara and November for the Kimberley region; the estimated spawning dates in each year were assigned as one week after the new moon based on literature (Table S1). The spawning date, date of capture and count of opaque bands were used to determine decimal ages for all individuals.

von Bertalanffy growth curves (VBGF) were fitted to the length-at-age data (both sexes pooled) for (i) each climate (temperate, subtropical and tropical) and for (ii) each location independently for both species (Table S2), based on the original VBGF parameterization using the R package *FSA* (R Core Team 2019, Ogle et al. 2020):

$L|t] = L\infty - (L\infty - L0)^{-Kt}$

Where $L|t]$ is the expected length at age t, $L\infty$ is the asymptotic length, K is the growth rate coefficient (yr−1) and $L0$ is the expected mean length at time zero (recruitment). Parameter values were estimated with non-parametric bootstrapping using the R package *nlstools* (Baty et al. 2015), except for L0 which was constrained to reported values of length at recruitment (age zero) for *S. fuscescens* (50 mm) and *S. rivulatus* (30 mm) to allow for a better comparison of the growth trajectories among locations (Lavina and Alcala 1974, Hasse et al. 1977, Kanashiro et al. 1999, Bariche et al. 2004). Average annual growth (mm y^{-1}) was extracted from the VBGF of each location for the years (age) shared by all climates for each species.

Maximum Size

Information about maximum size attained across different climate regimes for *S. fuscescens* was obtained from 45 studies reporting abundance and body length, which spanned 67 degrees of latitude (32°S-35°N) from Perth in Australia to Tateyama Bay in Japan; while 30 studies were obtained for *S. rivulatus*, spanning 10 degrees of latitude (28°N-39°N), from Jeddah in Saudi Arabia to Akbuk in Turkey (Fig. 1 & Table S3). Only studies that reported extensive sampling of individuals per location were

considered (n>30), including the studies of reproduction and growth. The maximum length reported in each published work was extracted for statistical analyses.

Environmental Variables

Time-series of environmental data spanning the time frames of each study of reproduction and growth rates of *S. fuscescens* and *S. rivulatus* were obtained from the European Union`s Copernicus Marine Service (EU's Earth Observation 2021) for average (m), maximum (*i.e.* summer: max) and minimum (*i.e.* winter: min) monthly sea surface temperature (C°) and primary productivity (mg m^{-2} day^{-1}) from the products GLORYS12V1 (1/12° horizontal resolution), GLOBAL_REANALYSIS_BIO_001_029 (1/4° horizontal resolution) and OCEANCOLOUR_GLO_CHL_L4 (1/27° horizontal resolution). For the analyses of maximum body size and longevity across temperature gradients, we obtained the long-term temperature variables for each location from the database BioOracle (Assis *et al*. 2018).

Statistical Analyses

Changes in the duration of spawning periods (number of months), minimum length at maturity, maximum body size and longevity were analyzed across thermal gradients (SSTm, SSTmin and SSTmax) with generalized linear models (GLM) using the R package *stats* (R Core Team 2019). Longevity was also analyzed with linear quantile regression (QLM) to the 80th and 90th percentile of the age distribution using the R package *lqmm* to evaluate differences specifically in the maximum ages attained by each population (Geraci 2014). Changes in fecundity were analyzed with GLMs considering an interaction between fork length and climate (temperate, subtropical and tropical). During data exploration, collinearity among temperature covariates was detected with scatterplots and Spearman's rank correlation coefficients. Thus, only SSTmin was selected for these statistical analyses due to its stronger correlation with the dependent variables and its greater significance for physiological processes and life-history traits across latitude (Osland *et al.* 2021; Taylor *et al.* 2019).

Changes in growth rates were evaluated with GLMs considering temperature and primary productivity (proxy for food abundance and nutrition) as explanatory covariates interacting with age. For the analyses of *S. fuscescens*, most of the covariates had collinearity, except between SSTmin and mean primary productivity (PPm, mg m^{-2} day^{-1}); thus, only these variables were used. Whereas in the case of *S. rivulatus*, all covariates had collinearity, masking the effect of each other on growth rates; thus, we carried independent analyses considering SSTmin and PPm as explanatory variables across different ages. In all cases, model fit was checked with AICc, R^2, graphical examination of predicted versus observed values and dispersion tests using the R package *DHARMa* (Hartig 2020) and p-values were calculated with Likelihood Ratio Tests with the R package *lme4* (Bates et al. 2015).

2.4. Results

Spawning phenology and length at maturity

The timing of the spawning periods of *S. fuscescens* differed between climates, with earlier reproductive onsets in warmer environments (Fig. 2A). In tropical locations, there were usually two spawning periods per year, starting in December-January followed by June-July. However, spawning began at higher latitudes only when temperatures increased above 20°C, in March-April at subtropical locations and in July-August at temperate locations. Representing a phenological shift of six months from tropical regions. Similar patterns were observed for *Siganus rivulatus*, where subtropical and temperate populations began to spawn in March-May in the Red Sea and June-July in the Mediterranean Sea, representing a shift of two months for the onset of reproduction (Fig. 2B).

The duration of the spawning period for both species had a significant positive correlation with winter temperatures, where populations had shorter spawning periods as temperature decreased and latitude increased (GLM, $p<0.01$, $R^2=0.78$; Fig. 2C). *S. fuscescens* in the tropics had spawning periods of up to seven months, while in subtropical and temperate locations, they lasted between 3-4 months and only 2 months, respectively. Similarly, the spawning period of *S. rivulatus* in the Red Sea lasted 4-7 months, whereas at higher latitudes in the Mediterranean Sea this was reduced to 1-2 months (GLM, $p<0.01$, $R^2=0.71$; Fig. 2D).

Minimum length at maturity (MLM) for *S. fuscescens* had a significant negative correlation with SSTmin (GLM, $p=0.01$, $R^2=0.59$; Fig. 2E). Reproductive *S. fuscescens* in the tropics (5°S-10°N) were as small as 120 ± 14 mm in length, whereas fish started to be reproductive at lengths of 150 ± 10 mm in the subtropics (22-27°N) and 199 ± 31 mm in temperate locations (33-35°N). This relationship was not found across the latitudinal range of *S. rivulatus* (GLM, $p=0.7$, $R^2<0.01$; Fig. 2F), where MLM did not differ significantly between populations in the Red Sea (21°N, 125 ± 13 mm) and the Mediterranean Sea (37°N, 133 ± 6 mm).
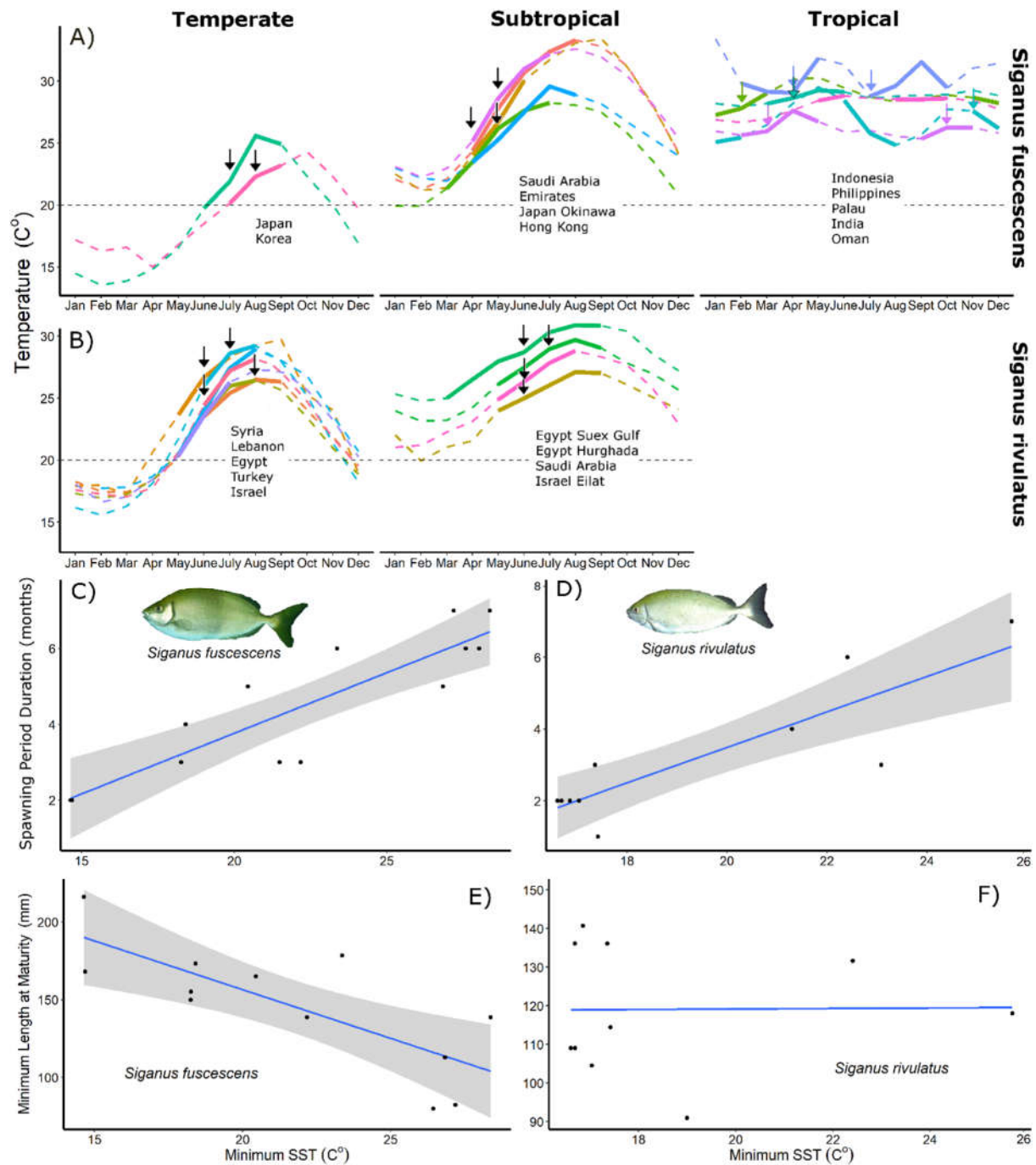
Figure 2. Period (continuous lines) and peak of spawning (arrows) with respect to sea surface temperature fluctuations (dashed lines; A, B) and duration of spawning period (C, D) and minimum length at maturity (E, F) across minimum annual temperature in different climates regimes for the rabbitfish *Siganus fuscescens* and *Siganus rivulatus*.

Fecundity

Fecundity varied according to the interaction between fish length and climate for both species of rabbitfish (GLMs, p<0.01, R^2=0.84, 0.73; Fig. 3). Populations of *S. fuscescens* in temperate locations had the greatest number of eggs per individual on average across all fish length classes. The highest

fecundity at maximum lengths (350 mm) in the tropics was 661,251 eggs ind-1, which was significantly lower than subtropical (1,164,209 eggs ind-1) and temperate individuals (1,063,377 eggs ind-1) of the same length (Fig. 3A). Similarly, populations of *S. rivulatus* from temperate climates had higher average fecundity than populations of the Red Sea, but only at higher length classes (Fig. 3B). The highest fecundity reported at subtropical locations was 488,408 eggs ind-1, while at temperate locations was 937,568 eggs ind-1 at comparable lengths (227 mm).
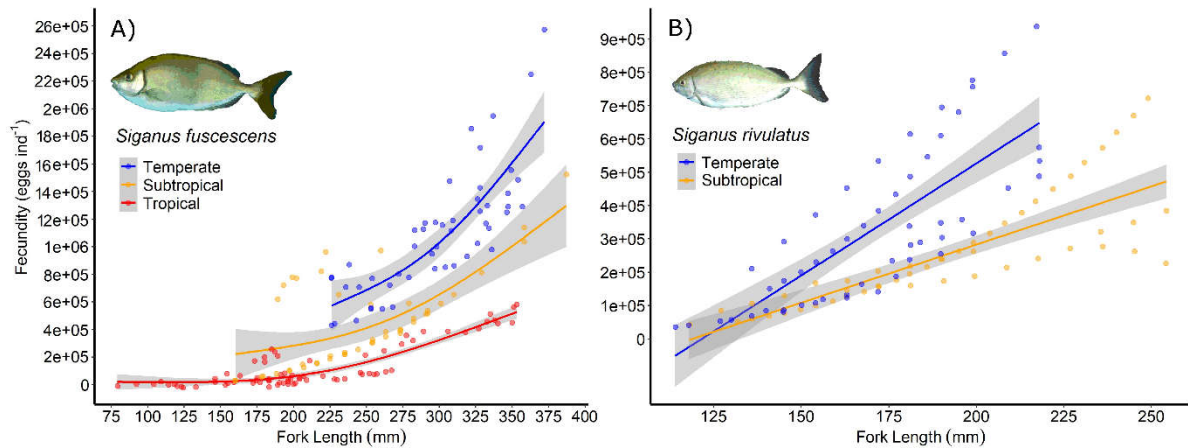
Figure 3. Relationships between fecundity of the range-extending *Siganus fuscescens* and *Siganus rivulatus* and fork length and climate (A, B) and winter sea surface temperatures (SST; C, D).

Growth rates, Maximum Size and Longevity

Temperate populations of *S. fuscescens* had lower von Bertalanffy growth coefficients (k, 0.4-0.6) but higher asymptotic lengths ($L\infty$, 300-326 mm) than subtropical (0.58-0.8, 300 mm) and tropical populations (1-1.16, 250-256 mm; Fig. 4A, Table S2). Growth rates in the first year of life were higher in the tropics (153 ± 21 mm), followed by the subtropical (134 ± 7.9 mm) and temperate populations (103 ± 8.6 mm). However, by the second year, length increments of tropical fish fell below other regions, and by the third and subsequent years temperate populations had the highest growth rates (Fig. 4C). This resulted in a significant interaction between SSTmin and Age (GLM, p= 0.018), where individuals grew faster under the warmer winter conditions of the tropics but only during their first year of life (Fig. 4E). Primary productivity (PPm) varied widely across the range of sampling locations but was not significantly related to growth rates (GLM, p= 0.53, Table S4, Fig. 4G).

On the other hand, temperate populations of *S. rivulatus* had lower k coefficients (0.14-0.27) and $L\infty$ (252-310 mm) than subtropical populations (0.33-0.72; 273-336 mm; Table S2, Fig. 4B). Growth rates in the first year of life were higher in the subtropical (100 ± 13.8 mm) versus the temperate locations (48.4 ± 7.9 mm). However, in contrast with *S. fuscescens,* this was maintained in the second (60.7 ± 3.4 vs 38.4 ± 5.5 mm) and third years (37.8 ± 4.6 vs 30.5 ± 3.8 mm), except for the fastest growing population in the Red Sea (Shalatein, Egypt), which also had the steepest decrease in growth rate with age, having lower length increments than temperate populations by the fourth year. The growth in other subtropical populations equaled those of temperate populations until the fifth year (20 ± 1 vs 19.4 ± 1.7 mm; Fig. 4D). SSTmin and PPm were higher in subtropical regions and both had a significant relationship with growth rates and significant interactions with age in independent statistical tests (GLM, p< 0.05, Table S4, Fig. 4F,H).
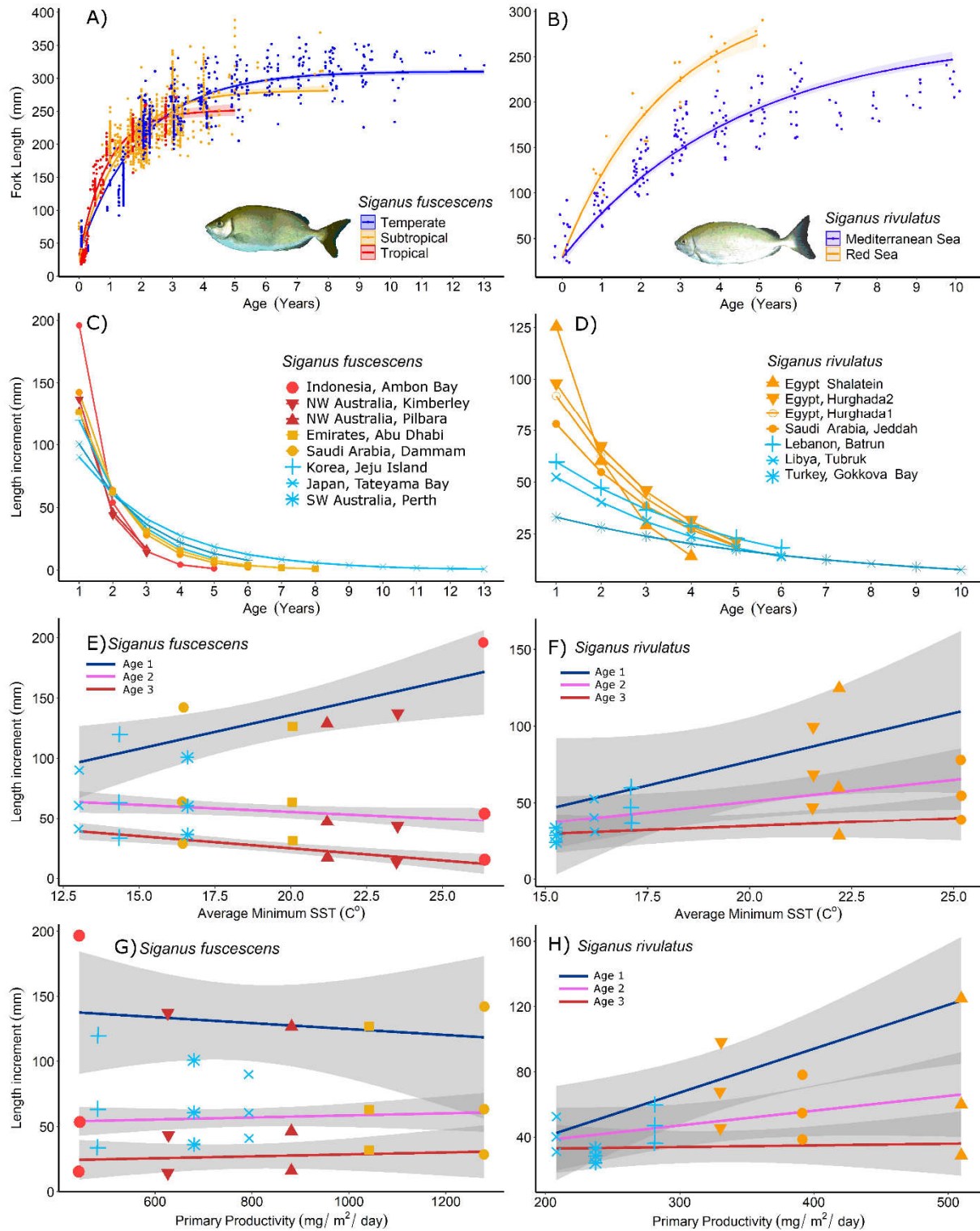
Figure 4. von Bertalanffy growth curves (A, B), corresponding average length increments by age (C, D) and the effect of winter temperatures (E, F) and primary productivity (G, H) on growth rates across latitude as reported in the literature for the rabbitfish *Siganus fuscescens* and *Siganus rivulatus* in temperate, subtropical and tropical locations. Maximum age reported in the tropics in panel A was 3 y/o, further years represent predicted length.

The maximum sizes of *S. fuscescens* had a significant negative correlation with SSTmin, where biggest sizes were found in colder climates, in agreement with the von Bertalanffy growth curves (GLM, p< 0.01, R^2=0.59, Fig. 5A). Similarly, longevity increased as winters got colder, from up to 3 years of age in the tropics to 8 years in the subtropics and 13 years in temperate locations at the highest latitude ($QLM_{0.9}$, p<0.01, GLM, p<0.01, R^2=0.3, Fig. 5C). The maximum sizes of *S. rivulatus* had a significant positive correlation with SSTmin, achieving bigger body sizes in warmer climates (GLM, p<0.01, R^2=0.28, Fig. 5B), while longevity increased from 4-5 years in the subtropics to 10 years in the coldest temperate location ($QLM_{0.8}$, p<0.01; GLM, p<0.01, R^2=0.13, Fig. 5H).
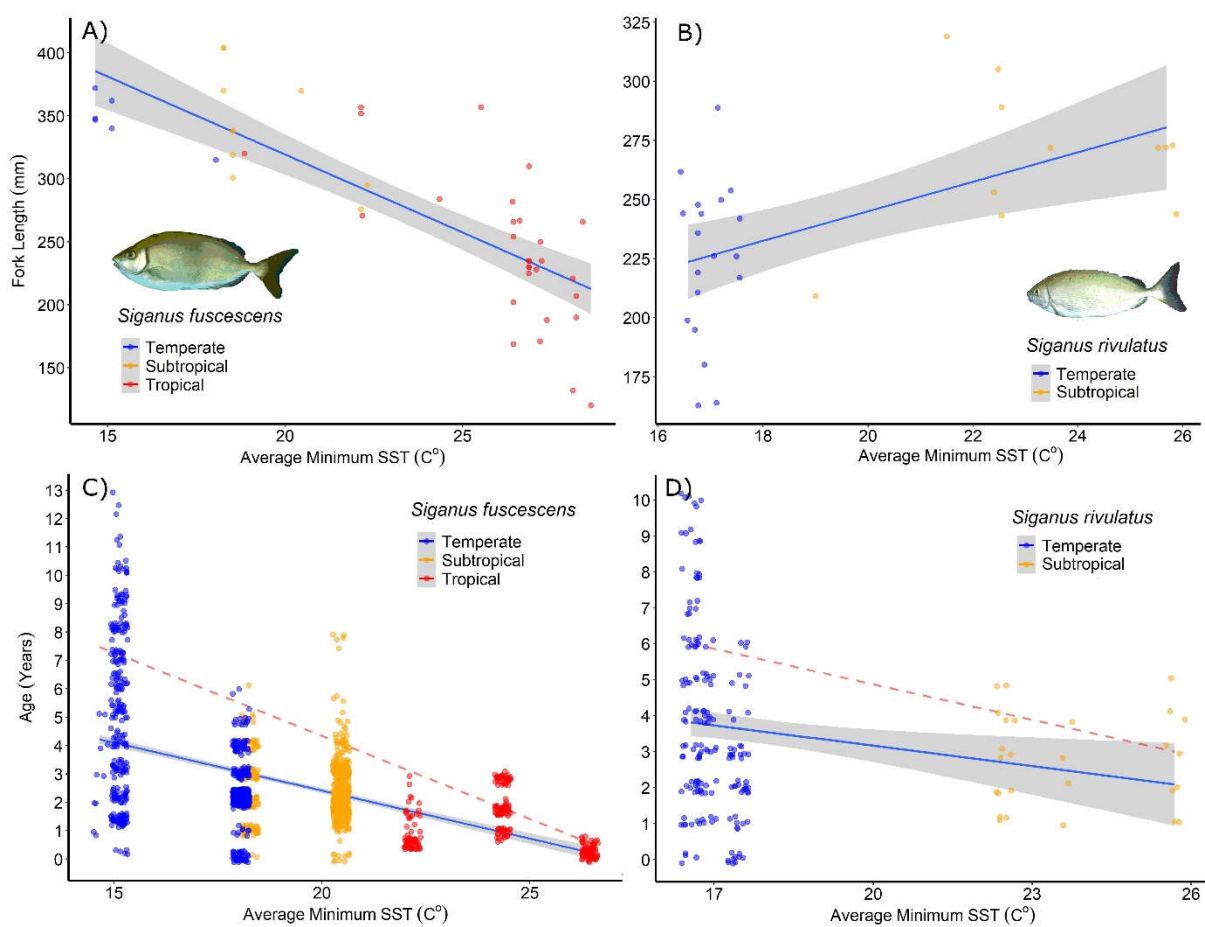
Figure 5. Relationships between maximum body size (A, B) and longevity (C, D) of the range-expanding rabbitfish *Siganus fuscescens* and *Siganus rivulatus* with winter sea surface in temperate, subtropical and tropical locations across their global distributions. Dotted lines in C and D represent quantile regression at the 90th percentile.

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2.5. Discussion

In this study we sought to advance our understanding on how life-history traits can change in response to shifts in distribution to higher latitudes. For this, we analyzed how the phenology and phenotype of two of the most successful range-expanding species of fish differed between their original warmer ecosystems and their temperate habitats. We found that most of our hypotheses were supported, with a few exceptions, as temperature and primary productivity changed across time (age) and space.

Our results on phenological changes showed that populations at the leading edge of range expansion had shorter reproductive periods with later onsets, similar to previous findings (Slesinger, Jensen & Saba 2021). Shorter reproductive periods at higher latitudes are suggested to be an adaptation to the seasonality of physical and biological factors (Conover 1992; Pankhurst & Porter 2003). Restricting spawning within the best conditions of temperature and food availability for larval development increases chances of survival, thereby maximizing recruitment success (Conover 1992; Pankhurst & Porter 2003). Many fish species at high latitudes spawn in spring and early summer, when temperatures are increasing, allowing longer growing seasons for their recruits and the ability to reach larger sizes. This increases their capacity to survive low temperatures and starvation and minimizes predation during the following winter (Sogard 1997). Progeny spawned in late summer or autumn would be exposed to low and potentially lethal temperatures in the subsequent winter, leading to higher mortality rates (Hurst 2007). We found that the spawning periods of rabbitfish populations started earlier and were reduced as winter temperatures decreased with increased latitude. Thermal seasonality in tropical regions was very low, within temperatures linked with peak spawning for *S. fuscescens* (~28°C). This results in long reproductive periods with bimodal peaks of spawning, similar to other species of rabbitfish in the tropics (Taylor, Gourley & Trianni 2017). On the other hand, rabbitfish experienced wide seasonal fluctuations in subtropical and temperate regions and lower temperatures associated with peak spawning, restricting their reproductive periods to the months when temperatures increased, becoming strict spring-spawners (Pankhurst & Porter 2003). Differences were lower between temperate and subtropical populations of *S. rivulatus* (1-3 vs 4-7 months, respectively), likely because maximum temperatures in the temperate Mediterranean Sea can reach similar values to the subtropical Red Sea during summer. However, increases and decreases in temperature are steeper in the temperate locations, providing narrower thermal windows for reproduction and growth, influencing the onset and duration of the spawning period.

The shorter spawning periods of populations of rabbitfish at higher latitudes were potentially compensated with an increase in fecundity per fish length, supporting our second hypothesis. This

trend has been found in other freshwater and marine species, where tropical populations have longer spawning seasons but lower fecundity (Vila-Gispert *et al.* 2002). The fecundity of both species of rabbitfish followed a similar pattern, where larger fish and colder winters resulted in higher egg production. Temperate populations of *S. fuscescens* had twice the fecundity in the smaller length class (FL, 220-250 mm) and three times greater fecundity at the biggest length class (300-350 mm) versus tropical populations; while differences between temperate and subtropical populations remained relatively stable across all length classes (1.5-1.8x). Similarly, the fecundity of temperate populations of *S. rivulatus* was higher by 1.4x in the lowest length class (110-150 mm) and by 2x in the biggest length class (>200 mm) vs subtropical populations. Fecundity has direct implications for recruitment success in natural environments; thus, greater egg production can be interpreted as an expression of counter gradient variation to maintain fitness by compensating for narrower reproductive windows in colder climates (Conover 1992). Because faster egg production can have important implications in the energy allocation for other biological processes, which are significantly modulated by temperature and nutrition (McBride *et al.* 2015).

Changes in the other life-history traits of *S. fuscescens* across the thermal gradient of its geographic distribution fit the expected patterns predicted by the Temperature-Size-Rule (TSR), corroborating the rest of our hypotheses. The biological processes explaining the TRS are still under debate; however, recent evidence supports the hypothesis that aquatic ectotherms with bigger bodies have limitations of oxygen supply under warmer environments (Verberk *et al.* 2011, 2021). This suggests that there might be selective pressures on individuals with genotypes prone to suffer oxygen supply limitations, favoring smaller body sizes and earlier maturity in warm environments (Rubalcaba *et al.* 2020; Pauly 2021). Energetic cost of oogenesis is high and its oxygen requirements are added to those of somatic maintenance and routine activities, reducing the aerobic scope of organisms and prompting earlier sexual maturation in warmer environments before reaching untenable levels of respiratory distress (Forster, Hirst & Atkinson 2012; Pauly 2021). The growth patterns of *S. fuscescens* across climates corroborated this, whereby tropical populations had faster initial growth but asymptoted to reach maturity sooner at smaller sizes compared with range-expanding populations experiencing colder winters. Higher latitude populations had lower growth rates, greater length/age at maturity, longer maximum sizes and lifespans.

Patterns of change in the life-history traits of *S. rivulatus* across climates did not meet the predicted outcomes by the TSR, except for changes in longevity. Range-extending populations had lower growth rates as expected; however, this did not translate into bigger body sizes and length at maturity than subtropical populations. A plausible explanation could be the differences found in primary

productivity and temperatures between regions. The Mediterranean Sea is considered one of the seas with lower levels of nutrients in the world (Azov 1991; Moutin & Raimbault 2002) and in combination with low temperatures could result in smaller bodies (Atkinson & Sibly 1997; Munday *et al.* 2008), maturation earlier than expected and increased longevity (Berrigan & Charnov 1994; Perrin 1995). Reaching maturity sooner could be a life-history adaptation to maximize their life-time reproductive output (Berrigan & Charnov 1994). Unlike populations living in warmer climates, temperate populations would not have limitations of aerobic scope, since metabolic rates would be low; however, given their very slow growth rates, reaching maturity at bigger sizes, as predicted by the TSR, would shorten their overall reproductive output considerably, carrying a high cost in fitness. For instance, maturing at the same size as temperate populations of *S. fuscescens* (200 mm) would take 5 years, risking complete reproductive failure for those individuals that perish before reaching maturation. This agrees with previous meta-analyses where a positive relationship was found between age at maturity and maximum age for all species of fish worldwide (Thorson *et al.* 2017).

The observed changes in longevity agreed with our hypothesis, where expanding populations of *S. rivulatus* and *S. fuscescens* experiencing the coldest winters had the oldest individuals (10-13 y/o respectively), in comparison with subtropical (5-8 y/o) and tropical populations (1-3 y/o). This pattern has been described for ectotherms and endotherms (Rollo 2002; Lee, Monaghan & Metcalfe 2013; Taylor *et al.* 2019), and its possible causes have been linked to intrinsic (senescence) and extrinsic processes (mortality rates) which can be modulated by temperature, such as higher cellular oxidative damage (Burraco *et al.* 2020) and higher predation rates in warmer environments related to higher metabolic demands in carnivorous species (Lima & Dill 1990; Werner & Anholt 1993). Predation rates on rabbitfish at the leading edge of range expansion is uncertain, since populations will interact with new and heterogeneous communities of predators in each location. Nonetheless, predation may be low given that rabbitfish possess poisonous spines and because native predators may not recognize them as prey (HilleRisLambers *et al.* 2013).

Fishing, like predation, increases mortality rates and can affect the size and age structure of fish populations in synergy with environmental variables (Hunter, Speirs & Heath 2015; Ahti, Kuparinen & Uusi-Heikkilä 2020; Morrongiello *et al.* 2021). We could not perform quantitative analyses of its effect in our study because species-specific information on fisheries landings of rabbitfish is lacking around the world; the Food and Agriculture Organization of the United Nations reports total yearly catches at low taxonomic (family) and geographic resolution (country) (FAO-FIGIS 2019). However, available evidence indicates that this could have a minimal impact in the general patterns found. For instance, in Western Australia rabbitfish are not commonly targeted and only are caught as bycatch, yet the

patterns between tropical and range-extending populations held. Fisheries effect on the traits of *S. rivulatus* may be low in the Red Sea, because individuals were larger (>250 mm) despite that trammel nets used in the region select for fishes >150 mm (Saber & Gewida 2020); however, we cannot discard a potential fishery effect in the Mediterranean Sea since nets target fishes > 200 mm, which could include the oldest and bigger individuals (Cerim, Soykan & Gülşahin 2020; Soykan 2020). Nonetheless, the global analyses of maximum sizes were robust. For instance, of the 45 studies examined about *S. fuscescens* across climates, maximum sizes below 250 mm were only reported in tropical locations from a total sample of 54,634 individuals. Likewise, of the 30 studies of *S. rivulatus*, maximum sizes below 200 mm were only reported in temperate locations from 32,563 fish individuals.

Ongoing climate change is influencing fish phenology, life-history traits and geographic distributions. Our results showed that these responses interplay in a way which can be generally predicted by ecogeographical rules, as most of our hypotheses were supported. However, we also found that effects can vary among species, depending on the interaction between changes in temperature and other important factors such as primary productivity and its related influence on nutrition. Rising temperatures at low latitudes are affecting fish populations by reaching upper critical thresholds for core biological activities, reducing fitness, and leading to range contractions. In contrast, populations at the leading edge of range expansions, experiencing stronger seasonal fluctuations with colder winters, will need to adapt their life-history strategies to maximize fitness. We showed that this may be reflected in range-expanding rabbitfish through shorter reproductive periods occurring only when temperatures are rising in spring, which increases the survival of their progeny. In addition, higher fecundity and greater longevity could maximize their lifetime reproductive output, favoring their persistence at higher latitudes and further range expansions in the future, as temperatures rise and oceanographic variables favor the dispersal of higher numbers of eggs and larvae to nursery grounds at higher latitudes. The results of this study reflect the phenological and phenotypic variation that some range-expanding species could have in terms of the interacting characteristics of reproduction, growth, and longevity. These are important aspects to consider when predicting future species redistributions and their related impacts on the functioning and productivity of natural ecosystems.

Acknowledgements

Author contributions

S.Z.P. conceived the study; S.Z.P. acquired the funding; D. F., C. D. and J.D. provided fish specimens; S.Z.P. dissected fish otoliths, R. A. mounted fish otoliths, S.Z.P. and B.T. aged fish otoliths; S.Z.P. conducted the literature review, analyzes, and wrote the first draft of the paper and all co-authors commented on the manuscript and gave final approval for publication.

2.6. References

Ahti, P.A., Kuparinen, A. & Uusi-Heikkilä, S. (2020) Size does matter – the eco-evolutionary effects of changing body size in fish. *Environmental Reviews*, **28**, 311–324.

Akiyama, S., Naganuma, M. & Katayama, S. (2009) Annual life cycle of rabbitfish Siganus fuscescens in Tateyama Bay, Chiba prefecture. *Fisheries Engineering*, **46**, 107–115.

Amarasekare, P. & Simon, M.W. (2020) Latitudinal directionality in ectotherm invasion success. *Proceedings. Biological Sciences / the Royal Society*, **287**, 20191411.

Angilletta, M.J., Steury, T.D. & Sears, M.W. (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, **44**, 498–509.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A. & De Clerck, O. (2018) Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, **27**, 277–284.

Atkinson, D. & Sibly, R.M. (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*, **12**, 235–239.

Azov, Y. (1991) Eastern Mediterranean—a marine desert? *Marine Pollution Bulletin*, **23**, 225–232.

Azzurro, E., Franzitta, G., Milazzo, M., Bariche, M. & Fanelli, E. (2017) Abundance patterns at the invasion front: the case of Siganus luridus in Linosa (Strait of Sicily, Central Mediterranean Sea). *Marine and Freshwater Research*, **68**, 697.

Bariche, M., Harmelin-Vivien, M. & Quignard, J.P. (2003) Reproductive cycles and spawning periods of two Lessepsian siganid fishes on the Lebanese coast. *Journal of Fish Biology*, **62**, 129–142.

Bariche, M., Letourneur, Y. & Harmelin-Vivien, M. (2004) Temporal fluctuations and settlement patterns of native and lessepsian herbivorous fishes on the lebanese coast (eastern mediterranean). *Environmental biology of fishes*, **70**, 81–90.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.

Baudron, A.R., Needle, C.L., Rijnsdorp, A.D. & Marshall, C.T. (2014) Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology*, **20**, 1023–1031.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J. & Saunders, B.J. (2015) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters*, **18**, 714–723.

Berrigan, D. & Charnov, E.L. (1994) Reaction norms for age and size at maturity in response to temperature: A puzzle for life historians. *Oikos*, **70**, 474.

Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C. & Finnegan, S. (2013) Climate change and the past, present, and future of biotic interactions. *Science*, **341**, 499–504.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Burraco, P., Orizaola, G., Monaghan, P. & Metcalfe, N.B. (2020) Climate change and ageing in ectotherms. *Global Change Biology*, **26**, 5371–5381.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J. & Richardson, A.J. (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.

Cerim, H., Soykan, O. & Gülşahin, A. (2020) Mortality and exploitation of marbled spinefoot, Siganus rivulatus (Actinopterygii: Perciformes: Siganidae), from southern Aegean Sea small-scale fishery. *Acta Ichthyologica Et Piscatoria*, **50**, 183–190.

Chaudhary, C., Richardson, A.J., Schoeman, D.S. & Costello, M.J. (2021) Global warming is causing a more pronounced dip in marine species richness around the equator. *Proceedings of the National Academy of Sciences of the United States of America*, **118**.

Cohen, J.M., Lajeunesse, M.J. & Rohr, J.R. (2018) A global synthesis of animal phenological responses to climate change. *Nature climate change*, **8**, 224–228.

Conover, D.O. (1992) Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology*, **41**, 161–178.

Daufresne, M., Lengfellner, K. & Sommer, U. (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 12788–12793.

Donelson, J.M., Sunday, J.M., Figueira, W.F., Gaitán-Espitia, J.D., Hobday, A.J., Johnson, C.R., Leis, J.M., Ling, S.D., Marshall, D., Pandolfi, J.M., Pecl, G., Rodgers, G.G., Booth, D.J. & Munday, P.L. (2019) Understanding interactions between plasticity, adaptation and range shifts in response to marine environmental change. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **374**, 20180186.

FAO-FIGIS. (2019) FAO Fisheries and Aquaculture Department. URL http://www.fao.org/fishery/topic/16140/en [accessed 18 April 2021]

Forster, J., Hirst, A.G. & Atkinson, D. (2012) Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 19310–19314.

Fox, R.J. & Bellwood, D.R. (2008) Remote video bioassays reveal the potential feeding impact of the rabbitfish Siganus canaliculatus (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs*, **27**, 605–615.

Froese, R. & Pauly, D. (2019) FishBase. URL http://www.fishbase.org [accessed 6 February 2021]

Geist, V. (1987) Bergmann's rule is invalid. *Canadian journal of zoology*, **65**, 1035–1038.

Hartig, F. (2020) *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models*. Computer software, R package.

HilleRisLambers, J., Harsch, M.A., Ettinger, A.K., Ford, K.R. & Theobald, E.J. (2013) How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences*, **1297**, 112–125.

Hunter, A., Speirs, D.C. & Heath, M.R. (2015) Fishery-induced changes to age and length dependent maturation schedules of three demersal fish species in the Firth of Clyde. *Fisheries Research*, **170**, 14–23.

Hurst, T.P. (2007) Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, **71**, 315–345.

IPCC. (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (eds V Masson-Delmotte, P Zhai, A Pirani, SL Connors, C Péan, S Berger, N Caud, Y Chen, L Goldfarb, MI Gomis, M Huang, K Leitzell, E Lonnoy, JBR Matthews, TK Maycock, T Waterfield, O Yelekçi, R Yu, and B Zhou). Cambridge University Press.

Kanashiro, K., Motonaga, F. & Kimura, M. (1999) Settlement of White-spotted Spinefoot, Siganus canaliculatus(Pisces: Siganidae), in the Coastal Waters off Okinawa Island, Japan. *NIPPON SUISAN GAKKAISHI*, **65**, 19–25.

Kumagai, N.H., García Molinos, J., Yamano, H., Takao, S., Fujii, M. & Yamanaka, Y. (2018) Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **115**, 8990–8995.

Lee, W.-S., Monaghan, P. & Metcalfe, N.B. (2013) Experimental demonstration of the growth rate--lifespan trade-off. *Proceedings. Biological Sciences / the Royal Society*, **280**, 20122370.

Lenanton, R.C.J., Dowling, C.E., Smith, K.A., Fairclough, D.V. & Jackson, G. (2017) Potential influence of a marine heatwave on range extensions of tropical fishes in the eastern Indian Ocean—Invaluable contributions from amateur observers. *Regional Studies in Marine Science*, **13**, 19–31.

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian journal of zoology*, **68**, 619–640.

McBride, R.S., Somarakis, S., Fitzhugh, G.R., Albert, A., Yaragina, N.A., Wuenschel, M.J., Alonso-Fernández, A. & Basilone, G. (2015) Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, **16**, 23–57.

McLean, M., Mouillot, D. & Auber, A. (2018) Ecological and life history traits explain a climate-induced shift in a temperate marine fish community. *Marine Ecology Progress Series*, **606**, 175–186.

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of biogeography*, **30**, 331–351.

Morales-Castilla, I., Rodríguez, M.Á. & Hawkins, B.A. (2012) Deep phylogeny, net primary productivity, and global body size gradient in birds. *Biological journal of the Linnean Society. Linnean Society of London*, **106**, 880–892.

Morrongiello, J.R., Horn, P.L., Ó Maolagáin, C. & Sutton, P.J.H. (2021) Synergistic effects of harvest and climate drive synchronous somatic growth within key New Zealand fisheries. *Global Change Biology*, **27**, 1470–1484.

Moutin, T. & Raimbault, P. (2002) Primary production, carbon export and nutrients availability in western and eastern Mediterranean Sea in early summer 1996 (MINOS cruise). *Journal of Marine Systems*, **33–34**, 273–288.

Munday, P.L., Kingsford, M.J., O'Callaghan, M. & Donelson, J.M. (2008) Elevated temperature restricts growth potential of the coral reef fish Acanthochromis polyacanthus. *Coral reefs (Online)*, **27**, 927–931.

Ogle, D.H., Wheeler, P. & Dinno, A. (2020) *FSA: Fisheries Stock Analysis*. Computer software, R.

Osland, M.J., Stevens, P.W., Lamont, M.M., Brusca, R.C., Hart, K.M., Waddle, J.H., Langtimm, C.A., Williams, C.M., Keim, B.D., Terando, A.J., Reyier, E.A., Marshall, K.E., Loik, M.E., Boucek, R.E., Lewis, A.B. & Seminoff, J.A. (2021) Tropicalization of temperate ecosystems in North America: The

northward range expansion of tropical organisms in response to warming winter temperatures. *Global Change Biology*.

Pankhurst, N.W. & Porter, M.J.R. (2003) Cold and dark or warm and light: variations on the theme of environmental control of reproduction. *Fish physiology and biochemistry*, **28**, 385–389.

Pauly, D. (2021) The gill-oxygen limitation theory (GOLT) and its critics. *Science Advances*, **7**.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J. & Williams, S.E. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, **355**.

Perrin, N. (1995) About Berrigan and Charnov's Life-History Puzzle. *Oikos*, **73**, 137.

Rollo, C.D. (2002) Growth negatively impacts the life span of mammals. *Evolution & Development*, **4**, 55–61.

Rubalcaba, J.G., Verberk, W.C.E.P., Hendriks, A.J., Saris, B. & Woods, H.A. (2020) Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, **117**, 31963–31968.

Saber, M.A. & Gewida, A.G.A. (2020) The influence of trammel net fishing on the Rabbit fish (Siganus rivulatus) stocks in Suez Gulf, Red Sea, Egypt. *Egyptian Journal of Aquatic Biology and Fisheries*, **24**, 135–145.

Sala, E., Kizilkaya, Z., Yildirim, D. & Ballesteros, E. (2011) Alien marine fishes deplete algal biomass in the Eastern Mediterranean. *Plos One*, **6**, e17356.

Sheridan, J.A. & Bickford, D. (2011) Shrinking body size as an ecological response to climate change. *Nature climate change*, **1**, 401–406.

Slesinger, E., Jensen, O.P. & Saba, G. (2021) Spawning phenology of a rapidly shifting marine fish species throughout its range. *ICES Journal of Marine Science*.

Sogard, S.M. (1997) Size-Selective Mortality in the Juvenile Stage of Teleost Fishes: A Review. *Bulletin of Marine Science*, **60**, 1129–1157.

Sommer, R.J. (2020) Phenotypic plasticity: from theory and genetics to current and future challenges. *Genetics*, **215**, 1–13.

Soykan, O. (2020) Maximum size of Marbled spinefoot (Siganus rivulatus Forsskal & Niebuhr, 1775) for Aegean Sea. *AQUATIC SCIENCES AND ENGINEERING*, 42–45.

Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., Edgar, G.J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R.A., Smale, D.A., Fulton, E.A., Slawinski, D., Feng, M., Radford, B.T., Thompson, P.A. & Bates, A.E. (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, **18**, 944–953.

Taylor, B.M., Choat, J.H., DeMartini, E.E., Hoey, A.S., Marshell, A., Priest, M.A., Rhodes, K.L. & Meekan, M.G. (2019) Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. *The Journal of Animal Ecology*, **88**, 1888–1900.

Taylor, B.M., Gourley, J. & Trianni, M.S. (2017) Age, growth, reproductive biology and spawning periodicity of the forktail rabbitfish (Siganus argenteus) from the Mariana Islands. *Marine and Freshwater Research*, **68**, 1088.

Thorson, J.T., Munch, S.B., Cope, J.M. & Gao, J. (2017) Predicting life history parameters for all fishes worldwide. *Ecological Applications*, **27**, 2262–2276.

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M.B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D.E., Nicotra, A.B., Poorter, H. & Zavala, M.A. (2014) The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, **17**, 1351–1364.

Verberk, W.C.E.P., Atkinson, D., Hoefnagel, K.N., Hirst, A.G., Horne, C.R. & Siepel, H. (2021) Shrinking body sizes in response to warming: explanations for the temperature-size rule with special emphasis on the role of oxygen. *Biological Reviews of the Cambridge Philosophical Society*, **96**, 247–268.

Verberk, W.C.E.P., Bilton, D.T., Calosi, P. & Spicer, J.I. (2011) Oxygen supply in aquatic ectotherms: partial pressure and solubility together explain biodiversity and size patterns. *Ecology*, **92**, 1565–1572.

Vila-Gispert, A., Moreno-Amich, R. & García-Berthou, E. (2002) Gradients of life-history variation: an intercontinental comparison of fishes. *Reviews in Fish Biology and Fisheries*.

Werner, E.E. & Anholt, B.R. (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *The American Naturalist*, **142**, 242–272.

Zarco-Perello, S., Langlois, T.J., Holmes, T., Vanderklift, M.A. & Wernberg, T. (2019) Overwintering tropical herbivores accelerate detritus production on temperate reefs. *Proceedings. Biological Sciences / the Royal Society*, **286**, 20192046.

Zarco-Perello, S., Wernberg, T., Langlois, T.J. & Vanderklift, M.A. (2017) Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports*, **7**, 820.

Zarco-Perello, S., Bosch, N.E., Bennett, S., Vanderklift, M.A. & Wernberg, T. (2021) Persistence of tropical herbivores in temperate reefs constrain kelp resilience to cryptic habitats. *The Journal of Ecology*, **00**, 1–14.

2.7. Supplementary Information

Table S1. Reproductive traits of species of siganids in temperate and tropical regions of the world. Juvs: juveniles, Obs: observations, Anec: anecdotical.

Species	Country/ Location	Spawning Period	Spawning Period Duration	Peak of Spawning	Fecundity (eggs/gonad)	Minimum Size at Maturity (mm)	Maximum Size (mm)	Number of Fish	Reference
Siganus fuscescens/ canaliculatus^	**Australia** Perth	Feb GSI April juvs		Jan-Feb					(Lenanton et al. 2017; Zarco-Perello and Wernberg 2019)
	Pilbara Kimberly	Oct-Dec		Nov					This study
	Indonesia South Sulawesi^	Jan-Dec?		Sept	5-131K	85F	284 TL	1821	(Tresnati et al. 2019)
	India Gulf of Mannar^	Nov-March (Feb-May recruits)	5	Jan-Feb	136-588K 34K - 285K	120F 150F	250 TL 250 TL 250 TL	503 873 129	(Anand and Reddy 2017; Jayasankar 1990)
	Oman Lakbi	Nov-Feb, Jun-Jul	6	Nov	242-607K	190F	375 TL	1014	(Al-Marzouqi et al. 2011)
	Singapore	Jan-April, Jul-Aug	6	Feb-March					Juvs (Lam 1974)
	Saudi Arabia Dammam^ Jubail^	April-June April-June March-May	3 3 3	April May April	42.2-1.1M 60-838K 62-983K	165F 150F	430 TL 360 TL 370 FL	2024 1625 241	(Wassef and Abdul Hady 1997; Wassef and Abdulhady 2001; Tharwat 2004) (Lin et al. 2019)

Siganus fuscescens/ canaliculatus	**United Arab Emirates** Ras Al Khaimah Abu Dhabi	March-May April-Jul; Nov	3 5	April April	650K-1M	110M, 120F 165F	286 SL 370 FL	918 763	(Grandcourt et al. 2007; Al-Ghais 1993)
	Japan Tateyama Bay	Jul-Aug	2	Aug		155M, 168F	340 FL	1770	(Akiyama et al. 2009)
	Korea Jeju Island	Jul-Aug June- Aug	2 2	Jul Jul	380,000 -2.6M 503K - 1.4M	230F	396 TL 369 TL	581	(Lee et al. 2019) (Hwang et al. 2004)
	Japan Okinawa	April-Jun *May-Jun* April-Jul	3 4	May	*500k-2.5M*			180 50	(Hoque et al. 1999) Tanks (Hoque et al. 1998) Field Obs (Kanashiro et al. 1999)
	Hong Kong	March-June	4	May	200-540K		290 SL	287	(Tseng and Chan 1982)
	Philippines Palompon Southern Negros Pujada Bay, Mindanao	Feb-May & Jul-Sept All year Feb-April, Sept-Nov	7 6	Apr & Jul May-Sept March & Oct	18.3K–306.8K 286-618.6K	55M, 71F 140F 75F	155 SL 155 SL 200 SL	669 64 550	(Paraboles and Campos 2018a) (Paraboles and Campos 2018b) Juvs (Lavina and Alcala 1974) (Jumawan-Nanual and Metillo 2008)
	Palau	Feb-May & June-July *Feb-June, Oct-Dec*	6	April	295.7K 30K-2M*	120F	230 SL		Juvs (Hasse et al. 1977) Tanks (Bryan et al. 1975) McVey 1972 and Drew 1971 in (Lam 1974)

Siganus rivulatus	**Lebanon** Batrun	June Juvs in Jul	1	June	100-550k	126F	250 TL	528-781 fishery	(Bariche et al. 2003; Bariche et al. 2009; Bariche et al. 2004)
	Egypt Alexandria Port Said Bardawil	July-Sept June-July June-July? June-July	3 2 2 2	Aug June June? June	103-396K 211K-1,12M 35-187K 57-356K	150F 150F 120F 11.5F	280 TL 240 TL 220 TL 240 TL	180 491 573	GSI (Hussein 1986) GSI (Fahmy 2019) GSI (Abdelhak et al. 2020) (Makbal et al. 2014)
	Turkey Yumurtalık and Karata Gokova Bay Gokova Bay	June- July June-July June-July	2 2 2	July June June	253-615K	155F 120F	270 TL 260 TL 261	473 721 240	GSI (Yeldan and Avşar 2000; Soykan et al. 2020; Engin et al. 2020) (Soykan et al. 2020) (Engin et al. 2020)
	Greece Leros	August?					380 TL		Anect (Lahnsteiner and Patzner 1999)
	Israel Jaffa	May-July (August recruits)	3	June-July					Field Obs (Popper and Gundermann 1975; Popper et al. 1979)
	Egypt Hurghada-Shalateen Hurghada Suez Gulf	May-Sept? May-Sept? May-August	5 4	June June July	18-735K 147-384K	145F 100F	280 TL 280TL	334	Larvae Obs (El-Regal 2013; Abu El-Regal et al. 2019) (Abdelhak et al. 2020) (Ramadan and Elhalfawy 2020)
	Israel Eilat	May-August (July-August recruits)	4	June					Field Obs (Popper and Gundermann 1975; Popper et al. 1979)
	Saudi Arabia Jeddah	March-September	7	June			300 TL	2177	(Amin 1985)
		March-September?			43-277K	130F	300 TL (most 200)	570	(Hashem 1983)

Table S2. Parameters of the von Bertalanffy equation and maximum age of Siganids from temperate and tropical regions. FL: Fork length, TL: Total length.

Species	Country/ Location	Latitude Longitude	Maximum Size (mm)	L∞ (mm)	K (year-1)	L0	Maximum age	Number of Fish	Reference
Siganus fuscescens/ Canaliculatus	**Australia** Perth	-31.8002 115.71849	345 TL 315 FL	300 FL	0.5183	50	6	387	This study
	Australia Pilbara	-20.78114 115.61806	298 TL 271 FL	250 FL	1	50	3	62	
	Australia Kimberley	-16.73042 122.19571	317 TL 284 FL	256 FL	1.164	50	3	109	
	Tropical Western Australia			253 FL	1	50		171	
	United Arab Emirates Abu Dhabi	24.73169 54.05259	370 FL	300 FL	0.7	50	7.8	763	(Grandcourt et al. 2007)
	Saudi Arabia Dammam	26.55941 50.32881	370 FL	300 FL	0.806	50	6	241	(Lin et al. 2019)
	Arabian Gulf			300 FL	0.578	50		1104	This study
	Japan Tateyama Bay	35.00984, 139.78342	362 FL	326 FL	0.3947	50	13	1781	(Katayama et al. 2009)
	Korea Jeju Island	33.36133, 126.54007	348 FL	300 FL	0.661	50	5	396	(Lee et al. 2014)
	Temperate East Asia			325 FL	0.401	50		2177	This study
	Indonesia Ambon Bay	-3.64586, 128.21464	267 FL	250 FL	1.3	30	1	185	(Mosse and Hutubessy 1996)

Siganus rivulatus	**Libya** Tubruk Benghazi	32.96439 21.92327	274 TL	252 FL	0.271	30	6	1672	(Shakman et al. 2008)
	Lebanon Batrun	34.25219, 35.6506	267 TL	310 FL	0.239	30	6	781	(Bariche 2005)
	Turkey Gokova Bay	36.95443, 27.96296	290 TL	264 FL	0.143	60	10	531	(Ergenler 2016) (Soykan 2020)
	Mediterranean Sea			270 FL	0.2247	30		2984	This study
	Egypt Shalatein Hurghada	23.16047, 35.76561	300 TL	273 FL	0.727	30	4	2000	(Mehanna et al. 2018)
		27.23348 34.03683	337 TL	**336 FL**	0.383	30	5	425	(Mehanna and Abdallah 2002)
			319 TL	**314 FL**	0.389	30	5	251	(El-Gammal 1988)
	Saudi Arabia Jeddah	21.53069 38.96739	302 TL	300 FL	0.334	30	5	2177	(Gabr et al. 2018)
	Red Sea			320 FL	0.367	30		4853	This study

Table S3. Additional studies used for analyses of changes in maximum size (length) of siganids in temperate and tropical regions of the world. TL: Total length.

Species	Country/ Location	Maximum Size (mm)	Number Of Fish	Reference
Siganus fuscescens/ canaliculatus	**Indonesia** Ulelhee Bay Banda Besar Selayar Island South Sulawesi Jeneponto Ambon Bay Ambon Bay Ambon Bay Ambon Bay Ambon Bay Kotania Bay Bua Uloulo Bone Bay	 117 TL 300 TL 228 FL 202 TL 284 TL - 283 TL 215 TL 180 TL 270 TL 200 TL 220 TL 141 TL 205 TL	 300 2711 50 1000 1821 2921 4603 1810 1050 1050 1163 1712 523 1686	 (Muchlisin et al. 2017) (Munira et al. 2010) (Masyahoro 2011) (Halid et al. 2016) (Tresnati et al. 2019) (Latuconsina et al. 2012) (Ambo-Rappe et al. 2013) (Latuconsina and Rappe 2013) (H Latuconsina et al. 2020) (Husain Latuconsina et al. 2020) (Latuconsina and Wasahua 2015) (Jalil and Ali 2003) (Suardi et al. 2016)
	New Caledonia	295 FL	481	(Kulbicki et al. 2005)
	India Ratnagiri Mannar	 330 TL 245 TL	 497 543	(Metar et al. 2017) (Anand and Reddy 2012; Anand and Reddy 2014)
	Saudi Arabia Jubail Qatif	 360 TL 320 TL	 1625 	 (Tharwat 2005) (Tharwat and Al-Owafeir 2003)
	Oman Lakbi	380 TL	3275	(Al-Marzouqi 2013)
	Kenya Diani-Vanga	380 TL	260	(Wambiji et al. 2008)

|				
Siganus rivulatus	**Egypt** Alexandria	276 TL	112	(Abdallah 2002)
	Turkey Antalya Mersin	215 TL 241 TL	521 355	(Bilecenoglu and Kaya 2002) (Taskavak and Bilecenoglu 2001)
	Libya Benghazi	181 TL	310	(Elbaraasi 2014)
	Saudi Arabia Qatif Jeddah	270 TL 340 TL	200	(Tharwat and Al-Owafeir 2003; Al-Qishawe et al. 2014)
	Jordan Gulf of Aqaba	353 TL	72	(Odat 2003)
	Egypt Gulf of Suez	231 TL	566	(Saber and Gewida 2020)
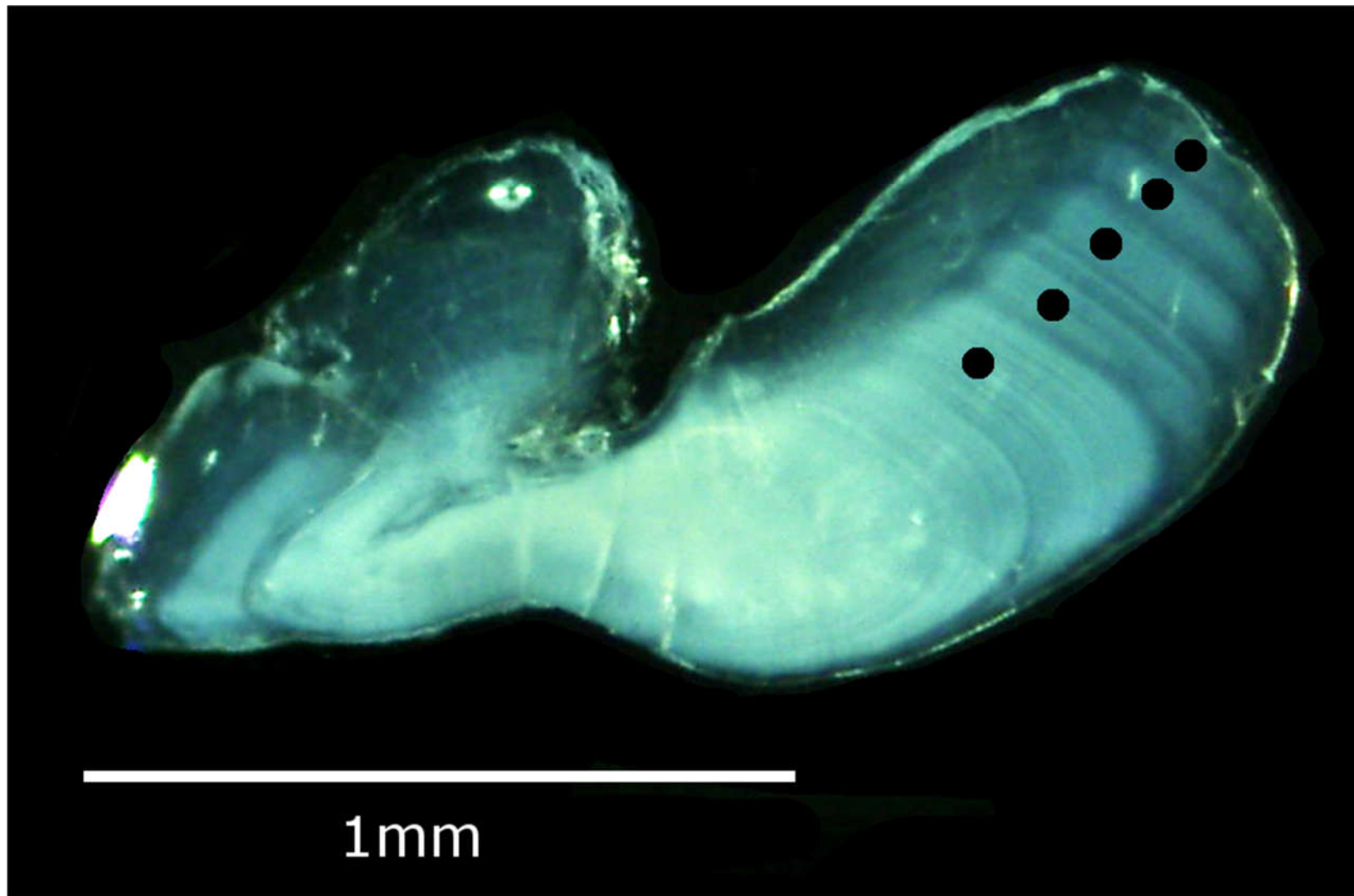
Figure S1. Transverse section of sagittal otolith of *Siganus fuscescens* from temperate reefs of Perth, Western Australia. Black dots mark the opaque bands representing seasonal growths during winter.

Table S4. Results of Generalized Linear Models (GLM) for spawning period duration, minimum size at maturity, fecundity, maximum body size and growth rates, and GLM and Quantile Regression (QR) for longevity of *Siganus fuscescens* and *Siganus rivulatus* in temperate, subtropical and tropical regions of the world.

Siganus fuscescens	*Siganus rivulatus*
Spawning Period Duration	

GLM. Spawning.Duration ~ SSTmin, family = Gamma(link = "identity").
 	
    Estimate   Std. Error   t value   Pr(>|t|)
(Intercept) -2.64028   0.85385   -3.092   0.0102 *
SSTmin   0.32028   0.04482   7.146   1.88e-05 ***
	GLM. Spawning.Duration ~ SSTmin, family = Gamma(link = "identity").
	
	    Estimate Std. Error t value Pr(>|t|)
	(Intercept) -5.8934 2.0343 -2.897 0.01768 *
	SSTmin 0.4672 0.1160 4.028 0.00298 **

Minimum Size at Maturity	

GLM. MLM ~ SSTmin, family = gaussian(link = "identity")
 	
    Estimate   Std. Error   t value   Pr(>|t|)
(Intercept) 281.845   36.235   7.778   1.5e-05 ***
SSTmin   -6.267   1.640   -3.821   0.00337 **
	GLM. MLM ~ SSTmin, family = gaussian(link = "identity")
	
	    Estimate Std. Error t value Pr(>|t|)
	(Intercept) 8.487e-03 2.507e-03 3.386 0.00956 **
	SSTmin -4.659e-06 1.332e-04 -0.035 0.97295

Fecundity	

GLM. Fecundity ~ FL*Climate, family = gaussian(link = "identity")
 	
         Estimate   Std. Error   t value   Pr(>|t|)
(Intercept)   -606057.16   398184.66   -1.522   0.13150
Fork Length   4073.91   1473.46   2.765   0.00691 **
ClimateTemperate   -527962.99   449134.17   -1.176   0.24289
ClimateTropical   -274068.62   469136.05   -0.584   0.56055
FL:ClimateTemperate 3373.71   1632.57   2.067   0.04165 *
FL:ClimateTropical   48.76   1703.71   0.029   0.97723
	GLM. Fecundity ~ FL*Climate, family = Gamma (link = "log")
	
	         Estimate Std. Error t value Pr(>|t|)
	(Intercept) 8.86623 0.38293 23.154 < 2e-16 ***
	Fork Length 0.01806 0.00215 8.399 6.55e-13 ***
	ClimateTemperate -0.65956 0.51492 -1.281 0.2036
	FL:ClimateTemperate 0.00724 0.00293 2.471 0.0154 *

Maximum Body Size	

GLM. Fork Length ~ SSTmin, family = Gamma(link = "identity").
 	
    Estimate   Std. Error   t value   Pr(>|t|)
(Intercept) 596.563   43.851   13.604   < 2e-16 ***
SSTmin   -13.627   1.734   -7.858   7.54e-10 ***
	GLM. Fork Length ~ SSTmin, family = Gamma(link = "identity").
	
	    Estimate Std. Error t value Pr(>|t|)
	(Intercept) 115.125 37.603 3.062 0.00482 **
	SSTmin 6.508 1.978 3.290 0.00271 **

Growth Rates	

GLM. Growth.log ~ PPm*SSTmin*Age, family=gaussian(link = "identity").

	Estimate Std.	Error	t value	Pr(>|t|)
(Intercept)	3.506e+00	1.277e+00	2.745	0.0144 *
PPm	1.889e-03	1.917e-03	0.986	0.3390
SSTmin	1.648e-01	6.624e-02	2.488	0.0243 *
Age	7.191e-01	5.914e-01	1.216	0.2416
PPm:SSTmin	-1.000e-04	1.038e-04	-0.964	0.3495
PPm:Age	-5.687e-04	8.874e-04	-0.641	0.5307
SSTmin:Age	-8.096e-02	3.066e-02	-2.641	0.0178 *
PPm:SSTmin:Age	3.091e-05	4.804e-05	0.643	0.5291

GLM. Growth.log ~ PPm*Age, family=gaussian(link = "identity").

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.8625945	0.4010697	9.631	5.93e-09 ***
PPm	0.0052425	0.0011736	4.467	0.000236 ***
Age	0.1760677	0.1464499	1.202	0.243313
PPm:Age	-0.0016257	0.0004286	-3.793	0.001140 **

GLM. Growth.log ~ SSTmin*Age, family=gaussian(link = "identity").

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.11634	0.67500	4.617	0.000167 ***
SSTmin	0.12552	0.03391	3.701	0.001413 **
Age	0.25263	0.24648	1.025	0.317608
SSTmin:Age	-0.03101	0.01238	-2.504	0.021035 *

Longevity	

GLM. Age ~ SSTmin, family = Gamma(link = "identity")

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	8.979817	0.174147	51.56	<2e-16 ***
SSTmin	-0.326054	0.006979	-46.72	<2e-16 ***

QR. Age ~ SSTmin, tau = 0.9

	Value Std.	Error	lower bound	upper bound	Pr(>|t|)
(Intercept)	9.420870	0.467419	8.481556	10.3602	< 2.2e-16 ***
SSTmin	-0.267289	0.020303	-0.308089	-0.2265	< 2.2e-16 ***

GLM. Age ~ SSTmin, family = Gamma(link = "inverse")

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.123535	0.112199	-1.101	0.272322
SSTmin	0.021893	0.006455	3.392	0.000851 ***

QR. Age ~ SSTmin, tau = 0.8

	Value	Std. Error	lower bound	upper bound	Pr(>|t|)
(Intercept)	7.797076	0.856228	6.076422	9.5177	4.096e-12 ***
SSTmin	-0.108991	0.040537	-0.190453	-0.0275	0.009775 **

Bibliography

Akiyama, S. 2007. Discards in large-scale set net in Tateyama Bay. *Nippon Suisan Gakkaishi (Japan)*.

Akiyama, S., Naganuma, M. and Katayama, S. 2009. Annual life cycle of rabbitfish Siganus fuscescens in Tateyama Bay, Chiba prefecture. *Fisheries Engineering* 46(2), pp. 107–115.

Al-Ghais, S.M. 1993. Some aspects of the biology of *Siganus canaliculatus* in the Southern Arabian Gulf. *Bulletin of Marine Science* 52(3), pp. 886–897.

Al-Marzouqi, A., Jayabalan, N., Al-Nahdi, A. and Al-Anbory, I. 2011. Reproductive biology of the white-spotted rabbitfish, *Siganus canaliculatus* (Park, 1797) in the Arabian Sea coast of Oman. *Western Indian Ocean Journal of Marine Science* 10(1), pp. 73–82.

Al-Qishawe, M.M.S., Ali, T.S. and Abahussain, A.A. 2014. Stock assessment of white spotted rabbitfish (*Siganus canaliculatus* Park, 1797) in Jubail marine wildlife sanctuary, Saudi Arabia. *International Journal of Fisheries and Aquatic Studies* 1(6), pp. 48–54.

Amin, E.M. 1985. Seasonal developmental changes in the ovaries of *Siganus rivulatus* from the Red Sea. *Bulletin of the National Institute of Oceanography and …*.

Anand, M. and Reddy, P. 2014. Age and growth studies on white-spotted rabbitfish *Siganus canaliculatus* (Park), from the Gulf of Mannar region South India. *Indian Journal of Geo-Marine Sciences* 43(3), pp. 427–433.

Anand, M. and Reddy, P.S.R. 2017. Reproductive biology of the rabbitfish (*Siganus canaliculatus*) in the Gulf of Mannar region, India.

Bariche, M. 2005. Age and growth of Lessepsian rabbitfish from the eastern Mediterranean. *Zeitschrift fur angewandte Ichthyologie = Journal of applied ichthyology* 21(2), pp. 141–145.

Bariche, M., Harmelin-Vivien, M. and Quignard, J.P. 2003. Reproductive cycles and spawning periods of two Lessepsian siganid fishes on the Lebanese coast. *Journal of Fish Biology* 62(1), pp. 129–142.

Bariche, M., Sadek, R. and Azzurro, E. 2009. Fecundity and condition of successful invaders: *Siganus rivulatus* and *S. luridus* (Actinopterygii: Perciformes: Siganidae) in the eastern Mediterranean Sea. *Acta Ichthyologica Et Piscatoria* 39(1), pp. 11–18.

Bryan, P.G., Madraisau, B.B. and Mcvey, J.P. 1975. Hormone induced and natural spawning of captive *Siganus canaliculatus* (Pisces: Siganidae) year round. *Micronesica* 11(2), pp. 199–204.

El-Gammal, F.I. 1988. Age, growth and mortality of the rabbitfish *Siganus rivulatus* (Forsk.,1775) from the Red Sea. *Bull. Inst. Oceanogr. & Fish.* 14, pp. 13–21.

Ergenler, A. 2016. The investigation of some biological characteristics of marbled spinefoot *Siganus rivulatus* (Forsskal 1775)) living In Iskenderun By . İskenderun Teknik Üniversitesi Fen Bilimleri Enstitüsü.

Fahmy, A.F. 2019. Variation in the reproductive biology of female rabbitfish *Siganus rivulatus* with histological and ultrastructural evidence. *Asian Journal of Biological Sciences*.

Froese, R. and Pauly, D. 2018. FishBase [Online]. Available at: http://www.fishbase.org [Accessed: 4 June 2018].

Gabr, M.H., Bakaili, A.S. and Mal, A.O. 2018. Growth, mortality and yield per recruit of the rabbit fish Siganus rivulatus (Forsskål 1775) in the red sea coast of Jeddah, Saudi Arabia. *International Journal of Fisheries and Aquatic Studies* 6(1), pp. 87–96.

Grandcourt, E., Al Abdessalaam, T., Francis, F. and Al Shamsi, A. 2007. Population biology and assessment of the white-spotted spinefoot, Siganus canaliculatus (Park, 1797), in the southern Arabian Gulf. *Zeitschrift fur angewandte Ichthyologie = Journal of applied ichthyology* 23(1), pp. 53–59.

Hashem, M. 1983. Biological studies on Siganus rivulatus (Forsk.) in the Red Sea. *Journal of The Faculty of Marine Science, King AbdulazizUniv: Jeddah, Saudi Arabia* 3, pp. 119–127.

Hasse, J.J., Madraisau, B.B. and Mcvey, J.P. 1977. Some aspects of the life history of *Siganus canaliculatus* (Park) (Pisces: Siganidae) in Palau. *Micronesica* 13(2), pp. 297–312.

Hoque, M., Takemura, A. and Takano, K. 1998. Annual changes in oocyte development and serum vitellogenin level in the rabbitfish *Siganus canaliculatus* (Park) in Okinawa, Southern Japan. *Fisheries Science* 64(1), pp. 44–51.

Hussein, K.A. 1986. Timing of spawning and fecundity of Mediterranean *Siganus rivulatus* (Forsk). *Bulletin of the National Institute of Oceanography and Fisheries* 12, pp. 175–186.

Jayasankar, P. 1990. Some aspects of biology of the white-spotted spine-foot, *Siganus canaliculatus* (Park, 1797) from the Gulf of Mannar. *Indian Journal of Fisheries* 37(1), pp. 9–14.

Katayama, S., Akiyama, S., Naganuma, M. And Shibata, R. 2009. Age and growth of rabbitfish *Siganus fuscescens* in Tateyama Bay, Japan. *Aquaculture ….*

Kulbicki, M., Guillemot, N. and Amand, M. 2005. A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybium* 29(3), pp. 235–252.

Lahnsteiner, F. and Patzner, R.A. 1999. Characterization of spermatozoa and eggs of the rabbitfish. *Journal of Fish Biology* 55(4), pp. 820–835.

Lakkis, S., Saad, A., Sabour, W. and Zeidane, R. 2004. Cycle sexuel et periodes de ponte chez deux especies de poissons exotiques: *Siganus luridus* et *S. rivulatus* (Siganidae) dans les eaux cotieres Syro-Lebanaises (Bassin Levantin). *Rapp. Comm. Int. Mer Medit.* 37.

Lee, S.-J., Kim, J.-B., Kim, M.-J. and Jung, S.-G. 2014. Age and growth of rabbit fish, Siganus fuscescens in the coast of Jeju island, Korea. *Journal of the Korean society of Fisheries Technology* 50(2), pp. 169–175.

Lee, S.J., Kim, M.J. and Han, S.H. 2019. Reproductive ecology of rabbit fish, *Siganus fuscescens* in the coastal waters off Jeju Island of Korea. *Journal of the Korean Society of Fisheries Ocean Technology* 55(4), pp. 349–355.

Masyahoro, A. 2011. Model pertumbuhan ikan beronang lingkis (*Siganus canaliculatus*) hasil tangkapan sero di Perairan Kepulauan Selayar. *J Agrisains* 12(1), pp. 50–56.

Mehanna, S. and Abdallah, M. 2002. Population dynamics of the rabbitfish *Siganus rivulatus* from the Egyptian sector of the Red Sea. *Marketing ZFP* 13(1), pp. 161–170.

Mehanna, S., S. Mohammad, A., M. El-Mahdy, S. and A.A. Osman, Y. 2018. Stock assessment and management of the rabbitfish *Siganus rivulatus* from the Southern Red Sea, Egypt. *Egyptian Journal of Aquatic Biology and Fisheries* 22(5 (Special Issue)), pp. 323–329.

Metar, S.Y., Nirmale, V.H., Chogale, N.D., Sadawarte, V.R., Satam, S.B., Singh, H. and Pai, R. 2017. Length-weight relationship and condition factor of the whitespotted rabbitfish *Siganus canaliculatus* (Park, 1797) From Ratnagiri Coast. In: Dapoli, 16-18 March 2017.

Muchlisin, Z.A., Fransiska, V., Muhammadar, A.A., Fauzi, M. and Batubara, A.S. 2017. Length-weight relationships and condition factors of the three dominant species of marine fishes caught by traditional beach trawl in Ulelhee Bay, Banda Aceh City, Indonesia. *Croatian Journal of Fisheries* 75(4), pp. 104–112.

Munira, Sulistiono and Zairion 2010. Length-weight relationship and growth of rabbit fish, *Siganus canaliculatus* (Park,1797) in the seagrass beds of Lonthoir Strait, Banda Archipelago, Maluku. *Jurnal Iktiologi Indonesia* 10(2), pp. 153–163.

Paraboles, L.C. and Campos, W.L. 2018a. Fecundity and oocyte development of the white-spotted rabbitfish *Siganus canaliculatus* (Park 1797) in Palompon, Leyte, Eastern Visayas, Philippines. *Asian fisheries science* 31, pp. 245–251.

Paraboles, L.C. and Campos, W.L. 2018b. Gonad development and reproductive cycle of the white-spotted rabbitfish *Siganus canaliculatus* (Park, 1797) in Palompon, Leyte, Eastern Visayas, Philippines. *Zeitschrift fur angewandte Ichthyologie = Journal of applied ichthyology* 34(4), pp. 878–887.

Popper, D. and Gundermann, N. 1975. Some ecological and behavioural aspects of siganid populations in the Red Sea and Mediterranean coasts of Israel in relation to their suitability for aquaculture. *Aquaculture* 6(2), pp. 127–141.

Popper, D., Pitt, R. and Zohar, Y. 1979. Experiments on the propagation of Red Sea siganids and some notes on their reproduction in nature. *Aquaculture* 16(2), pp. 177–181.

Shakman, E., Winkler, H., Oeberst, R. and Kinzelbach, R. 2008. Morphometry, age and growth of *Siganus luridus* Rüppell, 1828 and *Siganus rivulatus* Forsskål, 1775 (Siganidae) in the central Mediterranean (Libyan coast). *Revista de biología marina y oceanografía* 43(3).

Soykan, O., Gülşahin, A. and Cerim, H. 2020. Contribution to some biological aspects of invasive marbled spinefoot (*Siganus rivulatus* , Forsskål 1775) from the Turkish coast of southern Aegean Sea. *Journal of the Marine Biological Association of the UK*, pp. 1–8.

Suardi, Wiryawan, B., Taurusman, A.A., Santoso, J. and Riyanto, M. 2016. Variations in size and catch distribution of white spotted rabbit fish (*Siganus canaliculatus*) on bio-FADs from spatially and temporary point of view, at Luwu District, South Sulawesi, Indonesia. *Aquaculture, Aquarium, Conservation & Legislation* 9(6), pp. 1220–1232.

Tharwat, A. 2004. Reproductive cycle and mariculture potential of the rabbitfish *Siganus canaliculatus* in Saudi Arabia. *Egyptian Journal of Aquatic Biology and Fisheries* 8(4), pp. 123–143.

Tresnati, J., Omar, S.B.A. and Tuwo, A. 2019. Some reproductive biology studies of rabbitfish *Siganus canaliculatus* (Park, 1797) from the southern coastal waters of Jeneponto, South Sulawesi, Indonesia. *Biosciences, biotechnology research Asia* 16(3), pp. 617–624.

Tseng, W.Y. and Chan, K.L. 2009. The reproductive biology of the rabbitfish in Hong Kong. *Journal of the World Mariculture Society* 13(1-4), pp. 313–321.

Wassef, E. and Abdulhady, H. 2001. Some biological studies and gonadal development of rabbitfish *Siganus canaliculatus* (Park) and *Siganus spinus L.* (F: Siganidae) from the Gulf waters off Saudi Arabia. *Marketing ZFP* 12(1), pp. 189–208.

Wassef, E.A. and Abdul Hady, H.A. 1997. Breeding biology of rabbitfish *Siganus canaliculatus* (Siganidae) in mid Arabian gulf. *Fisheries Research* 33(1-3), pp. 159–166.

Yanagawa, H. 1994. Length-weight relationship of Gulf of Thailand fishes. *NAGA ICLARM Q* 17(4), pp. 48–52.

Yeldan, H. and Avşar, D. 2000. A preliminary study on the reproduction of the rabbitfish (*Siganus rivulatus* (Forsskal, 1775)) in the Northeastern Mediterranean. *Turkish Journal of Zoology* 24, pp. 173–182.

Chapter 3. Overwintering tropical herbivores accelerate detritus production on temperate reefs.

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3.1. Abstract

The tropicalization of temperate marine ecosystems can lead to increased herbivory rates, reducing the standing stock of seaweeds and potentially causing increases in detritus production. However, long-term studies analyzing these processes associated with the persistence of tropical herbivores in temperate reefs are lacking. We assessed the seasonal variation in abundances, macrophyte consumption, feeding modes and defecation rates of the range-extending tropical rabbitfish *Siganus fuscescens* and the temperate silver drummer *Kyphosus sydneyanus* and herring cale *Olisthops cyanomelas* on tropicalized reefs of Western Australia. Rabbitfish overwintered in temperate reefs, consumed more kelp and other macrophytes in all feeding modes and defecated more during both summer and winter than the temperate herbivores. Herbivory and defecation increased with rabbitfish abundance, but this was dependent on temperature, with higher rates attained by big schools during summer and lower rates in winter. Still, rabbitfish surpassed temperate herbivores, leading to a five-fold acceleration in the transformation of macrophyte standing stock to detritus, a function usually attributed to sea urchins in kelp forests. Our results suggest that further warming and tropicalization will not only increase primary consumption and affect the habitat structure of temperate reefs but also increase detritus production, with the potential to modify energy pathways.

3.2. Introduction

Primary consumption is fundamental for the transfer of energy across trophic levels and can exert a strong top-down control on the habitat structure and resilience of marine ecosystems, particularly in tropical regions [1]. Herbivores act as intermediate links between autotrophs, detritivores and secondary consumers, sustaining longer and more complex trophic chains in natural ecosystems [2]. At the same time, herbivores act as ecological engineers by regulating the cover of benthic macrophytes [3]. The intensity of herbivory follows a strong latitudinal pattern world-wide [4,5], in which tropical reefs dominated by corals have high rates of primary consumption mostly due to herbivorous fish [4,6–8], while temperate reefs dominated by large brown seaweeds experience lower rates of consumption, mostly caused by sea urchins and other mobile invertebrates [9]. Herbivorous fish are more abundant, more diverse and have more feeding strategies (*e.g.* browsers, grazers or scrapers) in the tropics than in temperate ecosystems [8,10–12], resulting in thousands of bites more on macrophytes per day [5,13–16]. However, as global climate change drives tropical species to shift their distribution towards higher latitudes, the guild of herbivorous fish in many temperate regions is

experiencing a process of tropicalization, where the proportion of warm-water species increase and past latitudinal patterns become blurred [17].

Global warming is changing the biodiversity configurations worldwide, causing poleward expansions of tropical species and creating new trophic interactions [18]. Among the marine vertebrates, herbivorous fish have been some of the most successful in expanding their distribution ranges [17]. Tropical herbivorous fish of the families Scaridae (parrotfish), Kyphosidae (sea chubs) and Siganidae (rabbitfish) have established populations in temperate ecosystems, increasing herbivory rates and having a direct effect on the structural complexity of these habitats, reducing seaweed and increasing turf and bare rock cover in the eastern Mediterranean Sea [19,20], southern Japan [21] and temperate Australia [22,23], with rabbitfish being the most successful taxon in all these regions [23–25]. In addition, it has been proposed recently that the process of tropicalization can also affect temperate ecosystems indirectly by modifying the energy transfer between trophic levels [26]. Kelp forests generate great amounts of detritus that are important sources of energy [27]. Currently, detritus is mainly generated by erosion or detachment of kelp sporophytes [28,29], with herbivory-derived detritus representing a small proportion and being mostly produced by sea-urchins [27,30]. Herbivores shred macrophyte biomass and transform it into particulate detrital matter of higher nutritional value for multiple consumers [31,32]. This process can be accelerated with the arrival of tropical herbivorous fish to temperate ecosystems by increasing the rates of defecation, with the potential of altering fluxes of biomass and the composition of the benthic community [30,33,34].

Despite the socio-ecological importance that the transformation of kelp forests to turf ecosystems can have [35,36] there is a lack of studies that integrally evaluate the persistence of tropical herbivores over multiple seasons, their direct and indirect effects and the interaction between these elements in tropicalized temperate ecosystems. Research to date has been restricted to assessments of seaweed consumption during warm (summer) conditions with no evaluations of its implication in detrital inputs on the temperate ecosystems or overwintering performance [16,19]. Assessments of these aspects across multiple seasons is of paramount importance since temperate winters can pose severe eco-physiological challenges to tropical fish adapted to more stable warmer environments [37,38]. Temperature modulate the metabolic rates of fish [39], consumption of macrophytes [40,41] and in extreme cases can lead to high mortality rates associated with physiological stress and starvation [42,43]. Still, some tropical herbivores seem to be extending their distribution polewards successfully but currently it is unknown how are they performing throughout the year in temperate reefs and how it compares to their temperate competitors and pre-tropicalization stages, information necessary to understand the magnitudes of change in current and future times. In this study we sought to answer

(i) whether rabbitfish overwintered in temperate reefs and suffered changes in abundances, (ii) which was their relative importance on transforming the standing-stock of kelp and other macrophytes into detritus over the seasons of the year and (iii) how this depended on the interaction between the number of herbivorous individuals and the environmental temperature, two factors that are predicted to increase in the future on temperate reefs. To test this, we assessed over multiple years (2016-2018) the seasonal variation in the abundances of the range-shifting tropical rabbitfish *Siganus fuscescens*, their herbivory rates in different feeding modes, their defecation rates, and compared these with the most important kelp consumers native of temperate reefs of western Australia: *Kyphosus sydneyanus* and *Olisthops cyanomelas.*

3.3. Materials and Methods

Location

The study was carried out at four temperate rocky reefs within Marmion Marine Park (Perth) in south-western Australia (31°49.4 S, 115°44.0 E), where the rabbitfish *Siganus fuscescens* has established populations following a marine heatwave in 2011 [23]: Cow Rocks, Wreck Rock, Whitfords Rock and The Lumps. These reefs are separated from each other by 1 ± 0.1 km and are characteristic of the inshore limestone reefs along the coast of south-western Australia, having similar environmental conditions associated with depth (~5m), wave exposure (1 km from land and subject to wind and oceanic swell of up to 4 m high) and substrate (limestone rock with reef flats, reef walls, crevices and overhangs). The reefs are dominated by the kelp *Ecklonia radiata* and the fucoids *Sargassum* spp., and are surrounded by meadows of the seagrasses *Posidonia sinuosa* and *Amphibolis* spp [44].

Herbivorous Fish Abundance and Rates of Herbivory

Fish abundance and herbivory rates were assessed during three consecutive years (2016, 2017 and 2018) in both the summer (November-April) and winter (July-September) seasons (summer: n = 19; winter: n = 16 days). During each sampling day at each reef, fish abundance was surveyed using Diver Operated Stereo-Video (S-DOV) before deploying bioassays of kelp filmed with Remote Underwater Videos (RUV). Three or four 25 × 5 m S-DOV transects were sampled along the ecotone between reef and seagrass, separating each transect by a minimum of ~10 m to ensure independence of replicates and ignoring fish appearing from behind the cameras to avoid double counting [45]. Using EventMeasure software (SeaGIS Pty Ltd), all individual fish were counted, measured (fork length) and identified to the lowest taxonomic level possible. Fish known to be consumers of kelp were classified

by climatic affinity (tropical: rabbitfish *S. fuscescens* and temperate: silver drummer *Kyphosus sydneyanus* and herring cale *Olisthops cyanomelas*). Herbivory on kelp was assessed through tethered bioassays consisting of a cluster of at least nine individual ~15 cm long lateral blades of *E. radiata* attached to 0.5 m rods simulating kelp canopy. One cluster was deployed per reef at each sampling day, representing one independent sampling unit. Tethers were deployed within the typical feeding timeframe of diurnal herbivorous fish, from the morning until the afternoon (8:00 – 16:00 hrs) [46] and filmed for 3-4 hours with GoPro cameras to identify the species responsible for the consumption of kelp, their relative abundances (MaxN), their bite rates on kelp (bites h^{-1}) and defecation rates (feces h^{-1}). During winter of 2018 (September) we deployed additional kelp tethers for three days to test if consumption rates would increase under a higher timeframe of exposure. In addition to herbivory on tethered kelps, bites on other macrophytes attached to the substratum and drifting in the water column were also registered during RUV analyses (*e.g.* kelp, seagrass, S*argassum* spp, *Ulva* spp., *Hypnea* spp.). We identified the species of fish feeding and classified their herbivory modes as: browsing (substrate attached macrophytes, including kelp tethers), kelp browsing (attached *E. radiata*), drifting (non-attached macrophytes) and total herbivory (browsing + drifting consumption).

Kelp lateral blades of bioassays were pressed between a white background and a perspex glass and photographed before and after deployment. The photographs of kelp were analyzed using the software ImageJ (rsb.info.nih.gov/ij/) to calculate the area consumed per time (cm^2 hr^{-1}) [23,44,47]. This was transformed to biomass (g hr^{-1}) using a linear area-weight regression. Herbivory and defecation rates were standardized for each species of the main kelp consumers (tropical rabbitfish: *S. fuscescens* and temperate silver drummers: *K. sydneyanus*). Bite rates estimates were multiplied by weight-specific bite sizes (cm^2), calculated from bite size-weight regressions using bite measures from specimens of both species donated by the Department of Primary Industries and Regional Development (Fisheries Research) and recreational fishermen (Supplementary Material), while defecation rates were multiplied by the mean weight of each species calculated from the corresponding S-DOV carried out immediately before each herbivory assay [48]. Underwater temperature data for each reef was recorded *in situ* during the fish and herbivory surveys using hobo data loggers. The full dataset used for analyzes is accessible at Dryad [49].

Statistical Analyses

We used mixed-effects linear regression analyses to evaluate (i) the effect of temperature on the abundance (S-DOV and MaxN) of tropical and temperate herbivorous fish, and the effect of both temperature and herbivorous fish abundance on (ii) kelp consumption rates, (iii) drift consumption rates and (iv) defecation rates of *S. fuscescens* and *K. sydneyanus*. Changes in fish abundance was

evaluated with negative binomial generalized linear mixed models using the R package glmmTMB [50]. Fish herbivory and defecation rates were analyzed with linear mixed effects models (LMEM) with the R package nlme [51]. Since the effect of multiple unmeasured factors in the natural environment can affect the phenomena of interest and increase the frequency of low values, masking the true effect of explanatory variables, we applied linear quantile mixed-effects regressions (LQMM) to the 90th percentile of the response distribution using the R package lqmm in addition to regressions based on the conditional mean of the response variables [52]. The use of quantile regression in ecological studies has increased since it is a more robust technique than the more common ordinary least squares approach and it allows a more complete analysis of the relationships between variables [53]. In all regressions, we included random intercepts based on Reefs and Years, but for herbivory and defecation rates we also included random slopes based on herbivorous fish abundance. Models with different structure of the random components were compared and the best was chosen based on AIC, BIC, Likelihood Ratio Test and graphical examination of predictions vs observations. Overdispersion, normality and homogeneity of the residuals of LMEM were assessed with histograms and fitted vs predicted scatterplots. When assumptions were not met, data was log transformed. In case of statistically significant effects of explanatory variables we used the R package sjPlot to graph the model predictions [54]; temperature was plotted as the moderator variable based on mean (18.59 °C) and ±SE values (20.85 and 16.33 °C). The R code of these analyzes is provided in the section of Supplementary Materials.

3.4. Results

Persistence during winter

Rabbitfish were present at temperate reefs in all surveys. There was no significant relationship between herbivorous fish abundance and temperature (Fig. 1). All herbivorous fish species were present in higher average abundances during summer, with tropical rabbitfish being the most abundant (MaxN: 25.8 ± 8.1; DOV: 12 ± 4 individuals 125 m^{-2}, mean ± SE), followed by silver drummers (MaxN: 10.2 ± 4.4, DOV: 3.5 ± 1.4 individuals 125 m^{-2}) and herring cale (MaxN: 0.4 ± 0.6, DOV: 0.4 ± 0.2 individuals 125 m^{-2}). Rabbitfish remained present during winter in waters as cold as 16°C, forming schools (MaxN: 17.3 ± 7.2, DOV: 5.8 ± 2.7 individuals 125 m^{-2}) of similar abundance as silver drummers (MaxN: 7 ± 3.1, DOV: 4.1 ±1.4 individuals 125 m^{-2}) but greater than herring cale (MaxN: 0.3 ± 0.1, DOV: 0.25 ± 0.2 individuals 125 m^{-2}) (Fig. 1). Rabbitfish average fork length was 28.5 ± 1.5 cm (Min: 20.5 cm and Max: 38.5 cm), while silver drummer average length was 43.2 ± 9.1 cm (Min: 18 cm and Max: 72.5 cm). Silver drummers had larger bite area than rabbitfish by 3 times within their comparable weight range (*i.e.* 200-400 g) and 6 times larger at bigger sizes (~7300 g) (Supplementary Material).
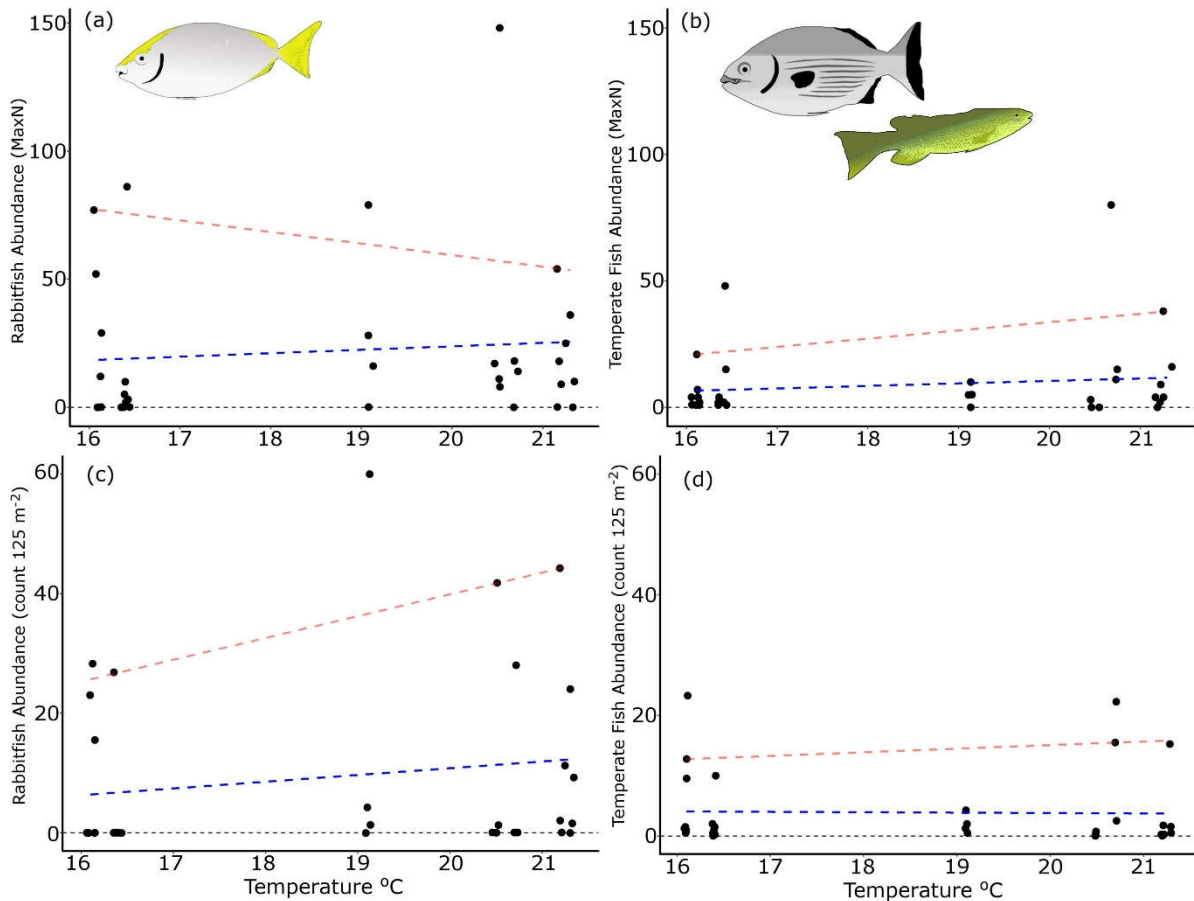
Figure 1. Relationship between the abundance of tropical (*Siganus fuscescens,* a, c) and temperate herbivorous fish (*Olisthops cyanomelas* and *Kyphosus sydneyanus,* b, d) and temperature changes through the year from RUV (a, b) and S-DOV (c, d). Regressions to the 0.9 quantile (red) and the mean (blue) were non-statistically significant (p > 0.5).

Primary Consumption Rates

Temperate and tropical herbivorous fish consumed kelp at higher rates in the warmest temperatures of summer (max T: 22 °C) than in the lower temperatures in winter (min T: 16 °C). Rabbitfish total consumption rate during summer was 244 ± 65 cm^2 hr^{-1} (mean ± SE) from 18092 total bites (426 bites hr^{-1}), while in winter the average rate was 7.4 ± 7.4 cm^2 hr^{-1} from 979 total bites (15.3 bites hr^{-1}). In comparison, silver drummers consumed macrophytes at a rate of 45.6 ± 22 cm^2 hr^{-1} in summer (715 bites: 21.2 bites hr^{-1}) and 1.7 ± 1.6 cm^2 hr^{-1} in winter (69 bites: 1.1 bites hr^{-1}). Herring cale had the lowest consumption rates with only 83 bites (1.6 bites hr^{-1}) in all summer surveys and zero consumption during winter (Fig. 2).
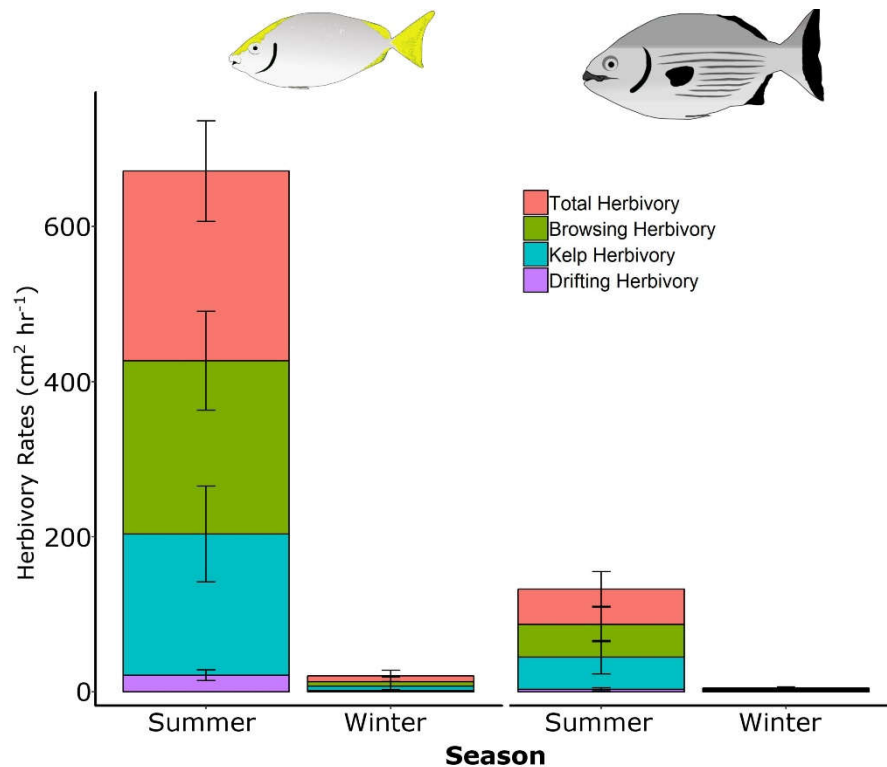
Figure 2. Rates of different modes of herbivory (mean ± SE) by temperate (*Kyphosus sydneyanus*) and tropical herbivorous fish (*Siganus fuscescens*) during winter (17-16 °C) and summer (19-21 °C) in temperate reefs of south-western Australia.

Rabbitfish browsing was 37 times higher during summer (223 ± 64 cm^2 hr^{-1}) than during winter (6 ± 5.9 cm^2 hr^{-1}). Similarly, although at lower rates, browsing by silver drummer was 26 times higher during summer (42 ± 22 cm^2 hr^{-1}) than in winter (1.7 ± 1.6 cm^2 hr^{-1}). Herring cale browsing was equivalent to their total consumption (Supplementary Material). Browsing was observed in seagrass, *Sargassum* and kelp. Seagrass was only consumed by rabbitfish in summer (4.6 ± 2.7 cm^2 hr^{-1}). Short thalli of *Sargassum* were mainly consumed by rabbitfish during both seasons (summer: 36.4 ± 22.4 cm^2 hr^{-1}, winter: 0.15 ± 0.15 cm^2 hr^{-1}), while silver drummer (0.8 ± 0.8 cm^2 hr^{-1}) and herring cale (45 bites: 0.8 ± 0.8 bites hr^{-1}) only consumed it during summer at lower rates. Consumption of kelp (tethered *Ecklonia radiata*) accounted for 82% of the total browsing. Rabbitfish bit kelp 13020 times and on average consumed 32 times more in summer (182 ± 67 cm^2 hr^{-1}) than during winter (5.7 ± 5.6 cm^2 hr^{-1}). Silver drummer bit kelp 616 times and consumed 24 times more kelp in summer (41 ± 23.5 cm^2 hr^{-1}) than in winter (1.7 ± 1.6 cm^2 hr^{-1}). Herring cale were rarely seen and only bit kelp 35 times during one survey in summer (0.75 ± 0.75 bites hr^{-1}). In terms of biomass, total consumption of tethered kelp in summer amounted to 529.5 g, equivalent to 10.4 ± 3.1 g h^{-1} (mean ± SE); while in winter total consumption was 37.7 g, equivalent to 0.6 ± 0.5 g h^{-1}. This was further confirmed with the results of 3-day tether deployments during winter of 2018 that yielded consumption values of 2.3 g hr^{-1}.

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Kelp consumption rates were correlated with rabbitfish abundance with a significant interaction with temperature (Fig. 3a; $LQMM_{0.9}$, p< 0.0001; LMEM, t_{28}= 5.18, p< 0.0001). Kelp consumption at 16°C during winter was low despite the presence of abundant rabbitfish schools of up to 50-80 individuals, registering a maximum consumption of 119 cm^2 hr^{-1}. In contrast, similar rabbitfish abundance in summer (19-21°C) was associated with kelp consumption rates of 782 cm^2 hr^{-1} (Fig. 3a). Consumption by silver drummer was not correlated with their abundance or with temperature, although the higher rates of consumption occurred at higher temperatures (Fig. 3b). Thus, although, temperate herbivores consumed more kelp biomass per bite, they had lower net consumption rates than tropical rabbitfish, which had five-fold higher bite rates and up to three-fold higher net consumption (Fig. 3).

While browsing accounted for most of the total herbivory registered during all surveys (89%), we also registered a considerable number of bites on seaweeds drifting in the water column, a behavior and ecological function generally disregarded in the ecological literature of fish herbivory. This accounted for 11% of the total primary consumption, with rabbitfish largely responsible for this mode of herbivory, consuming green, red and brown seaweed (*i.e. Ulva* spp., *Hypnea* spp., *Sargassum* spp., *Dictyopteris* spp. and kelp). Neither rabbitfish abundance nor temperature were significantly correlated with drift consumption, although most of the consumption was observed in summer ($LQMM_{0.9}$, p= 0.9148; LMEM, t_{28}= 0.33, p= 0.7418). In contrast to browsing, the highest rates of drift consumption were recorded when abundances of rabbitfish were low; the total number of bites recorded in summer were 1942 bites (21.4 ± 7 cm^2 hr^{-1}), in contrast to 202 bites during winter (1.5 ± 1.5 cm^2 hr^{-1}; Fig. 3c). No significant interaction was found between silver drummer abundance and temperature on their drifting herbivory rates ($LQMM_{0.9}$, p= 0.1098; LMEM, t_{28}= 2.0, p= 0.055); their consumption was only observed during summer at low frequency (3.4 ± 2 cm^2 hr^{-1}: 87 bites).
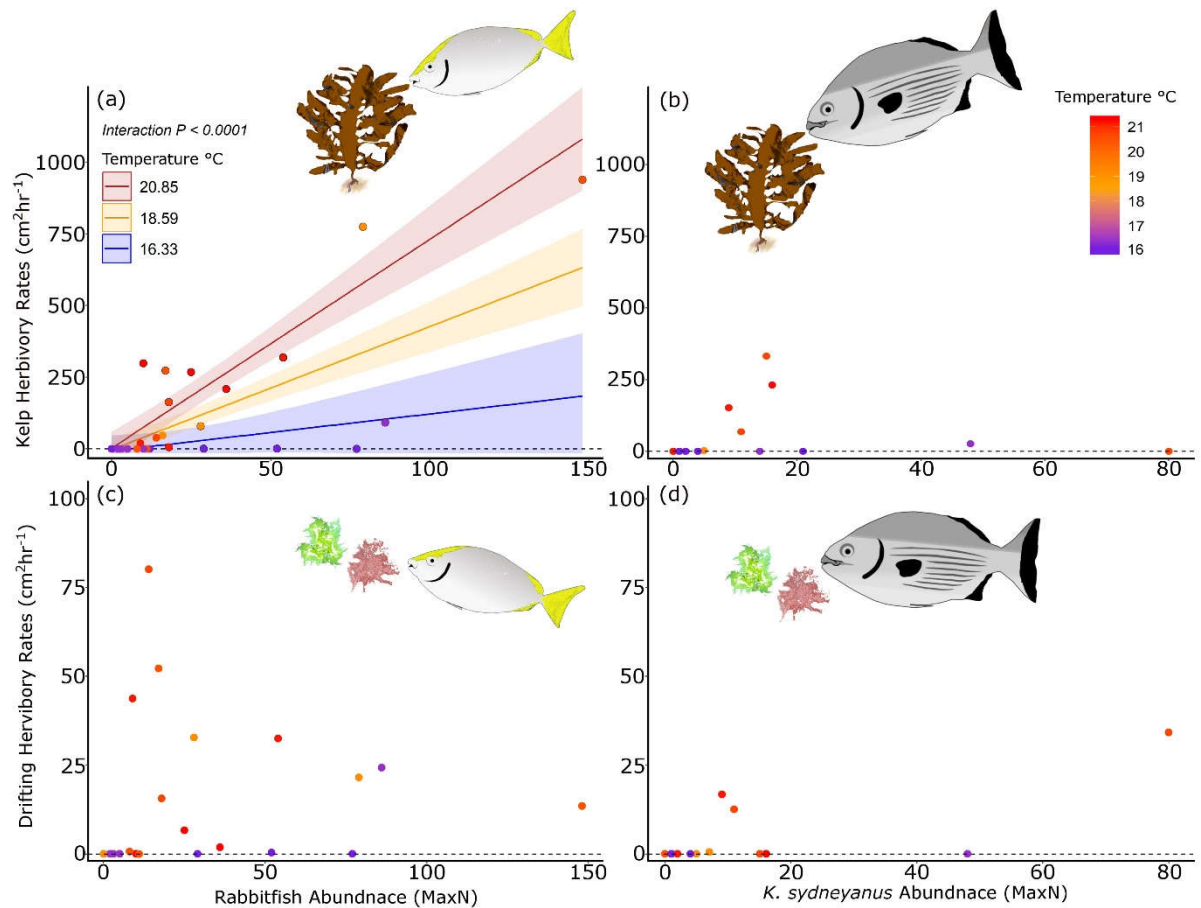
Figure 3. Relationship between kelp consumption (a, b) and drifting herbivory rates (*e.g. Ulva* spp. and *Hypnea* spp.; c, d) with temperature and abundances of herbivorous fish. A: Regressions (CI=95%) of kelp consumption based on a significant interaction between abundance of tropical rabbitfish (*Siganus fuscescens*) and temperature (mean ± SE). B: relationship between kelp consumption, abundance of temperate silver drummers (*Kyphosus sydneyanus*) and temperature. C: relationship between drifting herbivory, rabbitfish abundance and temperature. D: relationship between drifting herbivory, abundance of silver drummers and temperature.

Defecation rates

Defecation during summer accounted for 94.5% (*i.e.* 294) of all the observed defecations during our study, with the majority of these being from rabbitfish (97%) and the rest from silver drummer (2.3%), with no feces registered from herring cale. Defecation rates of rabbitfish had a significant interaction between their abundances and temperature (Fig. 4a; $LQMM_{0.9}$, p< 0.0001; LMEM, t_{28}= 3.85, p= 0.0006), and were strongly correlated with their total bite rates (p< 0.001). Defecation rates of silver drummers were not related with their abundances but were correlated with temperature (Fig. 4b; $LQMM_{0.9}$, p = 0.005) and bite rates (p< 0.001). Thus, as bite rates decreased with temperature during

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winter, we registered less defecations from all species (Fig. 4c-d). Defecation rates weighted by fish biomass, showed that rabbitfish produced eight time more feces on average (2.75 ± 0.6 feces kg hr^{-1}, 6 ± 1.27 feces hr^{-1}) than silver drummers in warm conditions (0.34 ± 0.17 feces kg hr^{-1}: 0.2 ± 0.1 feces hr^{-1}). In winter, defecation rates were lower; however, rabbitfish still produced five times more detritus (0.07 ± 0.07 feces kg hr^{-1}; 0.23 ± 0.23 feces hr^{-1}) than silver drummers (0.014 ± 0.014 feces kg hr^{-1}, 0.01 ± 0.01 feces hr^{-1}).
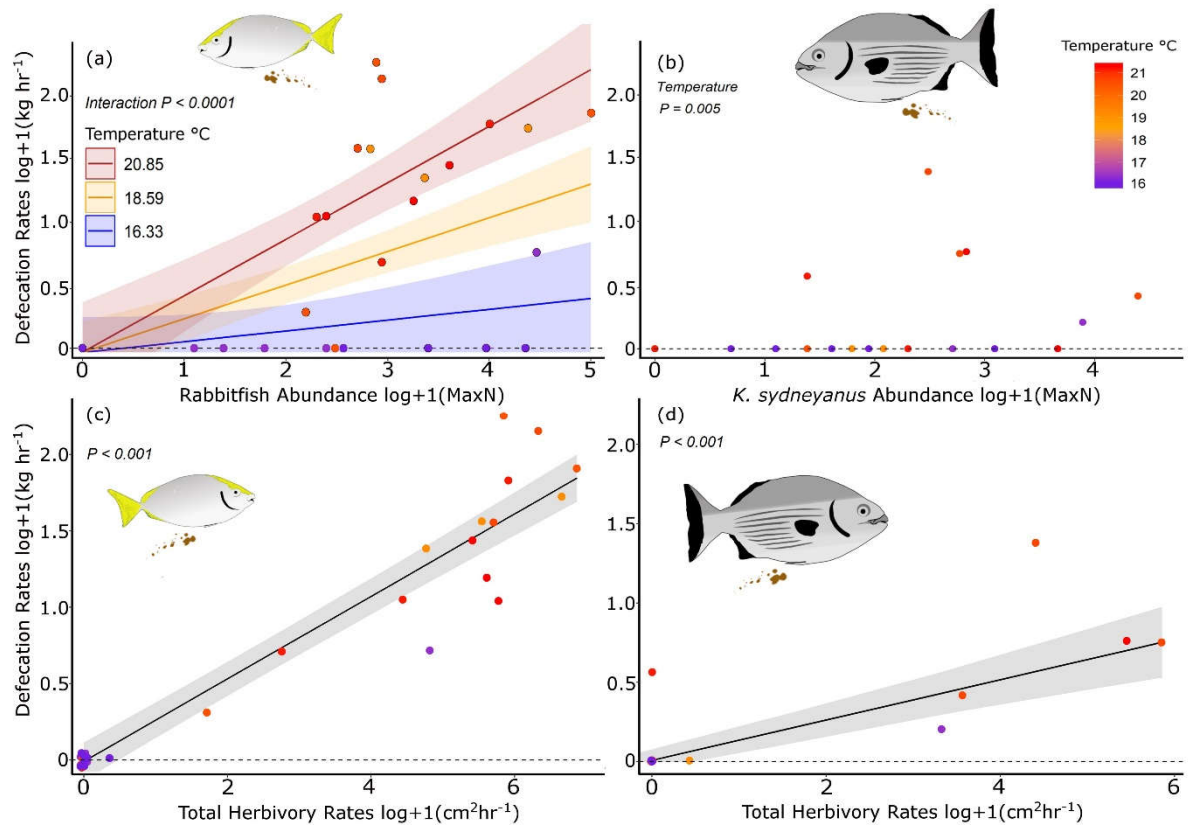
Figure 4. Relationship between defecation rates, abundance, temperature and total herbivory rates of tropical (a, c) and temperate herbivorous fish (b, d). A: regressions (CI=95%) of defecation rates of tropical rabbitfish (*Siganus fuscescens*) with a significant interaction between their abundance and temperature (mean ± SE). B: relationship between defecation rates of temperate silver drummers (*Kyphosus sydneyanus*), their abundance and temperature. C: Relationship between total herbivory rates and defecation rates of rabbitfish. D: Relationship between total herbivory rates and defecation rates of silver drummers.

3.5. Discussion

Our study investigated the ecological functions of tropical rabbitfish in their new temperate ecosystems (consumption of macrophytes and its transformation to detritus biomass) relative to native temperate herbivores and analyzed its variability through time according to key biological (abundance) and environmental variables (temperature). We found that rabbitfish persisted through the years, even during temperatures as low as 16 °C, overwintering in similar abundance as their most important temperate competitors silver drummers. Highly mobile fish species can relocate to more favorable thermal environments if they are suffering from thermal stress (*i.e.* behavioral thermoregulation) [38]. However, rabbitfish did not seem to migrate to warmer environments and did not suffer significant declines in population size. Although not reported elsewhere, this could be the same case for populations of rabbitfish inhabiting temperate reefs in Japan (*Siganus fuscescens;* [55,56]), the Mediterranean Sea (*Siganus luridus* and *Siganus rivulatus* [24]) and eastern Australia (*S. fuscescens* [57]), where their distributions have expanded.

Rabbitfish populations seem to be well established in the kelp forests of western Australia. However, their persistence in the future will depend on their recruitment success. *S. fuscescens* has expanded its distribution polewards in western Australia since 2011, aided by an extreme marine heatwave that intensified the transport of tropical waters towards higher latitudes [58]. Their presence in temperate environments has been reported during summers of subsequent years, including schools of juveniles, suggesting successful reproduction and recruitment events in their new temperate habitats [59]. All the rabbitfish observed during our S-DOV and RUV surveys were mature individuals (>20 cm FL). However, on two occasions during the summer of 2016 we observed schools of juveniles roaming through seagrass and kelp beds adjacent to our survey sites (Supplementary Materials). Breeding activity of tropical species in temperate ecosystems has been reported for some species but currently it is considered uncommon in a global context [60]. To our knowledge, rabbitfish are the only group of tropical herbivores documented as reproductively active at high latitudes [61]. *S. fuscescens* can recruit to kelp forests [62], indicating that temperate reefs are suitable for juveniles. Nevertheless, thermal tolerance is narrower in juvenile stages and extreme low temperatures can cause high rates of mortality [42,43]. For instance, many juvenile tropical fish appear during the summer in temperate reefs of eastern Australia, but most of them are not able to overwinter in the southernmost regions (*e.g* Merimbula) [63]. High mortality caused by cold spells have been reported for rabbitfish populations, however, well established and interconnected populations seem to be highly resilient, recovering in a short period of time when warmer conditions return [64].

Primary consumption and detritus production rates have been increased by rabbitfish throughout the year. The metabolic rates and energetic requirements of ectotherm organisms follow a positive exponential relationship with the environmental temperature [38]. Accordingly, consumption of macrophytes by fish fluctuates through the seasons of the year [40,41] and along latitudinal thermal gradients (18 - 27 °C) [12]. Feeding trials in aquarium experiments have shown that low temperatures decrease consumption rates (*e.g.* surgeonfish, 20 - 24 °C) [65–67] until a threshold is reached and individuals cease to feed (*e.g.* damselfish, 17-18.6 °C) [39]. Herbivory by rabbitfish was higher in summer and although it decreased during winter, it remained five-fold higher than silver drummers, their most important local competitors. Similarly, we found that tropical rabbitfish were the main producers of feces, having five to eight-fold higher defecation rates than silver drummers during winter and summer. Despite having smaller bite sizes than temperate herbivores, rabbitfish achieved a higher consumption efficiency as a function of higher bite rates. Although the bigger size of silver drummers suggest a high food intake for maintenance, larger animals tend to have lower feeding rates [68], as has been constantly described for this species in the region [44,47]. Similarly, herbivory rates by odacids have been lower than tropical fish in past studies, agreeing with our results regarding herring cale [69]. In contrast with past studies of rabbitfish herbivory in the Mediterranean Sea, where the native fish *Sarpa salpa* had a bigger impact on macrophytes during summer [19], our results suggest that rabbitfish can exert higher ecological impacts in temperate reefs throughout the year despite the reductions in herbivory during winter, since although net production of kelp in the region is positive during summer, kelp forests lose biomass during winter due to high rates of erosion [29].

Siganus fuscescens had the most flexible diet and was the most important herbivorous fish on all feeding modes. Rabbitfish browsed the most on kelp and sargassum, was the only species that consumed seagrass, and in addition to macrophytes, they can be avid consumers of cnidarians [70,71]. While they are usually categorized within one functional group, it is now known that they can be browsers [57,72] and grazers [16,19]. Our research adds an additional category to their feeding flexibility: drifting herbivory. We showed that 11% of herbivory was on detached macrophytes, demonstrating that herbivory by fish is more complex in temperate reefs than generally described. In tropical reefs drifting herbivory has rarely been considered [73], probably because detached macrophytes are either small or rare and the process itself might not be critical for reef resilience [74]. In contrast, consumption of detached macrophytes is recognized as an important process on temperate reefs [27,47] and temperate seagrass beds [44]. Here we observed rabbitfish consuming significant amounts of a diverse array of drifting seaweed in the water column, an herbivory mode not previously associated with them [74]. The ecological implications of drifting herbivory are important, since it implies that consumption of standing stock seaweed is reduced, alleviating the impact on the

habitat structure, and retaining biomass that otherwise would have been transported elsewhere, reducing the export of biomass and nutrients to inter-connected ecosystems [75].

Our study quantitatively modelled the interactions between changes in temperature, abundance of tropical herbivores and their rates of herbivory and defecation in temperate reefs. Based on our models and evidence of poleward migrations of tropical species [17], future increases in temperature and abundance of tropical herbivores due to climate change could further accelerate the transformation of macrophyte standing stocks to detritus biomass, altering historical ecological patterns and functioning of temperate reefs [26]. For instance, these analyses imply that a rise in temperature of 2°C, as predicted for the region of study by the end of the century under a business as usual scenario [76], could increase consumption and defecation rates of abundant schools of rabbitfish three-fold on average. Currently, herbivory-mediated detritus of kelp in temperate reefs is low compared with erosion-generated detritus [28] and is mainly produced by sea-urchins [27] with herbivorous fish playing a secondary role [69]. The increase of rates of herbivory and defecation by rabbitfish observed in our study suggest that this paradigm is already changing in temperate ecosystems with tropicalized herbivorous communities. Rabbitfish feces sink to the seafloor within the vegetation, where the nutrients likely will be recycled by a myriad of organisms. Marine herbivores shred macrophytes and enrich them in organic nutrients and minerals in its passage through the digestive system [30,34] and once released these could enter the microbial food web and be consumed by detritivorous organisms and higher trophic levels [31,33,77,78]. Further research into the detailed pathways that tropical fish feces could follow in temperate food-webs are necessary to assess their specific impact in the ecosystem.

Through seasonal surveys and feeding assays across three years our study provides new knowledge about the persistence of range-expanding tropical rabbitfish and their capacity to modify trophic processes in temperate reefs. We showed that rabbitfish populations in south-western Australia are able to withstand winter temperatures, remaining in the area with approximately similar abundances as summer months. Rabbitfish consumed more kelp, fed from more species of macrophytes on all feeding modes and produced more feces throughout the year than their temperate competitors. Rabbitifish browsed intensively in abundant schools but when they roved in small groups, they also consumed multiple drifting seaweed, a novel herbivory mode for these tropical herbivores. We report rabbitfish defecation rates for the first time in temperate ecosystems and found that they are significantly accelerating the herbivory derived detritus in the ecosystem, a function usually attributed to sea-urchins. Our study highlights that the ecological implication of herbivory in kelp forests goes beyond the sole process of reducing the cover of primary producers but the transformation of the ecological function of macrophyte biomass from habitat providers to nutrient sources for other

trophic groups as detritus. Predicted warming and increases in abundance and diversity of tropical herbivorous fish in the future due to climate change are likely to accelerate this process, with the potential to gradually drive temperate reefs to canopy-free states. This will depend on the specific relationship through time between the net primary consumption and net primary production of temperate reefs in different parts of the world.

Authors' Contributions

S.Z.-P. and T.W. conceived the study and acquired the funding; S.Z.-P. and T.W. collected the field data; S.Z.-P. analyzed the data and wrote the paper. All authors contributed to drafting the manuscript and gave final approval for publication.

Data Accessibility

The full dataset used for analyses is accessible from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tx95x69sg [49].

3.6. References

1. Steneck, R. S., Bellwood, D. R. & Hay, M. E. 2017 Herbivory in the marine realm. *Curr Biol* **27**, R484–R489. (doi:10.1016/j.cub.2017.04.021)
2. Bertness, M. D., Brisson, C. P., Coverdale, T. C., Bevil, M. C., Crotty, S. M. & Suglia, E. R. 2014 Experimental predator removal causes rapid salt marsh die-off. *Ecol Lett* **17**, 830–835. (doi:10.1111/ele.12287)
3. Gruner, D. S. et al. 2008 A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecol Lett* **11**, 740–755. (doi:10.1111/j.1461-0248.2008.01192.x)
4. Vergés, A., Doropoulos, C., Czarnik, R., McMahon, K., Llonch, N. & G. B. Poore, A. 2018 Latitudinal variation in seagrass herbivory: Global patterns and explanatory mechanisms. *Global Ecology and Biogeography* (doi:10.1111/geb.12767)

5. Longo, G. O., Hay, M. E., Ferreira, C. E. L. & Floeter, S. R. 2018 Trophic interactions across 61 degrees of latitude in the Western Atlantic. *Global Ecology and Biogeography* (doi:10.1111/geb.12806)

6. Hughes, T. P. et al. 2007 Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* **17**, 360–365. (doi:10.1016/j.cub.2006.12.049)

7. Bellwood, D. R., Hughes, T. P. & Hoey, A. S. 2006 Sleeping functional group drives coral-reef recovery. *Curr Biol* **16**, 2434–2439. (doi:10.1016/j.cub.2006.10.030)

8. Bellwood, D. R., Hughes, T. P., Folke, C. & Nyström, M. 2004 Confronting the coral reef crisis. *Nature* **429**, 827–833. (doi:10.1038/nature02691)

9. Filbee-Dexter, K. & Scheibling, R. E. 2014 Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Mar. Ecol. Prog. Ser.* **495**, 1–25. (doi:10.3354/meps10573)

10. Meekan, M. G. & Choat, J. H. 1997 Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs. *Mar. Biol.* **128**, 373–383. (doi:10.1007/s002270050103)

11. Floeter, S. R., Ferreira, C. E. L., Dominici-Arosemena, A. & Zalmon, I. R. 2004 Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *J Fish Biol* **64**, 1680–1699. (doi:10.1111/j.0022-1112.2004.00428.x)

12. Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddack, M. J. & Horn, M. H. 2005 Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar. Biol.* **147**, 1435–1447. (doi:10.1007/s00227-005-0027-0)

13. Ferreira, D. E. L., Peret, A. C. & Coutinho, R. 1998 Seasonal grazing rates and food processing by tropical herbivorous fishes. *J Fish Biol* **53**, 222–235. (doi:10.1111/j.1095-8649.1998.tb01029.x)

14. Polunin, N. V. C., Harmelin-Vivien, M. & Galzin, R. 1995 Contrasts in algal food processing among five herbivorous coral-reef fishes. *J Fish Biol* **47**, 455–465. (doi:10.1111/j.1095-8649.1995.tb01914.x)

15. Hoey, A. S. & Bellwood, D. R. 2009 Limited Functional Redundancy in a High Diversity System: Single Species Dominates Key Ecological Process on Coral Reefs. *Ecosystems* **12**, 1316–1328. (doi:10.1007/s10021-009-9291-z)

16. Bennett, S., Wernberg, T., Harvey, E. S., Santana-Garcon, J. & Saunders, B. J. 2015 Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecol Lett* **18**, 714–723. (doi:10.1111/ele.12450)

17. Vergés, A. et al. 2014 The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proc Biol Sci* **281**, 20140846. (doi:10.1098/rspb.2014.0846)

18. Pecl, G. T. et al. 2017 Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355**. (doi:10.1126/science.aai9214)

19. Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z., Dendrinos, P., Karamanlidis, A. A., Spiegel, D. & Sala, E. 2014 Tropical rabbitfish and the deforestation of a warming temperate sea. *J Ecol* **102**, 1518–1527. (doi:10.1111/1365-2745.12324)

20. Sala, E., Kizilkaya, Z., Yildirim, D. & Ballesteros, E. 2011 Alien marine fishes deplete algal biomass in the Eastern Mediterranean. *PLoS ONE* **6**, e17356. (doi:10.1371/journal.pone.0017356)

21. Kumagai, N. H., García Molinos, J., Yamano, H., Takao, S., Fujii, M. & Yamanaka, Y. 2018 Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proc Natl Acad Sci U S A* **115**, 8990–8995. (doi:10.1073/pnas.1716826115)

22. Ling, S. D., Barrett, N. S. & Edgar, G. J. 2018 Facilitation of Australia's southernmost reef-building coral by sea urchin herbivory. *Coral Reefs* **37**, 1053–1073. (doi:10.1007/s00338-018-1728-4)

23. Zarco-Perello, S., Wernberg, T., Langlois, T. J. & Vanderklift, M. A. 2017 Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Sci. Rep.* **7**, 820. (doi:10.1038/s41598-017-00991-2)

24. Azzurro, E., Franzitta, G., Milazzo, M., Bariche, M. & Fanelli, E. 2017 Abundance patterns at the invasion front: the case of Siganus luridus in Linosa (Strait of Sicily, Central Mediterranean Sea). *Mar. Freshwater Res.* **68**, 697. (doi:10.1071/MF16024)

25. Takao, S., Kumagai, N. H., Yamano, H., Fujii, M. & Yamanaka, Y. 2015 Projecting the impacts of rising seawater temperatures on the distribution of seaweeds around Japan under multiple climate change scenarios. *Ecol Evol* **5**, 213–223. (doi:10.1002/ece3.1358)

26. Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M. A., Wernberg, T., Ainsworth, T. & Steinberg, P. D. 2019 Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. *Funct Ecol* (doi:10.1111/1365-2435.13310)

27. Wernberg, T. & Filbee-Dexter, K. 2018 Grazers extend blue carbon transfer by slowing sinking speeds of kelp detritus. *Sci. Rep.* **8**, 17180. (doi:10.1038/s41598-018-34721-z)

28. Krumhansl, K. A. & Scheibling, R. E. 2012 Production and fate of kelp detritus. *Mar. Ecol. Prog. Ser.* **467**, 281–302. (doi:10.3354/meps09940)

29. De Bettignies, T., Wernberg, T., Lavery, P. S., Vanderklift, M. A. & Mohring, M. B. 2013 Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus. *Limnol. Oceanogr.* **58**, 1680–1688. (doi:10.4319/lo.2013.58.5.1680)

30. Sauchyn, L. K. & Scheibling, R. E. 2009 Degradation of sea urchin feces in a rocky subtidal ecosystem: implications for nutrient cycling and energy flow. *Aquat. Biol.* **6**, 99–108. (doi:10.3354/ab00171)

31. Yorke, C. E., Page, H. M. & Miller, R. J. 2019 Sea urchins mediate the availability of kelp detritus to benthic consumers. *Proc Biol Sci* **286**, 20190846. (doi:10.1098/rspb.2019.0846)

32. Dethier, M. N., Hoins, G., Kobelt, J., Lowe, A. T., Galloway, A. W. E., Schram, J. B., Raymore, M. & Duggins, D. O. 2019 Feces as food: The nutritional value of urchin feces and implications for benthic food webs. *Journal of Experimental Marine Biology and Ecology* **514-515**, 95–102. (doi:10.1016/j.jembe.2019.03.016)

33. Pinnegar, J. K. & Polunin, N. V. C. 2006 Planktivorous damselfish support significant nitrogen and phosphorus fluxes to Mediterranean reefs. *Mar. Biol.* **148**, 1089–1099. (doi:10.1007/s00227-005-0141-z)

34. Wotton, R. S. & Malmqvist, B. 2001 Feces in aquatic ecosystems. *Bioscience* **51**, 537. (doi:10.1641/0006-3568(2001)051[0537:FIAE]2.0.CO;2)

35. Bennett, S., Wernberg, T., Connell, S. D., Hobday, A. J., Johnson, C. R. & Poloczanska, E. S. 2016 The "Great Southern Reef": social, ecological and economic value of Australia's neglected kelp forests. *Mar. Freshwater Res.* **67**, 47. (doi:10.1071/MF15232)

36. Filbee-Dexter, K. & Wernberg, T. 2018 Rise of turfs: A new battlefront for globally declining kelp forests. *Bioscience* (doi:10.1093/biosci/bix147)

37. Pörtner, H. O. & Farrell, A. P. 2008 Ecology. Physiology and climate change. *Science* **322**, 690–692. (doi:10.1126/science.1163156)

38. Pörtner, H. O. & Peck, M. A. 2010 Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J Fish Biol* **77**, 1745–1779. (doi:10.1111/j.1095-8649.2010.02783.x)

39. Eme, J. & Bennett, W. A. 2008 Low temperature as a limiting factor for introduction and distribution of Indo-Pacific damselfishes in the eastern United States. *J Therm Biol* **33**, 62–66. (doi:10.1016/j.jtherbio.2007.10.003)

40. Clements, K. D. & Choat, J. H. 1993 Influence of season, ontogeny and tide on the diet of the temperate marine herbivorous fish Odax pullus (Odacidae). *Mar. Biol.* **117**, 213–220. (doi:10.1007/BF00345665)

41. Tomas, F., Turon, X. & Romero, J. 2005 Seasonal and small-scale spatial variability of herbivory pressure on the temperate seagrass Posidonia oceanica. *Mar. Ecol. Prog. Ser.* **301**, 95–107. (doi:10.3354/meps301095)

42. Hurst, T. P. 2007 Causes and consequences of winter mortality in fishes. *J Fish Biol* **71**, 315–345. (doi:10.1111/j.1095-8649.2007.01596.x)

43. Zarco-Perello, S., Pratchett, M. & Liao, V. 2012 Temperature-growth performance curves for a coral reef fish, *Acanthochromis polyacanthus*. *Galaxea, Journal of Coral Reef Studies* **14**, 97–103. (doi:10.3755/galaxea.14.97)

44. Wernberg, T., Vanderklift, M. A., How, J. & Lavery, P. S. 2006 Export of detached macroalgae from reefs to adjacent seagrass beds. *Oecologia* **147**, 692–701. (doi:10.1007/s00442-005-0318-7)

45. Goetze, J. S. et al. 2019 A field and video analysis guide for diver operated stereo-video. *Methods Ecol Evol* **10**, 1083–1090. (doi:10.1111/2041-210X.13189)

46. Fox, R. J., Sunderland, T. L., Hoey, A. S. & Bellwood, D. R. 2009 Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. *Mar. Ecol. Prog. Ser.* **385**, 261–269. (doi:10.3354/meps08059)

47. Vanderklift, M. A., Lavery, P. S. & Waddington, K. I. 2009 Intensity of herbivory on kelp by fish and sea urchins differs between inshore and offshore reefs. *Mar. Ecol. Prog. Ser.* **376**, 203–211. (doi:10.3354/meps07811)

48. Shantz, A. A., Ladd, M. C., Schrack, E. & Burkepile, D. E. 2015 Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecol Appl* **25**, 2142–2152. (doi:10.1890/14-2209.1)

49. Zarco-Perello, S. & Wernberg, T. 2019 Overwintering tropical herbivores accelerate detritus production on temperate reefs. *Dryad*. https://doi.org/10.5061/dryad.tx95x69sg

50. Brooks, M., E., Kristensen, K., Benthem, K., J.,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M. & Bolker, B., M. 2017 glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J.* **9**, 378. (doi:10.32614/RJ-2017-066)

51. Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. 2019 *nlme: Linear and nonlinear mixed effects models*. R Core Team.

52. Geraci, M. 2014 Linear quantile mixed models: thelqmm package for laplace quantile regression. *J Stat Softw* **57**, 1–29. (doi:10.18637/jss.v057.i13)

53. Cade, B. S. & Noon, B. R. 2003 A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* **1**, 412–420. (doi:10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2)

54. Lüdecke, D., Bartel, A. & Schwemmer, C. 2019 *sjPlot: Data Visualization for Statistics in Social Science*. R Project.

55. Fujita, D. 2010 Current status and problems of isoyake in Japan. *Bull. Fish. Res. Agen* , 33–42.

56. Nakamura, Y., Feary, D. A., Kanda, M. & Yamaoka, K. 2013 Tropical fishes dominate temperate reef fish communities within western Japan. *PLoS ONE* **8**, e81107. (doi:10.1371/journal.pone.0081107)

57. Vergés, A. et al. 2016 Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc Natl Acad Sci U S A* **113**, 13791–13796. (doi:10.1073/pnas.1610725113)

58. Pearce, A. F. & Feng, M. 2013 The rise and fall of the "marine heat wave" off Western Australia during the summer of 2010/2011. *Journal of Marine Systems* **111-112**, 139–156. (doi:10.1016/j.jmarsys.2012.10.009)

59. Lenanton, R. C. J., Dowling, C. E., Smith, K. A., Fairclough, D. V. & Jackson, G. 2017 Potential influence of a marine heatwave on range extensions of tropical fishes in the eastern Indian

Ocean—Invaluable contributions from amateur observers. *Regional Studies in Marine Science* **13**, 19–31. (doi:10.1016/j.rsma.2017.03.005)

60. Tose, K., Hirata, T., Kotera, Y., Kanda, M. & Nakamura, Y. 2017 Occurrence and reproduction of tropical fishes in ocean warming hotspots of Japanese temperate reefs. *Environ. Biol. Fishes* **100**, 617–630. (doi:10.1007/s10641-017-0590-5)

61. Azzurro, E., Carnevali, O., Bariche, M. & Andaloro, F. 2007 Reproductive features of the non-native Siganus luridus (Teleostei, Siganidae) during early colonization at Linosa Island (Sicily Strait, Mediterranean Sea). *J. Appl. Ichthyol.* **23**, 640–645. (doi:10.1111/j.1439-0426.2007.00864.x)

62. Beck, H. J., Feary, D. A., Nakamura, Y. & Booth, D. J. 2017 Temperate macroalgae impacts tropical fish recruitment at forefronts of range expansion. *Coral Reefs* **36**, 639–651. (doi:10.1007/s00338-017-1553-1)

63. Booth, D. J., Beretta, G. A., Brown, L. & Figueira, W. F. 2018 Predicting Success of Range-Expanding Coral Reef Fish in Temperate Habitats Using Temperature-Abundance Relationships. *Front. Mar. Sci.* **5**. (doi:10.3389/fmars.2018.00031)

64. Hsu, T.-H. & Gwo, J.-C. 2017 Fine-scale genetic structure of rabbitfish, Siganus fuscescens, in Penghu Archipelago following a mass mortality event caused by extreme cold winter weather. *Genes Genomics* **39**, 645–652. (doi:10.1007/s13258-017-0530-y)

65. Basford, A. J., Feary, D. A., Truong, G., Steinberg, P. D., Marzinelli, E. M. & Vergés, A. 2016 Feeding habits of range-shifting herbivores: tropical surgeonfishes in a temperate environment. *Mar. Freshwater Res.* **67**, 75. (doi:10.1071/MF14208)

66. Booth, D. J., Figueira, W. F., Gregson, M. A., Brown, L. & Beretta, G. 2007 Occurrence of tropical fishes in temperate southeastern Australia: Role of the East Australian Current. *Estuarine, Coastal and Shelf Science* **72**, 102–114. (doi:10.1016/j.ecss.2006.10.003)

67. Figueira, W. & Booth, D. 2010 Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Glob Chang Biol* **16**, 506–516. (doi:10.1111/j.1365-2486.2009.01934.x)

68. Moran, D. & Clements, K. D. 2002 Diet and endogenous carbohydrases in the temperate marine herbivorous fish Kyphosus sydneyanus. *J Fish Biol* **60**, 1190–1203. (doi:10.1111/j.1095-8649.2002.tb01714.x)

69. Choat, J. H. & Clements, K. D. 1993 Daily feeding rates in herbivorous labroid fishes. *Mar. Biol.* **117**, 205–211. (doi:10.1007/BF00345664)

70. Kuo, F.-W., Kuo, C.-Y., Fan, T.-Y., Liu, M.-C. & Chen, C. A. 2015 Hidden ecosystem function of rabbitfishes? Siganus fuscescens feeds on the soft coral, Sarcophyton sp. *Coral Reefs* **34**, 57–57. (doi:10.1007/s00338-014-1250-2)

71. Bos, A. R., Cruz-Rivera, E. & Sanad, A. M. 2017 Herbivorous fishes Siganus rivulatus (Siganidae) and Zebrasoma desjardinii (Acanthuridae) feed on Ctenophora and Scyphozoa in the Red Sea. *Mar. Biodiv.* **47**, 243–246. (doi:10.1007/s12526-016-0454-9)

72. Fox, R. J. & Bellwood, D. R. 2008 Remote video bioassays reveal the potential feeding impact of the rabbitfish Siganus canaliculatus (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs* **27**, 605–615. (doi:10.1007/s00338-008-0359-6)

73. Littler, M. M., Taylor, P. R. & Littler, D. S. 1983 Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* **2**, 111–118. (doi:10.1007/BF02395281)

74. Bellwood, D. R., Streit, R. P., Brandl, S. J. & Tebbett, S. B. 2018 The meaning of the term "function" in ecology: a coral reef perspective. *Funct Ecol* (doi:10.1111/1365-2435.13265)

75. Hyndes, G. A., Nagelkerken, I., McLeod, R. J., Connolly, R. M., Lavery, P. S. & Vanderklift, M. A. 2014 Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biol Rev Camb Philos Soc* **89**, 232–254. (doi:10.1111/brv.12055)

76. Hope, P. et al. 2015 Southern and South-Western Flatlands Cluster Report.

77. Rothans, T. C. & Miller, A. C. 1991 A link between biologically imported particulate organic nutrients and the detritus food web in reef communities. *Mar. Biol.* **110**, 145–150. (doi:10.1007/BF01313101)

78. Robertson, D. R. 1982 Fish feces as fish food on a pacific coral reef. *Mar. Ecol. Prog. Ser.* **7**, 253–265. (doi:10.3354/meps007253)

3.7. Supplementary Information

Herbivory rates

Table S1. Number of bites, bite rates and standardized consumption rates by bite size of tropical (*Siganus fuscescens* and temperate herbivorous fish (*Kyphosus sydneyanus and Olisthops cyanomelas*) on different herbivory categories.

		Total herbivory	Browsing herbivory	Kelp herbivory	Drifting herbivory
Siganus fuscescens	Summer	18092 bites 426 bites hr^{-1} 244 ± 65 cm^2 hr^{-1}	16150 bites 389 ± 107 bites hr^{-1} 223 ± 64 cm^2 hr^{-1}	13020 bites 314 ± 102 bites hr^{-1} 182 ± 62 cm^2 hr^{-1}	1942 bites 37.5 ± 12 bites hr^{-1} 21.4 ± 7 cm^2 hr^{-1}
	Winter	979 bites 15.3 bites hr^{-1} 7.4 ± 7.4 cm^2 hr^{-1}	777 bites 12 ± 12 bites hr^{-1} 6 ± 5.9 cm^2 hr^{-1}	757 bites 12 ± 12 bites hr^{-1} 5.7 ± 5.6 cm^2 hr^{-1}	202 bites 3.1 ± 3.1 bites hr^{-1} 1.5 ± 1.5 cm^2 hr^{-1}
Kyphosus Sydneyanus	Summer	715 bites 21.2 bites hr^{-1} 45.6 ± 22 cm^2 hr^{-1}	628 19.7 ± 10.4 bites hr^{-1} 42 ± 22 cm^2 hr^{-1}	616 bites 19.4 ± 10 bites hr^{-1} 41 ± 23.5 cm^2 hr^{-1}	87 bites 1.4 ± 0.8 bites hr^{-1} 3.4 ± 2 cm^2 hr^{-1}
	Winter	69 bites 1.1 bites hr^{-1} 1.7 ± 1.6 cm^2 hr^{-1}	69 1 ± 1 bites hr^{-1} 1.7 ± 1.6 cm^2 hr^{-1}	69 1 ± 1 bites hr^{-1} 1.7 ± 1.6 cm^2 hr^{-1}	0
Olisthops cyanomelas	Summer	83 bites 1.6 bites hr^{-1}	83 bites 1.6 bites hr^{-1}	35 bites 0.75 bites hr^{-1}	0
	Winter	0	0	0	0

Herbivorous fish body and bite sizes

On average rabbitfish were 60% smaller than temperate silver drummer. Rabbitfish average fork length was 28.5 ± 1.5 cm, with a minimum observed size of 20.5 cm and a maximum of 38.5 cm, while silver drummer average length was 43.2 ± 9.1 cm, with a minimum size of 18 cm and a maximum of 72.5 cm. Bite size of both species followed a power relationship with weight but silver drummers had larger bite area than rabbitfish by 3 times within their comparable weight range (*i.e.* 200-400 g) and 6 times larger at bigger sizes (~7300 g) (Fig. S1).
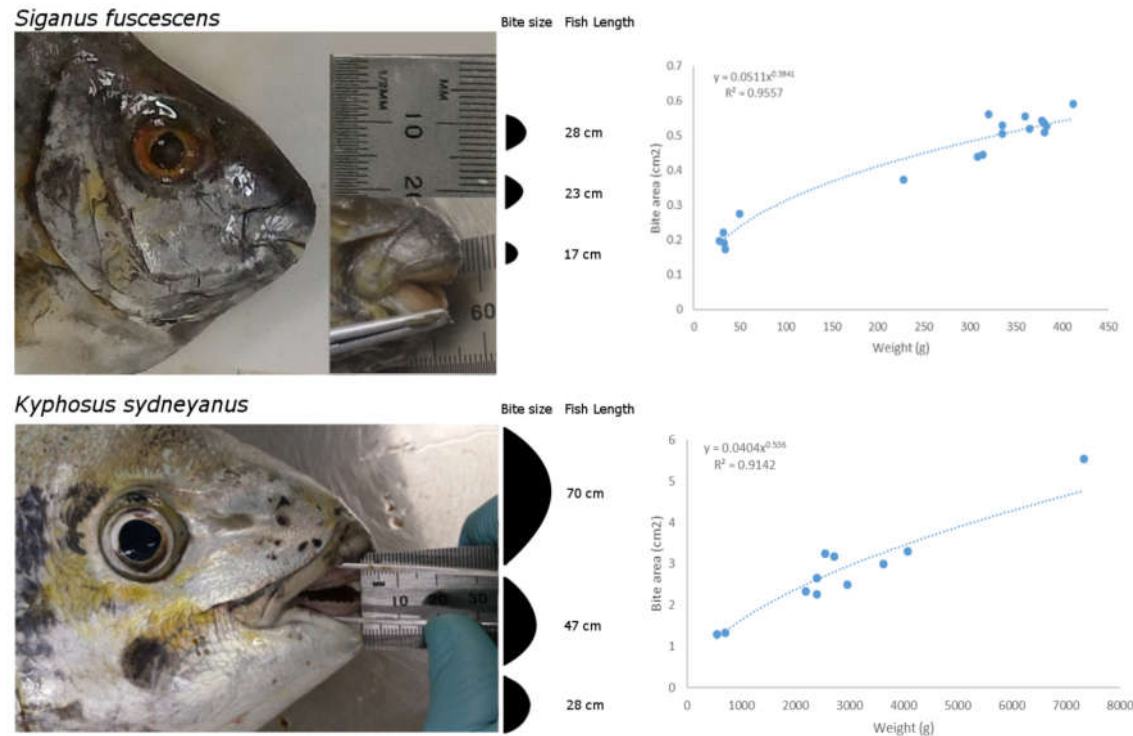
Figure S1. Dentition photographs, bite size per fish length diagrams and bite area per fish weight relationships of the tropical *Siganus fuscescens* and the temperate herbivore *Kyphosus sydneyanus*.

Recruitment of rabbitfish in temperate western Australia

Figure S2. School of juvenile *Siganus fuscescens* in a temperate reef of Western Australia during summer of 2016.

Chapter 4. Range-extending tropical herbivores increase diversity, intensity, and extent of herbivory functions in temperate marine ecosystems.

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4.1. Abstract

Climate change is modifying species distributions around the world, forcing some species poleward, where they can alter trophic interactions. Many tropical herbivorous fishes have successfully expanded their ranges into temperate ecosystems, and while it is clear they drive increases in herbivory rates in specific localities, little is known about how they might affect the diversity of herbivory functions across large spatial scales, considering their interaction with assemblages of native herbivores in temperate habitats. We assessed the spatial overlap and habitat associations of native temperate and range-expanding tropical herbivorous fishes in six sub-regions of south-western Australia to determine how incursions of tropical species may have affected the diversity, redundancy (index of uniqueness) and the 'spatial extent' (addition of functions in new areas) and 'intensity' (increasing density of functional groups) of specific herbivory functions in recipient ecosystems. Tropical herbivores had high abundances in temperate ecosystems, forming schools from 40 (parrotfish) to 200 (rabbitfish) individuals strongly associated with seagrass meadows and reefs with high cover of turf algae. Overlap with temperate herbivores was highest in the northern sub-regions, forming unique assemblages, with no apparent species displacements. The addition of tropical species increased functional diversity and uniqueness (the complement of redundancy), introducing novel herbivory functions to many locations. Seagrass browsing increased in spatial extent (27%) and intensity (15 x), while seaweed browsing and grazing increased in intensity by up to 2.5 x in regions with high abundances of tropical herbivores. Our results suggest that the diversity, intensity and spatial extent of different herbivory functions can change as tropical species with different habitat affinities, behaviors and diets shift their distributions poleward. Changes in functional redundancy are likely to be heterogeneous in space and might not increase initially because the diversity of herbivory functions is relatively low in some temperate marine ecosystems. However, there is the potential for greater redundancy as further tropical species arrive, their abundances increase and the spatial and functional overlap of communities rises.

4.2. Introduction

Evidence is mounting about the impact of climate change on the distribution of marine and terrestrial species (Pecl *et al.* 2017). While species' ranges are expanding, contracting or shifting locally, overall there is a global trend for species' addition at higher latitudes (Blowes *et al.* 2019). This trend has seen an increase in the proportion of species of tropical affinity in temperate ecosystems, a process often referred to as 'tropicalization' (Wernberg *et al.* 2012; García Molinos *et al.* 2015). Tropicalization has

been particularly strong in marine ecosystems (Vergés *et al.* 2014), where climate-change velocities and species range-shifts are advancing at higher rates than in terrestrial environments (Sorte, Williams & Carlton 2010; Burrows *et al.* 2011). Range expansion of tropical species into temperate regions alters the species composition of recipient ecosystems, potentially changing the diversity and intensity of ecological functions, in ways that depend on the outcomes of novel species interactions and the overall balance between species extirpations and additions in the ecosystem (Albouy *et al.* 2014; Ockendon *et al.* 2014).

As novel species assemblages emerge, ecological processes can be modified by ecological engineers (Blois *et al.* 2013). Temperate seagrass meadows and kelp forests are forecast to change as the ocean warms, because top-down forces are expected to intensify with the addition of tropical herbivores (Hoekman 2010; Hyndes *et al.* 2016). Herbivory is a key ecological function which regulates the bottom-up energy flow between trophic levels and the top-down control on habitat structure by reducing seagrass and seaweed canopy cover and mediating competition for space between sessile taxa (Poore *et al.* 2012; Nowicki, Fourqurean & Heithaus 2018). Consequently, the strengthening of herbivory by range-extending tropical herbivores could shift temperate habitats primarily regulated by production towards states regulated by consumption (Vergés *et al.* 2014), thereby accelerating the integration of biomass from habitat-forming macrophytes into the food chain (Zarco-Perello *et al.* 2019) and increasing the cover of turf seaweed and sessile invertebrates (Filbee-Dexter & Wernberg 2018; Ling, Barrett & Edgar 2018).

The effect of range-expanding tropical herbivores will likely depend on the magnitude of functional overlap with existing temperate herbivore assemblages. Novel species associations can result in competition, causing replacements of species and ecological functions (Milazzo *et al.* 2013), or creating new assemblages that augment certain ecological processes (Marshak & Heck 2017). Herbivorous fishes, particularly species from the family Siganidae, have been some of the most successful at expanding their distributions poleward (Vergés *et al.* 2014). Current evidence suggests that where they have expanded, there has not been a displacement of temperate species but rather additions of new populations (Vergés *et al.* 2014; Bennett *et al.* 2015; Zarco-Perello *et al.* 2017, 2019).

Herbivory is carried out by species with different feeding behaviors that are generally classified into two broad functional groups: 'grazers', which bite on reef substrata and regulate recruitment rates of sessile taxa by consuming turf seaweed, sediment and particulate organic matter; and 'browsers', which bite at canopy-forming macrophytes, engineering the three-dimensional habitat structure of the ecosystem (Bellwood *et al.* 2019). Consequently, increases in the number of herbivorous species could intensify herbivory by adding to the number and richness of functional groups present.

However, considering that species have specific habitat associations, diet preferences, consumption rates and population sizes (Ruttenberg *et al.* 2019), high spatial variation in functional changes and in the degrees of ecological impacts on primary producers can be expected as novel guilds of herbivores are formed.

Knowledge of the habitat associations of range-shifting species is needed in order to evaluate their interactions, identify which habitats are more likely to be affected and which ones are likely to facilitate further range expansions of tropical species. However, this has rarely been considered in range-shift predictions (Parravicini *et al.* 2015) and currently we lack an understanding of how range-shifting tropical species can affect herbivory functions in different habitats across large spatial scales (Bonebrake *et al.* 2018). The spatial overlap of temperate and range-expanding tropical herbivores will determine changes in functional diversity and redundancy of herbivory; however, since many species have functional plasticity (*i.e.* they can graze or browse on different macrophytes) (Bennett *et al.* 2015; Zarco-Perello *et al.* 2019; Ebrahim *et al.* 2020), the execution of each function also depends on the spatial overlap between consumers and food resources. The concept of spatial overlap within ecological communities has been applied to estimate trophic interactions between species of predators and their prey (*e.g.* Carroll *et al.* 2019), but has not been applied to functional analyses of herbivory. Here, we use this approach to assess novel species interactions between potential competitors (tropical and temperate herbivores) and their associated effects on herbivory in temperate marine habitats experiencing tropicalization (Wernberg *et al.* 2016). For this, we evaluated (i) the habitat associations and spatial overlap of temperate and range-expanding tropical herbivores, (ii) the relative effect of tropical herbivores on functional diversity and (iii) changes in the spatial extent (addition of functions in new areas), and intensity (increasing density of functional groups) of specific herbivory functions.

4.3. Materials and Methods

Study Location

The composition of fish assemblages in coastal habitats of western Australia has changed following a marine heatwave that struck the region in 2011 (Wernberg *et al.* 2016). Tropical rabbitfish (*Siganus fuscescens*) have since formed self-recruiting populations in temperate ecosystems (Lenanton *et al.* 2017; Zarco-Perello *et al.* 2019) while parrotfish (*Scarus ghobban* and S. *schlegeli*) became more abundant (Parker *et al.* 2019). To identify the effects of these changes, surveys of herbivorous fish were conducted over inshore habitats along the coastline of south-western Australia during summer (April-May) of 2018 and 2019, from the Perth metropolitan area to Cape Naturaliste in the south of

the state. The ecosystems along the coast consist of carbonate reefs interspersed with boulder reefs, seagrass meadows and sandy plains. Survey locations were restricted to shallow habitats (depth 1-9 m; up to 6 km from the shoreline), where the abundance of herbivorous fish is highest (Hoey, Brandl & Bellwood 2013).

Herbivorous Fish Abundance and Habitat Associations

The abundances of temperate (*Girella zebra*, *Olisthops cyanomelas*, *Pelates octolineatus*, *Kyphosus cornelii* and *Kyphosus sydneyanus*) and tropical herbivorous fish (*Scarus* spp. and *Siganus fuscescens*) were measured via a GPS-tracked roving underwater visual census with 15 minutes per sampling location. This method is effective to estimate the abundance of schooling herbivorous fish and has proven to be efficient for range-shifting species (Fox & Bellwood 2008; Beck *et al.* 2014). One roving survey was performed per site, where one surveyor swam at a constant pace, registering all individuals of the species of interest in an approximate area of 2000 m^2. A second surveyor followed the same path recording the seascape with an underwater camera for subsequent assessment of habitat features. Videos were analyzed with the program TransectMeasure (SeaGIS), each video transect was paused at one minute intervals (n=15 per transect) to extract information on topographic complexity (Wilson, Graham & Polunin 2007), substrate type, species composition, species diversity, and abundance of morpho-functional groups of sessile biota based on the CATAMI classification scheme (Althaus *et al.* 2015). A total of 69 sites were surveyed across six sub-regions: North Perth (31.8°S, n=13), Rottnest Island (32°S, n=18), South Perth (32.2°S, n=13), Rockingham (32.4°S, n=11), Bunbury (33.3°S, n=5) and Geographe Bay (33.6°S, n=9). The relationship between the herbivorous fish assemblage and selected measurements of habitat was assessed using a Canonical Correspondence Analysis (CCA) (Borcard, Gillet & Legendre 2011) with the R package Vegan (Oksanen *et al.* 2019).

Fish abundance was standardized to density (individuals 125 m^{-2}); however, we also considered a new metric: MaxS (maximum number of fish per school in each survey), a similar approach to abundance assessments of pelagic schooling fish (*i.e.* school size; Beare 2002) and abundance estimates from static video methods (*i.e.* MaxN; Cappo *et al.* 2003). In addition to abundance information, MaxS can be a proxy for reproductive behaviour (Azzurro *et al.* 2017) and ecological impact, since certain species have positive correlations between school size and *per capita* consumption rates (Michael *et al.* 2013; Basford *et al.* 2016). For simplicity, we report the highest MaxS and the average MaxS (MaxSm) per subregion in the text. Changes in abundance of temperate and tropical herbivorous fish across latitude were evaluated in separate models with negative binomial generalized linear models using the R package glmmTMB (Brooks *et al.* 2017).

Herbivorous Fish Spatial Overlap

The potential strength of ecological interactions between tropical and temperate herbivorous fish species was estimated by calculating their spatial overlap with the 'local index of colocation' (Pianka's *O*, Pianka 1973; Carroll *et al.* 2019). This metric assesses the correlation between the proportions of the densities of two groups across sites, and can be considered a proxy for their encounter rate (Pianka 1973; Carroll *et al.* 2019). For this analysis we pooled the densities of all tropical herbivorous species and all temperate herbivorous species and calculated the overlap between the two groups within each sub-region. A resampling jackknife method was applied to estimate mean and standard errors of overlap within each sub-region, where we repeatedly recalculated Pianka's *O*, each time excluding a different site from the calculations (Manly *et al.* 2007).

Diversity and Spatial Overlap of Herbivory Functions

We classified herbivory functions based on the tendency of species to feed on different groups of macrophytes that affect different ecological processes: (i) grazing of turf (impacting sessile taxa recruitment), (ii) browsing on seaweed canopy (impacting habitat structure) and (iii) browsing of seagrass canopy (impacting nursery grounds). Because each herbivorous species contributes differently to each function (Hoey & Bellwood 2009), we assigned them a species-specific weight based on herbivory rates and stomach content analyses reported in the scientific literature, as well as observations during our surveys in the region (Table S1 in Supplementary Material). Changes in overall herbivory functions in each temperate subregion were assessed by calculating functional diversity (FD) based on attribute diversity (t = d_{mean} and *q* = 1; (Chao *et al.* 2019) and functional uniqueness (U, the complement of redundancy), employing the function *uniqueness* with Euclidean distance (Table S2 in Supplementary Material) using the software R (R Core Team 2019): U = Q / D, where U is uniqueness, Q is Rao quadratic entropy (an index of functional diversity) and D is the Simpson index of biological diversity (Ricotta *et al.* 2016). The creators of the U index exemplify its application to analyze the vulnerability of ecosystems to population declines or species extinction due to disturbances, here we apply it to analyze the impact of species additions due to range shifts.

To assess changes in specific herbivory functions, we performed spatial overlap analyses to calculate addition of functions in new areas (*i.e.* increase in spatial extent) and increase in intensity of existing functions across space (*i.e.* increase in density). Functional weights were not scaled for these calculations and only adult individuals were included in these analyses, since herbivory rates of juveniles of most species are uncertain.

Herbivory intensity was calculated with a modified version of community weighted mean of trait values (Laliberté & Legendre 2010) that incorporates spatial overlap. We refer to this as the overlapped community weighted mean of trait values (oCWM), where we accounted for the execution

of specific herbivory functions only when there was overlap between each functional group of herbivores (*e.g.* seagrass browsers) and the group of macrophytes they consume (*e.g.* seagrass), similar to analyses of predator-prey interactions (Fig. 1a; Pianka 1973; Carroll *et al.* 2019). For each herbivory function we defined the spatial range of its corresponding macrophyte type (seagrass, turf and canopy seaweed) based on whether it occurred at each survey site across the region. Within the range where the macrophyte was present, the densities of each temperate and tropical herbivorous species were multiplied by their weight value for that function. For instance, species with a weight value of 0 for seagrass browsing did not contribute to that function despite them being very abundant, whereas species with values > 0 contributed only where the populations overlapped with seagrass meadows. The effect of tropical herbivores for each herbivory function in each sub-region was then determined as the increase in oCWM including tropical species (mixed ensemble), relative to the oCWM of temperate species alone (Fig. 1). Statistical significance of observed variations between temperate and mixed ensembles in all functional indices within each sub-region were tested with Permutational Multivariate Analysis of Variance (PERMANOVA) using the function *adonis* of the R package vegan (Oksanen *et al.* 2019). Herbivory extent was calculated as the 'range overlap' between each macrophytes and its consumers (Carroll *et al.* 2019). For this, we took the spatial range for each macrophyte and then determined their overlap with their corresponding herbivory function considering the presence of only a) temperate consumers, b) tropical consumers and c) either temperate or tropical consumers. The difference between temperate consumer overlap and the overlap between either temperate or tropical consumers represented the increase in herbivory extent attributable to the addition of tropical herbivores (Fig. 1).
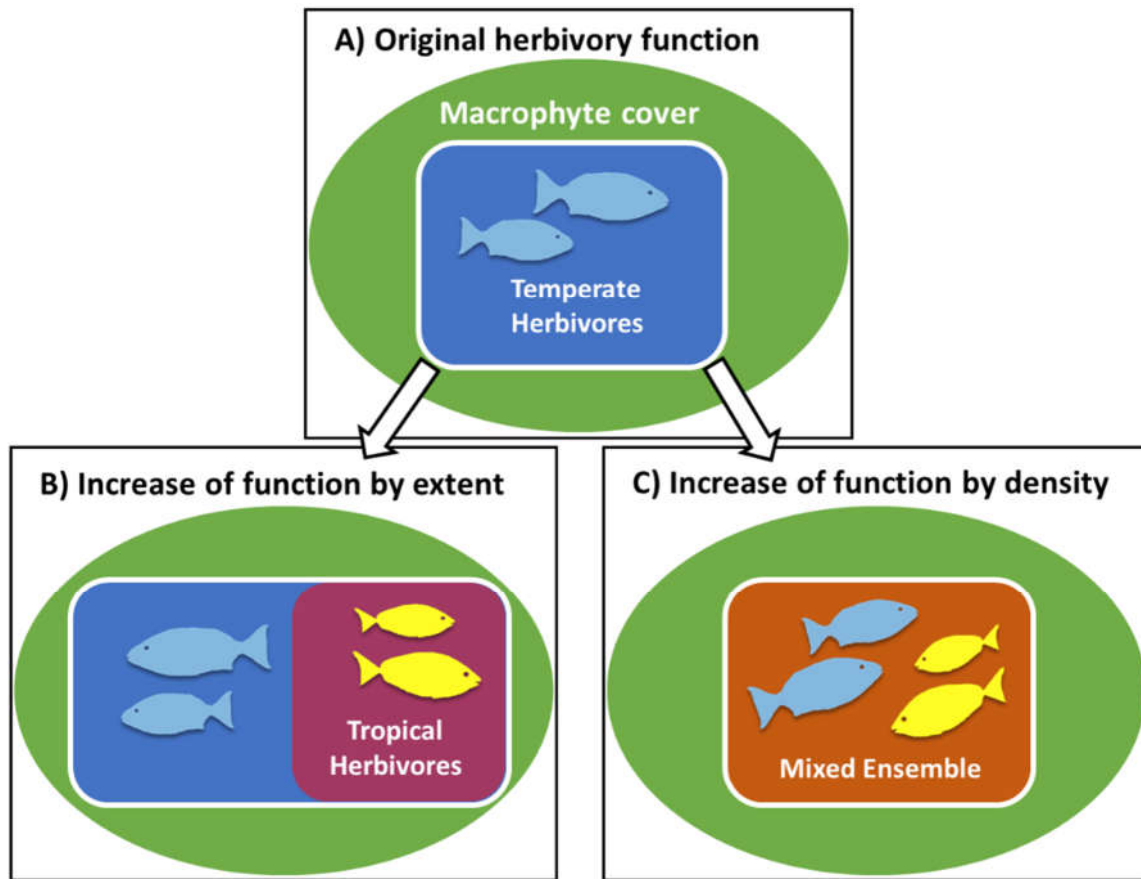
Figure 1. Conceptual diagram of the overlap analyses used to assess changes in herbivory functions in temperate ecosystems due to the overlap of tropical and temperate herbivores and the macrophytes they consume (A). Changes in *spatial extent*: changes in area overlap between herbivory functions and corresponding macrophytes by the arrival of tropical species (B), and *intensity (density)*: calculated as overlapped weighted mean of traits of functional groups of temperate and tropical herbivores (mixed ensemble) within spatial ranges of corresponding macrophytes (C).

4.4. Results

Spatial overlap of temperate and tropical herbivores

Abundance of tropical herbivores declined as latitude increased (GLM, $p < 0.01$), as did the abundance of temperate herbivores (GLM, $p = 0.035$). Temperate herbivores were more abundant than tropical herbivores in all subregions (Fig. 2a). Tropical rabbitfish were frequently seen at North Perth (MaxSm: 60 ± 19 (mean individuals school^{-1}), MaxS: 207 (maximum school size)) and around Rottnest Island (MaxSm: 24 ± 9.5; MaxS: 158). In South Perth rabbitfish were recorded less frequently (MaxSm: 10 ± 8; MaxS: 100) but here we registered the only school of juveniles (MaxS: 100). No rabbitfish were

recorded at Rockingham or Bunbury, but they were observed at Geographe Bay (MaxSm: 10.4 ± 7.9; MaxS: 100). Parrotfish populations were only recorded at Rottnest Island, where they were generally abundant (MaxSm: 6 ± 2.3; MaxS: 39). Temperate herbivores were recorded at all study sites but with varying abundances. *Kyphosus sydneyanus* was observed across the entire latitudinal gradient and was most abundant at North Perth (MaxSm: 35.4 ± 8; MaxS: 96), Rottnest Island (MaxSm: 45.1 ± 23.5; MaxS: 404) and Rockingham (MaxSm: 38.5 ± 13.9; MaxS: 141). *Kyphosus cornelii* had similar patterns, having high abundances at North Perth (MaxSm: 39.5 ± 11.5; MaxS: 130), Rottnest Island (MaxSm: 99.5 ± 15.0; MaxS: 290) and Rockingham (MaxSm: 38 ± 18; MaxS: 162). *Pelates octolineatus* was most abundant at South Perth (MaxSm: 48.4 ± 27.5; MaxS: 360), Rockingham (MaxS mean: 102.9 ± 46.5; MaxS: 465), and Geographe Bay (MaxSm: 24.1 ± 10.2; MaxS: 95). *Girella zebra* was abundant at Rottnest Island (MaxSm: 15.3 ± 9.3; MaxS: 153) and Geographe Bay (MaxSm: 2.2 ± 1.1; MaxS: 10). *Olisthops cyanomelas* was recorded in all the regions; however, as the only non-schooling herbivorous species in the study it generally had the lowest abundances, except for Geographe Bay (Fig. 2b). Spatial overlap between temperate and tropical herbivores was highest in the most northerly sub-regions (Pianka's *O* at North Perth = 0.46 ± 0.01, Rottnest Island = 0.38 ± 0.01 and South Perth = 0.73 ± 0.06), with overlap decreasing towards the south (Pianka's *O* at Rockingham = 0, Bunbury = 0, Geographe Bay = 0.28 ± 0.01) (Fig. 2c).
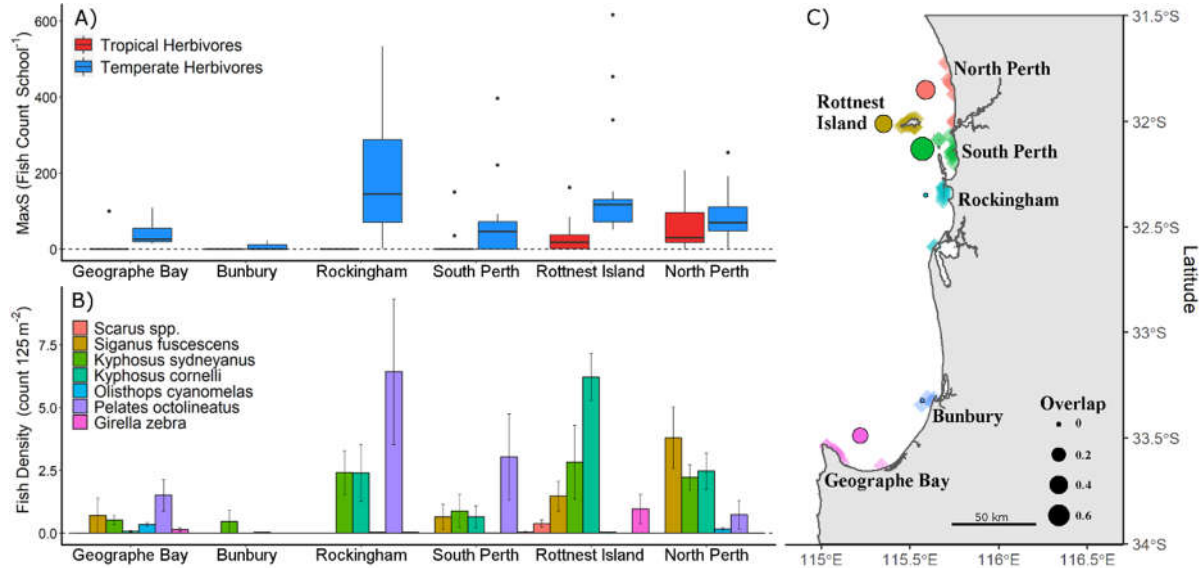

Figure 2. Abundance patterns as MaxS (school size) (A) and density (B) of herbivorous fish of tropical (*Scarus* spp. and *S. fuscescens*) and temperate climate affinity (*Kyphosus* spp., *O. cyanomelas*, *P. octolineatus* and *G. zebra*) and (c) their spatial overlap (Pianka's O) along the temperate sub-regions of Western Australia. Colored diamonds in map represent surveyed sites.

Habitat Associations

Canonical Correspondence Analysis of the herbivorous fish community and habitat variables accounted for 82% of the total constrained inertia in the first two axes. The first axis represented a gradient from high latitude habitats dominated by canopy-forming and coarse-branching seaweed species (*e.g. Ecklonia radiata* and *Sargassum* spp.) to lower latitude sites with higher cover of turf (small-mixed seaweed); while the second axis represented a gradient of topographic complexity, from seagrass meadows to consolidated reef substrates covered by seaweeds (Figure 3). Along these gradients, the species scores aggregated in three main groups of herbivores; (1) *P. octolineatus* and *O. cyanomelas* were more strongly associated with habitats having higher cover of large brown seaweed at higher latitudes. However, *P. octolineatus* associated more with seagrass, whereas *O. cyanomelas* associated more with reefs. (2) *K. cornelii* and *K. sydneyanus* were associated more with reef sites with medium canopy-cover, while (3) *G. zebra*, *Scarus spp*. and the rabbitfish *S. fuscescens* were associated more with sites with seagrass meadows and reefs with higher cover of turf seaweed. Nonetheless, schools of parrotfish and especially rabbitfish, were also found at sites with high canopy cover, over reefs associated with low seagrass density and habitats with low and high topographic complexity, co-occurring with all temperate species in several sites (Figure 3).
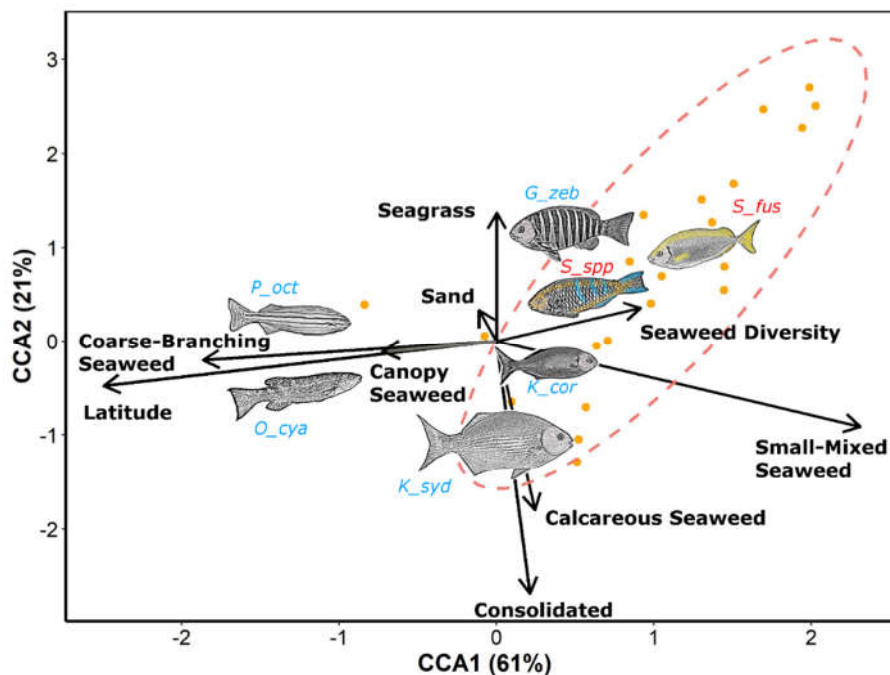

Figure 3. Canonical correspondence analysis of herbivorous fish species and habitat variables (arrows) of temperate ecosystems in southwestern Australia. Ellipse encloses sites (dots) where rabbitfish (*S_fus*) were recorded. *P_oct = Pelates octolineatus*; *O_cya = Olisthops cyanomelas*; *K_syd = Kyphosus sydneyanus*; *K_cor = Kyphosus cornelii*; *G_Zeb = Girella zebra*; *S_spp = Scarus* spp. and *S_fus = Siganus fuscescens*.

Functional diversity

The addition of tropical species increased average functional diversity (FD) and functional uniqueness whenever they established abundant populations (Fig. 4). Considering only temperate herbivores, we found that Geographe Bay (1.68 ± 0.09) and North Perth (1.73 ± 0.14), the subregions at the highest and lowest latitudes respectively, had the highest FD; however, the addition of tropical species shifted the highest values towards lower latitudes, with high increases in North Perth (33% higher; 2.3 ± 0.2; PERMANOVA p=0.037) and Rottnest Island (25% higher; 1.75 ± 0.11; PERMANOVA p=0.017) with smaller or no increases in other regions with fewer or no tropical herbivores (South Perth = 1.3%, Rockingham = 0%, Bunbury = 0%, Geographe Bay = 2.5%; Fig. 4a). Average functional uniqueness values were very similar in four out of six subregions considering only temperate communities, but as with FD, the inclusion of tropical species shifted the highest values towards northern latitudes, with North Perth being the highest (109% higher; PERMANOVA p<0.001), followed by Rottnest Island (47% higher; PERMANOVA p<0.02; Fig. 4b).
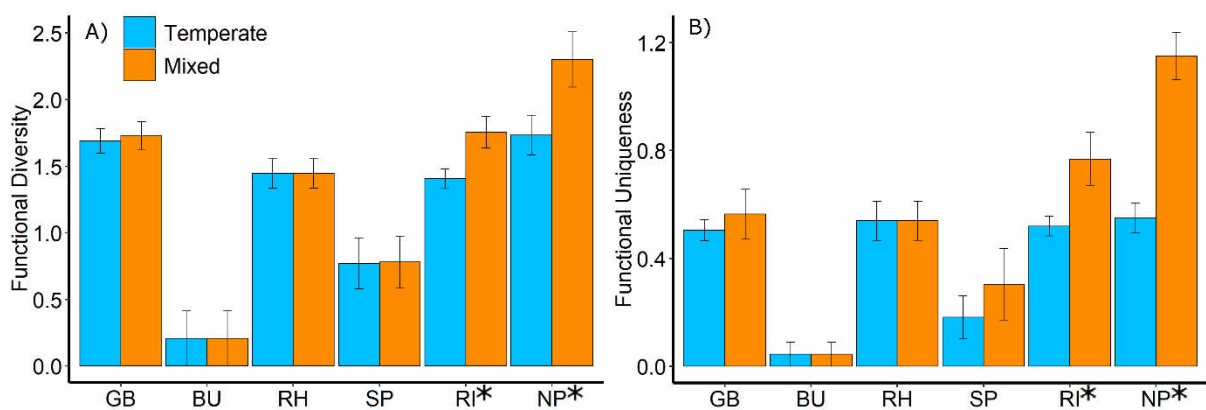
Figure 4. Variation (mean ± SE) of functional diversity (A) and functional uniqueness (B) considering communities of temperate herbivorous fish only, and with the addition of populations of tropical species (mixed) in south western Australia (GB: Geographe Bay, BU: Bunbury: RH: Rockingham, SP: South Perth, RI: Rottnest Island, NP: North Perth). Asterisks on bar charts mark statistically significant differences between temperate and mixed herbivorous communities (PERMANOVA p<0.05).

Herbivory functions

The addition of tropical herbivores contributed to a 27% increase in spatial extent of potential seagrass browsing. Of the 157.5 km^2 that was surveyed during this study, 106 km^2 represented sites where seagrass was present; of this area, 55% overlapped with temperate seagrass consumers, 47% overlapped with tropical seagrass consumers, and 74% overlapped with either temperate or tropical seagrass consumers. Turf seaweeds were present across 147.5 km^2; of this area, 82% overlapped with

temperate grazers, 45% with tropical grazers, and 85% with either temperate or tropical grazers, thus representing an increase of 3% in spatial extent of potential seaweed grazing with the addition of tropical species. Canopy seaweeds were present across 129 km^2 of the survey area, 94% of this overlapped with temperate seaweed browsers, 48% with tropical seaweed browsers, and 96% with either temperate or tropical seaweed browsers, representing an increase of 2% in spatial extent of potential seaweed browsing due to tropical herbivores.
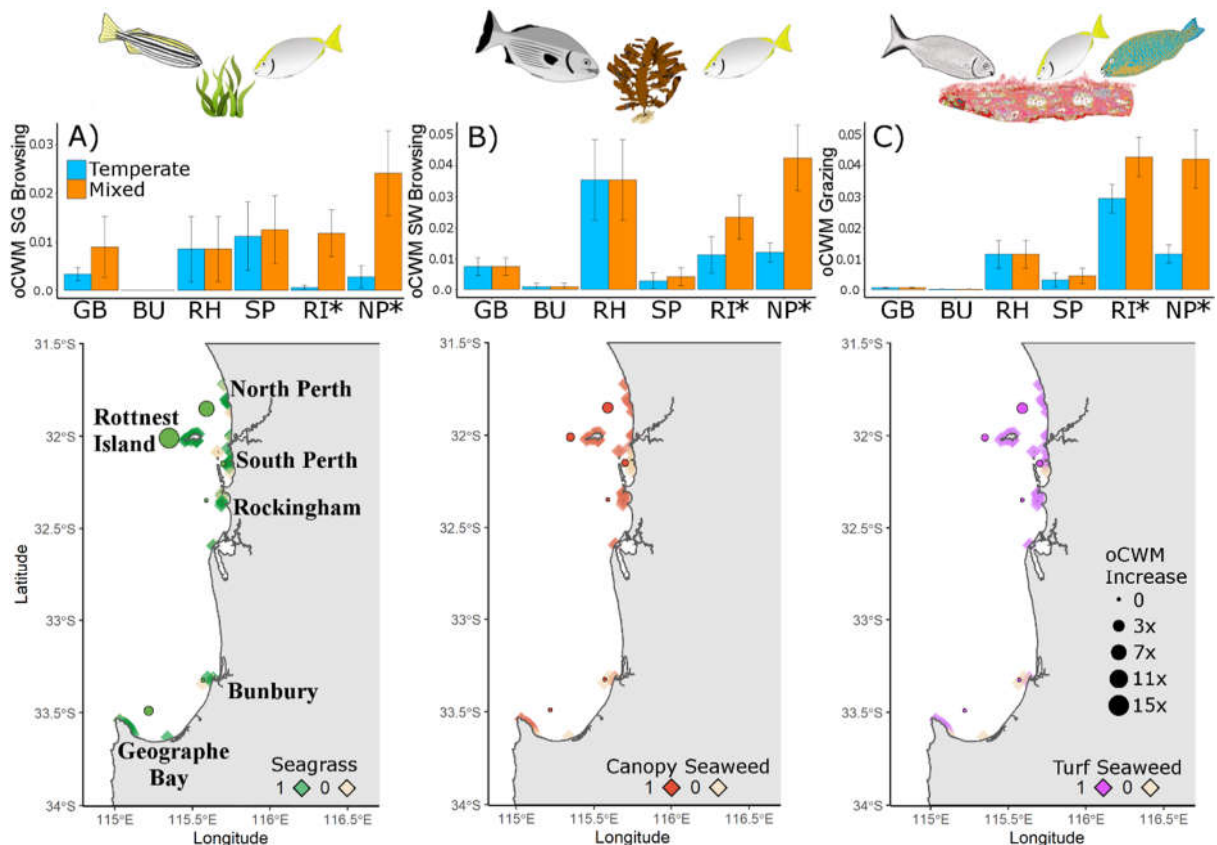
Figure 5. Variation in values (bars; mean ± SE) and relative increases (maps) of functional metrics considering communities of temperate herbivorous fish only, and with the addition of populations of tropical species (mixed). Overlapped Community Weighted Means of Traits for seagrass browsing (a), seaweed browsing (b) and seaweed grazing (c) across temperate western Australia (GB: Geographe Bay, BU: Bunbury: RH: Rockingham, SP: South Perth, RI: Rottnest Island, NP: North Perth). Asterisks on bar charts mark statistically significant differences between temperate and mixed herbivorous communities (PERMANOVA $p < 0.5$). The size of the bubbles in the maps represent proportional increase in herbivory functions with the addition of tropical species, colored diamonds represent presence/absence of macrophytes at sampling sites.

Overlapped Community Weighted Means of Traits (oCWM) for all herbivory functions increased in the northern sub-regions (Fig. 5; PERMANOVA $p<0.02$). In the absence of tropical species, seagrass and seaweed browsing oCWM were highest at mid-latitude sub-regions, while seaweed grazing was highest at Rottnest Island. However, when tropical herbivores were mixed in the communities, Rottnest Island and North Perth had significant increases for average seagrass browsing (15x and 9x respectively; PERMANOVA $p=0.02$), seaweed browsing (1x and 2.5x respectively; PERMANOVA $p=0.02$) and seaweed grazing (0.4x and 2.6x respectively; PERMANOVA $p<0.01$). Southern sub-regions had small or no changes in herbivory functions, except for Geographe Bay, which had an increase in seagrass browsing (1.6x), albeit not statistically significant (PERMANOVA $p=0.97$).

4.5. Discussion

Our study assessed the spatial interactions between tropical and temperate herbivores and evaluated their effects on herbivory functions within temperate marine habitats along a latitudinal gradient. The range expansion and increase in abundance of tropical herbivores into higher latitudes did not appear to modify the abundance of temperate herbivores or cause species replacements. The northern sub-regions had the highest abundances and species diversity of temperate herbivores, but also had the highest abundances of tropical herbivores, as reflected in their high overlap values. This indicates that there is no negative relationship between temperate and tropical herbivores at the densities observed.

These results align well with the resource partitioning and empty niche theories proposed to explain the success of many invasive species (Lowry *et al.* 2012). This is particularly relevant for herbivorous species because temperate ecosystems generally have a surplus of macrophyte production and low competition (Mann 2000). For instance, the Mediterranean Sea has extensive and productive seagrass and seaweed habitats (Sales & Ballesteros 2012), yet hosts only two native herbivorous fish species (*Sarpa salpa* and *Sparisoma cretense*), which likely has eased the expansion of tropical herbivores in the region. *Scarus ghobban* remains uncommon in the Mediterranean Sea, but the occurrence of this species has extended from Israel to Greece (Erguden *et al.* 2018), while the rabbitfish *Siganus luridus* and *Siganus rivulatus* have become abundant in many locations, attaining MaxS of ~100 individuals at the edge of their expansion in Linoza, Italy (Azzurro *et al.* 2017). The region of our study has a higher diversity, with five dominant species, but still lags far behind herbivore assemblages in the tropics with 30 to 100 species (Steneck, Bellwood & Hay 2017).

Our results on habitat associations also indicate that the different behaviors and diet of each species can facilitate coexistence of competitors. Some species were associated with reefs with different cover of canopy-forming and turf seaweed, and some were also more strongly associated with seagrass. Thus, although tropical and temperate species inhabit the same location, their overlap decreases at finer spatial scales (Streit, Cumming & Bellwood 2019). Moreover, specific feeding behaviors can also increase niche dissimilarity among species; for instance, species that tend to feed on drifting macrophytes, such as *S. fuscescens*, reduce resource competition in the benthic space (Zarco-Perello *et al.* 2019). Hence, there seem to be ample niche spaces available in temperate ecosystems for range-shifting tropical herbivores to occupy, without directly competing against their temperate counterparts (Vergés *et al.* 2019).

The addition of tropical herbivorous fish to temperate ecosystems changed the spatial patterns of functional diversity, functional uniqueness, and the intensity of specific herbivory functions in our study. Changes in species richness caused by climate change have been forecast and described by multiple studies, with tropical regions expected to suffer losses in biodiversity, while temperate regions are likely to experience increases in species richness that could modify ecological processes (Blowes *et al.* 2019). Our results expanded on this from a functional perspective, showing that the expansion of tropical species to temperate ecosystems could initially lead to general increases in functional diversity (FD) at sites where they establish permanent and abundant populations. This can lead to increases in functional redundancy but also to the introduction of new herbivory functions. The low number of temperate species per herbivory function implies that some functions are not performed at many sites, and that the arrival of tropical species could fill these empty functional niches. This explains the increase in functional uniqueness (U) that we observed in sub-regions where tropical herbivores had established. However, increments were heterogeneous in space depending on how functionally redundant tropical ensembles were in relation to the temperate communities they overlapped with.

While increments in FD were similar between Rottnest Island and North Perth (24% and 33%), the increment in U was double in the latter (47% vs 109%). This shows that there was a higher redundancy of functions at Rottnest Island, and conversely that there were more sites in North Perth where rabbitfish brought new functions (Ricotta *et al.* 2016). Among these, seagrass browsing seemed to be the main driver of change, since it was the only function that increased significantly in spatial extent and up to 3x and 32x more in intensity than seaweed grazing and browsing in North Perth and Rottnest Island respectively. This is understandable since only the trumpeter *Pelates octolineatus* has been identified as an important temperate seagrass consumer (Bessey & Heithaus 2015), reflecting

historically low rates of herbivory in seagrass meadows of the region (White, Westera & Kendrick 2011).

Knowledge of the baseline abundance and functional role of herbivorous species in recipient ecosystems is crucial to accurately assess and forecast changes in functional processes under tropicalization. While tropical species drove increases in all functions, the total intensity was strongly determined by the native temperate assemblages. From a species diversity perspective, Rottnest Island is the most tropicalized sub-region of south-western Australia, being the only one hosting both rabbitfish and parrotfish. Nonetheless, from a functional perspective it had similar diversity to Geographe Bay, and substantially lower functional diversity than North Perth, owing to the more diverse temperate communities in those regions prior to the addition of tropical rabbitfish. Likewise, Rottnest Island experienced by far the highest increase in seagrass browsing intensity but maintained similar overall mean values to other sub-regions not hosting tropical species. Additionally, seaweed browsing and grazing increased the most in North Perth, but overall Rockingham had similar levels for the former and Rottnest Island for the latter, since both had strong temperate communities in these functions.

The fact that the average intensities of seaweed browsing were similar between some tropicalized and non-tropicalized areas indicates that consumption rates in the region have not yet reached levels that pose a significant risk of regime-change at extensive spatial scales. However, shifts could occur in the future as tropical herbivores further expand their distribution and abundance in temperate ecosystems. High densities of tropical herbivores at local spatial scales have been correlated with increases in herbivory, declines in biomass of kelp (Zarco-Perello *et al.* 2017) and the maintenance of canopy-free states and high turf cover following environmental disturbances, resulting in a positive feedback loop that favors the persistence of tropical herbivores and decreases the seascape resilience of temperate ecosystems (Bennett *et al.* 2015). This is consistent with ecological theories indicating that ecosystem processes are strongly determined by the abundance of species with high importance in certain ecological functions (Mokany, Ash & Roxburgh 2008). Species composition and dominance within ecosystems are therefore likely to be highly significant, and the impact of the tropicalization of herbivorous communities could be driven in great part by the expansion of keystone species of tropical herbivores (Hoey & Bellwood 2009)*,* in combination with the establishment of abundant populations of other species with lower impact *per capita* (Ruttenberg *et al.* 2019)*.*

Our study shows empirically how range-shifting tropical species can affect herbivory in temperate habitats across large spatial extents. The high overlap with temperate species that we observed is not surprising considering that tropical coral reefs have fewer macrophyte resources shared among a

higher number of species and populations than temperate ecosystems do. Consequently, we can expect that resource limitation in the form of space and food will not constrain further tropicalization of temperate ecosystems under climate change, with reefs with high turf cover and seagrass meadows facilitating the range-expansion and persistence of tropical fish in temperate regions. By assessing novel species interactions in three levels of overlap between temperate herbivores, tropical herbivores and temperate macrophytes, we found that in a first stage of tropicalization, temperate marine ecosystems will experience increases in the diversity, intensity and spatial extent of different herbivory functions as tropical species with different habitat affinities, feeding behaviors and diets shift their distribution poleward. Functional redundancy will be heterogeneous and might not necessarily increase initially in many sites due to the low abundance and diversity of herbivory functions in some temperate ecosystems, but it will likely do so more broadly as further tropical species arrive, their abundance increase and both the spatial and functional overlap of the communities rise.

4.6. References

Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D. & Gravel, D. (2014) From projected species distribution to food-web structure under climate change. *Global change biology*, **20**, 730–741.

Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C.H.L., Stuart-Smith, R., Barrett, N., Edgar, G., Colquhoun, J., Tran, M., Jordan, A., Rees, T. & Gowlett-Holmes, K. (2015) A Standardised Vocabulary for Identifying Benthic Biota and Substrata from Underwater Imagery: The CATAMI Classification Scheme. *Plos One*, **10**, e0141039.

Azzurro, E., Franzitta, G., Milazzo, M., Bariche, M. & Fanelli, E. (2017) Abundance patterns at the invasion front: the case of Siganus luridus in Linosa (Strait of Sicily, Central Mediterranean Sea). *Marine and Freshwater Research*, **68**, 697.

Basford, A.J., Feary, D.A., Truong, G., Steinberg, P.D., Marzinelli, E.M. & Verges, A. (2016) Feeding habits of range-shifting herbivores: tropical surgeonfishes in a temperate environment. *Marine and Freshwater Research*, **67**, 75.

Beare, D. (2002) Spatio-temporal patterns in herring (Clupea harengus L.) school abundance and size in the northwest North Sea: modelling space–time dependencies to allow examination of the impact of local school abundance on school size. *ICES Journal of Marine Science*, **59**, 469–479.

Beck, H.J., Feary, D.A., Figueira, W.F. & Booth, D.J. (2014) Assessing range shifts of tropical reef fishes: a comparison of belt transect and roaming underwater visual census methods. *Bulletin of Marine Science*, **90**, 705–721.

Bellwood, D.R., Streit, R.P., Brandl, S.J. & Tebbett, S.B. (2019) The meaning of the term "function" in ecology: a coral reef perspective. *Functional ecology,* **33**, 948-961.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J. & Saunders, B.J. (2015) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters*, **18**, 714–723.

Bessey, C. & Heithaus, M.R. (2015) Ecological niche of an abundant teleost Pelates octolineatus in a subtropical seagrass ecosystem. *Marine Ecology Progress Series*, **541**, 195–204.

Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C. & Finnegan, S. (2013) Climate change and the past, present, and future of biotic interactions. *Science*, **341**, 499–504.

Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I.H., Winter, M., Bjorkman, A.D., Bowler, D.E., Byrnes, J.E.K., Gonzalez, A., Hines, J., Isbell, F., Jones, H.P., Navarro, L.M., Thompson, P.L., Vellend, M., Waldock, C. & Dornelas, M. (2019) The geography of biodiversity change in marine and terrestrial assemblages. *Science*, **366**, 339–345.

Bonebrake, T.C., Brown, C.J., Bell, J.D., Blanchard, J.L., Chauvenet, A., Champion, C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Dell, A.I., Donelson, J.M., Evengård, B., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Jarzyna, M.A., Lee, E., Lenoir, J., Linnetved, H., Martin, V.Y., McCormack, P.C., McDonald, J., McDonald-Madden, E., Mitchell, N., Mustonen, T., Pandolfi, J.M., Pettorelli, N., Possingham, H., Pulsifer, P., Reynolds, M., Scheffers, B.R., Sorte, C.J.B., Strugnell, J.M., Tuanmu, M.-N., Twiname, S., Vergés, A., Villanueva, C., Wapstra, E., Wernberg, T. & Pecl, G.T. (2018) Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biological Reviews of the Cambridge Philosophical Society*, **93**, 284–305.

Borcard, D., Gillet, F. & Legendre, P. (2011) *Numerical Ecology with R*. Springer New York, New York, NY.

Brooks, M., E., Kristensen, K., Benthem, K., J.,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M. & Bolker, B., M. (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R journal*, **9**, 378.

Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J. & Richardson, A.J. (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–655.

Cappo, M., Harvey, E., Malcolm, H. & Speare, P. (2003) Potential of video techniques to monitor diversity, abundance and size of fish in studies of Marine Protected Areas. *Proc World Congr on Aquat Protected Areas* (eds J.P. Beumer, A. Grant & D.C. Smith), pp. 455–464. Australian Society for Fish Biology, North Beach, Western Australia.

Carroll, G., Holsman, K.K., Brodie, S., Thorson, J.T., Hazen, E.L., Bograd, S.J., Haltuch, M.A., Kotwicki, S., Samhouri, J., Spencer, P., Willis-Norton, E. & Selden, R.L. (2019) A review of methods for quantifying spatial predator–prey overlap. *Global Ecology and Biogeography*, **28**, 1561-1577.

Chao, A., Chiu, C., Villéger, S., Sun, I., Thorn, S., Lin, Y., Chiang, J. & Sherwin, W.B. (2019) An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. *Ecological monographs*, **89**, e01343.

Ebrahim, A., Martin, T.S.H., Mumby, P.J., Olds, A.D. & Tibbetts, I.R. (2020) Differences in diet and foraging behaviour of commercially important rabbitfish species on coral reefs in the Indian Ocean. *Coral Reefs*, **39**, 977-988.

Erguden, D., Bayhan, Y.K., Alagöz Erguden, S. & Altun, A. (2018) Range extension of blue-barred parrotfish Scarus ghobban Forsskal, 1775 along the Mediterranean Coast of Turkey. *Acta Biologica Turcica*, **31**, 82–85.

Filbee-Dexter, K. & Wernberg, T. (2018) Rise of turfs: A new battlefront for globally declining kelp forests. *Bioscience*, **68**, 64-76.

Fox, R.J. & Bellwood, D.R. (2008) Remote video bioassays reveal the potential feeding impact of the rabbitfish Siganus canaliculatus (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs*, **27**, 605–615.

García Molinos, J., Halpern, B.S., Schoeman, D.S., Brown, C.J., Kiessling, W., Moore, P.J., Pandolfi, J.M., Poloczanska, E.S., Richardson, A.J. & Burrows, M.T. (2015) Climate velocity and the future global redistribution of marine biodiversity. *Nature climate change*, **6**, 83–88.

Hoekman, D. (2010) Turning up the heat: temperature influences the relative importance of top-down and bottom-up effects. *Ecology*, **91**, 2819–2825.

Hoey, A.S. & Bellwood, D.R. (2009) Limited Functional Redundancy in a High Diversity System: Single Species Dominates Key Ecological Process on Coral Reefs. *Ecosystems (New York, N.Y.)*, **12**, 1316–1328.

Hoey, A.S., Brandl, S.J. & Bellwood, D.R. (2013) Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs*, **32**, 973–984.

Hyndes, G.A., Heck, K.L., Vergés, A., Harvey, E.S., Kendrick, G.A., Lavery, P.S., McMahon, K., Orth, R.J., Pearce, A., Vanderklift, M., Wernberg, T., Whiting, S. & Wilson, S. (2016) Accelerating tropicalization and the transformation of temperate seagrass meadows. *Bioscience*, **66**, 938–948.

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.

Lenanton, R.C.J., Dowling, C.E., Smith, K.A., Fairclough, D.V. & Jackson, G. (2017) Potential influence of a marine heatwave on range extensions of tropical fishes in the eastern Indian Ocean—Invaluable contributions from amateur observers. *Regional Studies in Marine Science*, **13**, 19–31.

Ling, S.D., Barrett, N.S. & Edgar, G.J. (2018) Facilitation of Australia's southernmost reef-building coral by sea urchin herbivory. *Coral Reefs*, **37**, 1053–1073.

Lowry, E., Rollinson, E.J., Laybourn, A.J., Scott, T.E., Aiello-Lammens, M.E., Gray, S.M., Mickley, J. & Gurevitch, J. (2012) Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and evolution*, **3**, 182–196.

Manly, B., Chatfield, C., Tanner, M., Carlin, B. & Zidek,, J. (2007) *Randomization, bootstrap and monte carlo methods in biology*, 3rd ed. Chapman and Hall/CRC.

Mann, K.H. (2000) *Ecology of coastal waters: with implications for management*, 2nd ed. John Wiley & Sons, Hoboken, NJ.

Marshak, A.R. & Heck, K.L. (2017) Interactions between range-expanding tropical fishes and the northern Gulf of Mexico red snapper Lutjanus campechanus. *Journal of Fish Biology*, **91**, 1139–1165.

Michael, P.J., Hyndes, G.A., Vanderklift, M.A. & Vergés, A. (2013) Identity and behaviour of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef. *Marine Ecology Progress Series*, **482**, 227–240.

Milazzo, M., Mirto, S., Domenici, P. & Gristina, M. (2013) Climate change exacerbates interspecific interactions in sympatric coastal fishes. *The Journal of Animal Ecology*, **82**, 468–477.

Mokany, K., Ash, J. & Roxburgh, S. (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.

Nowicki, R.J., Fourqurean, J.W. & Heithaus, M.R. (2018) The role of consumers in structuring seagrass communities: direct and indirect mechanisms. *Seagrasses of australia: structure, ecology and conservation* (eds A.W.D. Larkum, G.A. Kendrick & P.J. Ralph), pp. 491–540. Springer International Publishing, Cham.

Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E.A., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Butchart, S.H.M., Doswald, N., Foden, W., Gill, D.J.C., Green, R.E., Sutherland, W.J., Tanner, E.V.J. & Pearce-Higgins, J.W. (2014) Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global change biology*, **20**, 2221–2229.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2019) Vegan: Community Ecology Package. R package version 2.5-6. *http://cran. r-project. org> ….*

Parker, J.R.C., Saunders, B.J., Bennett, S., DiBattista, J.D., Shalders, T.C. & Harvey, E.S. (2019) Shifts in Labridae geographical distribution along a unique and dynamic coastline. *Diversity & distributions*, **25**, 1787-1799.

Parravicini, V., Azzurro, E., Kulbicki, M. & Belmaker, J. (2015) Niche shift can impair the ability to predict invasion risk in the marine realm: an illustration using Mediterranean fish invaders. *Ecology Letters*, **18**, 246–253.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.I., Martin, V.Y.,

McCormack, P.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettorelli, N., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J.M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E. & Williams, S.E. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, **355**.

Pianka, E.R. (1973) The Structure of Lizard Communities. *Annual review of ecology and systematics*, **4**, 53–74.

Poore, A.G.B., Campbell, A.H., Coleman, R.A., Edgar, G.J., Jormalainen, V., Reynolds, P.L., Sotka, E.E., Stachowicz, J.J., Taylor, R.B., Vanderklift, M.A. & Duffy, J.E. (2012) Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters*, **15**, 912–922.

R Core Team. (2019) *R: A language and environment for statistical computing*. Computer software, R Foundation for Statistical Computing, Vienna, Austria.

Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E.L. & Pavoine, S. (2016) Measuring the functional redundancy of biological communities: a quantitative guide. *Methods in ecology and evolution / British Ecological Society*, **7**, 1386–1395.

Ruttenberg, B.I., Adam, T.C., Duran, A. & Burkepile, D.E. (2019) Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales. *Ecological Applications*, **29**, e01893.

Sales, M. & Ballesteros, E. (2012) Seasonal dynamics and annual production of *Cystoseira crinita* (Fucales: Ochrophyta)-dominated assemblages from the northwestern Mediterranean. *Scientia marina*, **76**, 391–401.

Sorte, C.J.B., Williams, S.L. & Carlton, J.T. (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, **19**, 303–316.

Steneck, R.S., Bellwood, D.R. & Hay, M.E. (2017) Herbivory in the marine realm. *Current Biology*, **27**, R484–R489.

Streit, R.P., Cumming, G.S. & Bellwood, D.R. (2019) Patchy delivery of functions undermines functional redundancy in a high diversity system. *Functional ecology*, **33**, 1144-1155.

Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M.A., Wernberg, T., Ainsworth, T. & Steinberg, P.D. (2019) Tropicalisation of temperate reefs: Implications for ecosystem functions and management actions. *Functional ecology*, **33**, 1000–1013.

Vergés, A., Steinberg, P.D., Hay, M.E., Poore, A.G.B., Campbell, A.H., Ballesteros, E., Heck, K.L., Booth, D.J., Coleman, M.A., Feary, D.A., Figueira, W., Langlois, T., Marzinelli, E.M., Mizerek, T., Mumby, P.J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A.S., Smale, D.A., Tomas, F., Wernberg, T. & Wilson, S.K. (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings. Biological Sciences / the Royal Society*, **281**, 20140846.

Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C.J., Hovey, R.K., Harvey, E.S., Holmes, T.H., Kendrick, G.A., Radford, B., Santana-Garcon, J., Saunders, B.J., Smale, D.A., Thomsen, M.S., Tuckett, C.A., Tuya, F., Vanderklift, M.A. & Wilson, S. (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science*, **353**, 169–172.

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S. & Rousseaux, C.S. (2012) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature climate change*, **3**, 78–82.

White, K.S., Westera, M.B. & Kendrick, G.A. (2011) Spatial patterns in fish herbivory in a temperate Australian seagrass meadow. *Estuarine, Coastal and Shelf Science*, **93**, 366–374.

Wilson, S.K., Graham, N.A.J. & Polunin, N.V.C. (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine biology*, **151**, 1069–1076.

Zarco-Perello, S., Langlois, T.J., Holmes, T., Vanderklift, M.A. & Wernberg, T. (2019) Overwintering tropical herbivores accelerate detritus production on temperate reefs. *Proceedings of the Royal Society B*, **286**, 20192046.

Zarco-Perello, S., Wernberg, T., Langlois, T.J. & Vanderklift, M.A. (2017) Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports*, **7**, 820.

Zarco-Perello, S., Wernberg, T (2020) Data from: range-extending tropical herbivores increase diversity, intensity and extent of herbivory functions in temperate marine ecosystems. Dryad Digital Repository: https://doi.org/10.5061/dryad.8w9ghx3hx.

4.7. Supporting Information

Table S1. Weights of herbivory functions (columns in color) for each species of tropical and temperate fish inhabiting temperate ecosystems of Western Australia based on published literature indicating herbivory rates, stomach contents analyses and field observations. Information indicated that rabbitfish is the top consumer in all functions in temperate ecosystems in the region and was assigned the maximum value as 1, this was used to scale the weights of the rest of the species. ***** Information based on closely related species. FO: field observations of our study appear *in italics*; *bites min^{-1}* calculated as *per capita* following fish individuals for 5 min. Information of **bites h^{-1}** are from recent unpublished herbivory assays carried out by SZP.

Species	Seaweed Grazer W	Seaweed Browser W	Seagrass Browser W	Turf Feeding	Canopy Feeding	Seagrass Feeding	Type of information	References
Siganus fuscescens	1	1	1	**15.4 bites h^{-1}** 50-60% *27 bites min^{-1}*	426 bites h^{-1} 10-30% *18 bites min^{-1}*	8 bites h^{-1} 32% *19 bites min^{-1}*	Herbivory assays Stomach content Field observations	(Zarco-Perello et al. 2019; Avenant 2018; Bennett et al. 2015; Nakayama 1999), FO.
Scarus spp.	0.5	0.25	0.1	**11.5 bites h^{-1}** 92% *15 bites min^{-1}*	- 8% *9 bites min^{-1}*	- 2% *5 bites min^{-1}*	Herbivory assays Stomach content Field observations	(Bennett et al. 2015; Jeeramani et al. 2010; De la Torre-Castro et al. 2009), FO.
Kyphosus sydneyanus	0.1	0.5	0	*0.2 bites h^{-1}* *Few bites*	21.2 bites h^{-1} 80% *Few bites*	0 0 0	Herbivory assays Stomach content Field observations	(Zarco-Perello et al. 2017; Zarco-Perello et al. 2019; Salter et al. 2010; Moran and Clements 2002), FO.

Kyphosus cornelii	0.5	0	0	8.4 bites h^{-1} - *Many bites*	0 - 0	0 - 0	Herbivory assays Stomach content Field observations	(Zarco-Perello et al. 2019; Ferguson et al. 2017; Berry and Playford 1992; Rimmer 1986), FO.
Girella zebra*	0.3	0	0.1	0 80% *Few bites*	0 0 0	0 Present *Few bites*	Herbivory assays Stomach content Field observations	(Ferguson et al. 2016; Clements and Choat 1997; Burchmore et al. 1984), FO.
Pelates octolineatus	0	0.5	0.5	- 0 0	- 50±50% *Few bites*	- 50±50 % *Frequent bites*	Herbivory assays Stomach content Field observations	(Bessey and Heithaus 2015), FO.
Olisthops cyanomelas	0	0.3	0	0 0 0	1.6 bites h^{-1} 56-86% 2.1 bites min^{-1}	0 0 0	Herbivory assays Stomach content Field observations	(Zarco-Perello et al. 2019; Shepherd and Baker 2008; Jones and Andrew 1990)

Table S2. Dissimilitude (euclidean distances) in herbivory functions between tropical (orange cells) and temperate herbivorous fish species of south western Australia.

	Scarus spp.	Kyphosus sydneyanus	Kyphosus cornelli	Olisthops cyanomelas	Pelates octolineatus	Girella zebra	Siganus fuscescens
Scarus spp.	0						
Kyphosus sydneyanus	0.57	0					
Kyphosus cornelli	0.14	0.64	0				
Olisthops cyanomelas	0.55	0.22	0.58	0			
Pelates octolineatus	0.75	0.51	0.86	0.54	0		
Girella zebra	0.22	0.55	0.22	0.44	0.71	0	
Siganus fuscescens	1.37	1.43	1.50	1.58	1.22	1.51	0

Bibliography

Avenant, C. 2018. Diet of the Tropicalised Herbivore Siganus fuscescens Across a Broad Latitudinal Gradient and Comparisons With Temperate Seagrass-associated Omnivorous Fishes. Edith Cowan University.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J. and Saunders, B.J. 2015. Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters* 18(7), pp. 714–723.

Berry, P.F. and Playford, P.E. 1992. Territoriality in a subtropical kyphosid fish associated with macroalgal polygons on reef platforms at Rottnest Island, Western Australia. *JR Soc West Aust*.

Bessey, C. and Heithaus, M.R. 2015. Ecological niche of an abundant teleost Pelates octolineatus in a subtropical seagrass ecosystem. *Marine Ecology Progress Series* 541, pp. 195–204.

Burchmore, J.J., Pollard, D.A. and Bell, J.D. 1984. Community structure and trophic relationships of the fish fauna of an estuarine Posidonia Australis seagrass habitat in port hacking, new South Wales. *Aquatic Botany* 18(1-2), pp. 71–87.

Clements, K.D. and Choat, J.H. 1997. Comparison of herbivory in the closely-related marine fish genera Girella and Kyphosus. *Marine biology* 127(4), pp. 579–586.

Ferguson, A.M., Harvey, E.S. and Knott, N.A. 2017. Herbivore abundance, grazing rates and feeding pathways on Australian temperate reefs inside and outside marine reserves: How are things on the west coast? *Journal of Experimental Marine Biology and Ecology* 493, pp. 49–56.

Ferguson, A.M., Harvey, E.S. and Knott, N.A. 2016. Herbivore abundance, site fidelity and grazing rates on temperate reefs inside and outside marine reserves. *Journal of Experimental Marine Biology and Ecology* 478, pp. 96–105.

Jeeramani, T., Rani, V., Kesanan, K. and Balasubramanian, T. 2010. Food and Feeding Habit of the Parrotfish Scarus ghobban Forsskal, 1775 (Family: Scaridae) from Nagapattinam, South East Coast of India. *World Journal of Fish and Marine Sciences* 2, pp. 147–151.

Jones, G.P. and Andrew, N.L. 1990. Herbivory and patch dynamics on rocky reefs in temperate Australasia: The roles of fish and sea urchins. *Austral ecology* 15(4), pp. 505–520.

Moran, D. and Clements, K.D. 2002. Diet and endogenous carbohydrases in the temperate marine herbivorous fish Kyphosus sydneyanus. *Journal of Fish Biology* 60(5), pp. 1190–1203.

Nakayama, Y. 1999. Grazing of the brown alga Ecklonia cava by three herbivorous fishes on the coast of Nakagi, South Izu, central Japan. *Japanese Journal of Phycology* (47), pp. 105–112.

Rimmer, D.W. 1986. Changes in diet and the development of microbial digestion in juvenile buffalo bream, Kyphosus cornelii. *Marine biology* 92(3), pp. 443–448.

Salter, Z.T., Harvey, E.S., Kendrick, G.A. and Murray, K. 2010. The effect of kelp bed disturbance on the abundance and feeding behaviour of fishes on high-relief reefs. *Marine and freshwater behaviour and physiology* 43(2), pp. 109–125.

Shepherd, S.A. and Baker, J.L. 2008. Investigator group expedition 2006: flexible foraging ecologyofa temperate herbivore, the herring cale, *olisthops cyanomelas* , in south australia. *Transactions of the Royal Society of South Australia* 132(2), pp. 147–162.

De la Torre-Castro, M., Björk, M., Eklöf, J. and Rönnbäck, P. 2009. Seagrass Importance in Food Provisioning Services: Fish Stomach Content as a Link between Seagrass Meadows and Local Fisheries. *Western Indian Ocean Journal of Marine Science* 7(1).

Zarco-Perello, S., Langlois, T.J., Holmes, T., Vanderklift, M.A. and Wernberg, T. 2019. Overwintering tropical herbivores accelerate detritus production on temperate reefs. *Proceedings. Biological Sciences / the Royal Society* 286(1915), p. 20192046.

Zarco-Perello, S., Wernberg, T., Langlois, T.J. and Vanderklift, M.A. 2017. Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports* 7(1), p. 820.

Chapter 5. Persistence of tropical herbivores in temperate reefs constrain kelp resilience to cryptic habitats

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5.1. Abstract

Global warming is facilitating the range-expansion of tropical herbivores, causing a tropicalization of temperate marine ecosystems, where tropical herbivores can suppress habitat-forming macrophytes, supporting the resilience of canopy-free ecosystem states. However, currently we lack a thorough understanding of the mechanisms that, on one hand, support the persistence of tropical herbivores and on the other support the recovery of temperate foundation species in tropicalized ecosystems, a required knowledge to predict potential regime-shifts and reversals to the baseline state of the ecosystem. This study tested processes behind the persistence of the tropicalization of temperate reefs which experienced a complete loss of their kelp forests and an influx of tropical herbivores following a marine heatwave in 2011. For this, we assessed the feedback mechanisms that maintain turf-dominated states (recruitment of tropical herbivores, browsing and grazing rates and turf cover) and those that resist it (kelp recruitment, survival, and reproductiveness). We found that the reefs remained tropicalized with high cover of turf and high abundance of tropical herbivores after nine years from the regime shift. The most important herbivores, the rabbitfish *Siganus fuscescens* and the chub *Kyphosus bigibbus*, persisted with high abundances. This was supported by the adjacent reef lagoon, where seagrass meadows and the backreef habitats hosted juveniles of both species, particularly rabbitfish. Tropical herbivores exerted a strong top-down control on turf seaweed and kelp during herbivory assays, rapidly consuming kelp individuals in open areas. However, in topographical refuges in the reefs, herbivory was low and kelp individuals survived, with some having reproductive tissue. *Synthesis*: Our findings incorporate the importance of nursery grounds for tropical herbivores and herbivory refugia for kelp individuals into the tropicalization model, where the former increases the resilience of canopy-free states and the latter might facilitate recovering kelp populations. The restoration of abundant warm-resistant kelp populations in shelters could provide local sources of propagules to recolonize open spaces, however, our results suggest that the reduction of herbivory and the provision of turf-free substratum would be necessary to boost the recovery of kelp forests.

5.2. Introduction

Kelps (Phaeophyta, order Laminariales) are foundation species on temperate reefs, where they provide high habitat complexity and trophic resources supporting diverse biological communities (Steneck *et al.* 2002). They have among the highest rates of primary productivity, most of which becomes detritus and is consumed by detritivores, sustaining secondary productivity of reefs and

connected ecosystems (*e.g.* seagrass meadows) (Mann 2000; Krumhansl & Scheibling 2012). This high productivity and biodiversity translates into ecosystem services such as coastal protection, nutrient cycling, carbon fixation and a myriad of resources for recreational users and commercial industries conservatively valued between US $434 million to $7 billion year^{-1} for regional economies (Vásquez *et al.* 2014; Bennett *et al.* 2016; Blamey & Bolton 2017). However, substantial reductions in the abundance of kelp have occurred in several places around the world. Declines have been attributed to physical and biological stressors which have increased mortality rates and hindered recruitment, eroding resilience and driving the system towards canopy-free ecosystem states (Wernberg *et al.* 2019). This has prompted calls for further understanding of the mechanisms behind regime-shifts, their persistence and the development of strategies for the restoration of kelp forests (Layton *et al.* 2020; Morris *et al.* 2020).

Regime shifts have occurred in multiple places around the world, with two types of mechanisms implicated in all cases: (1) stressors which cause kelp loss and (2) processes which inhibit kelp recovery. Large-scale disappearance of kelp has been caused by high temperatures, pollution, eutrophication, overharvesting, intense grazing and invasive and range extending species (Filbee-Dexter & Wernberg 2018). The nature, spatial extents and temporal durations of these disturbances differ widely, but declines of kelp abundance have occurred in 40-60% of the studied kelp forests of the world (Krumhansl *et al.* 2016; Wernberg *et al.* 2019). The resilience of kelp dominated states is density dependent because high abundances of kelp maintain positive feedback loops that ensure the survival of adults and recruits (high spore supply, facilitation of recruitment and low herbivory rates) (Bennett *et al.* 2015; Filbee-Dexter & Wernberg 2018). When severe disturbances cause substantial decreases in kelp abundance, the supply of propagules and survival may become too low to maintain kelp populations, triggering positive feedback loops that favour canopy-free states (low spore supply, low recruitment and intense herbivory rates *per capita*). Under low cover of kelp, assemblages of opportunistic species of small filamentous and foliose seaweed known as turf (Connell, Foster & Airoldi 2014) quickly dominate hard substrates, hindering the settlement and survival of new kelp propagules (Gorman & Connell 2009; Feehan, Grace & Narvaez 2019). In some systems with high abundance of herbivores, kelp recruits would be eaten even if they can settle successfully onto turf, preventing kelp recovery and enforcing canopy-free states (O'Brien, Scheibling & Krumhansl 2015; Bennett *et al.* 2015).

Herbivory is an important ecological process that can modify the composition of primary producers and the functioning of temperate reef ecosystems. In terrestrial forests, herbivores such as insects, rodents and ungulates can inflict considerable damage to plants (Beschta 2005); in kelp forests, herbivores such as molluscs, sea urchins or fish can damage kelp blades, making them susceptible to

breakage and lower their reproductive output (Andrew & Jones 1990; O'Brien & Scheibling 2016). However, herbivory in general has been lower in temperate reefs compared with tropical reefs (Longo *et al.* 2018), and large-scale herbivore damage has only occurred exceptionally due to outbreaks of sea urchins which consume the base of kelps, causing their detachment and extensive deforestations denominated "urchin barrens" (Breen & Mann 1976; Filbee-Dexter & Scheibling 2014). Nonetheless, herbivory in temperate reefs is rising due to the redistribution of species and novel biological interactions caused by climate change (Blowes *et al.* 2019). The abundance and diversity of herbivores in several temperate regions of the world are increasing due to the poleward range extension of tropical species as a result of the intensification of warm currents that transport tropical propagules to higher latitudes (Vergés *et al.* 2014). This has increased the intensity and the functional diversity of herbivory (Zarco-Perello *et al.* 2020), accelerating the transformation of kelp and other macrophytes to detrital biomass (Zarco-Perello *et al.* 2019). While there is no clear evidence at this point that range-extending tropical herbivores have been the primary cause of shifts to canopy free states, there is clear evidence that they have increased kelp consumption, contributing to reduce kelp abundance (Bennett *et al.* 2015; Vergés *et al.* 2016; Zarco-Perello *et al.* 2017) and maintenance of turf-dominated states (Bennett *et al.* 2015) with predictions of further increases of consumption under future warmer conditions (Vergés *et al.* 2019; Zarco-Perello *et al.* 2019).

The persistence of regime-shifts and tropicalization of kelp forests is one of the main questions in current conservation research of temperate reefs (Vergés *et al.* 2019). Sea urchin barren states are caused and enforced by high rates of herbivory, while turf-dominated states have been caused by environmental disturbances (*e.g.* pollution and warming) and enforced by turf seaweed that inhibit kelp recruitment. Tropicalized turf-dominated states combine elements of these two alternative states, where tropical herbivores contribute to reduce the abundance of kelp together with environmental disturbances and enforce the canopy free state together with turf mats by inhibiting settlement and survival of recruits (Vergés *et al.* 2014; Bennett *et al.* 2015). To date, there have not been reports of kelp recovery when the ecosystem has shifted to turf-dominated states, let alone under the enforcement of tropical herbivores (Filbee-Dexter & Wernberg 2018). However, kelp forests have been able to recover from urchin barren states after the abundance of sea urchins has decreased due to increases in predation, diseases or fishing, reducing herbivory rates and enhancing kelp recruitment success (Filbee-Dexter & Scheibling 2014). Thus, it is important to understand the capacity of range-shifting herbivores to persist and enforce canopy-free states in temperate reefs.

It has been suggested that turf dominated reefs can promote the persistence of range-extending tropical herbivorous fish, because they have a tendency to occupy habitats with less canopy (Hoey & Bellwood 2011; Bennett *et al.* 2015). However, fish species also need nursery grounds that provide

suitable environments for recruitment, such as seagrass meadows and algal beds (Zarco-Perello & Enríquez 2019; Fulton *et al.* 2020). To date, nursery habitats have not been integrated in the ecological model of the tropicalization of temperate reefs. On the other hand, under high herbivory intensity, macrophytes are likely to persist if they are unpalatable to consumers or settle in habitats inaccessible to herbivores (Lubchenco & Gaines 1981). Such refuges can enhance the resilience of communities by providing protection from disturbances (Sedell *et al.* 1990). Examples of refugia against herbivory exist in land (Beschta 2005), freshwater (Bergey 2005), coral reefs (Bennett, Vergés & Bellwood 2010; Brandl, Hoey & Bellwood 2014; Puk *et al.* 2020) and temperate reefs (Franco *et al.* 2015). However, the role of topographic refugia for kelp has not been explored in temperate reefs experiencing tropicalization and phase-shifts to turf-dominated states, despite the capacity of refuges to function as natural propagule banks that in the cessation of disturbances could repopulate new areas (Gorman & Connell 2009).

In this study, we assessed the ecological feedbacks that resist (kelp recruitment, survival, and reproduction) and maintain canopy-free states (recruitment of tropical herbivores, browsing and grazing rates and turf cover) on tropicalized reefs which experienced severe loss of kelp and increases in abundance of tropical herbivorous fish following a marine heatwave (Bennett *et al.* 2015). We assessed: (i) the benthic community structure and the recruitment of new kelp individuals, (ii) the abundance of recruits and adults of tropical herbivores and tested the persistence of their populations since the marine heatwave until today and (iii) the herbivory rates of kelp in exposed and sheltered habitats in the reefs. We hypothesized that (1) kelp could persist if settlement occurs in topographical shelters, (2) tropical herbivores would persist if recruitment occurred in lagoon systems with nursery grounds (*e.g.* seagrass meadows), (3) herbivory on kelp and turf would remain dominated by tropical browsers (consumers of canopy-forming macrophytes) and grazers (consumers of turf) and (4) herbivory on kelp would be significantly higher in exposed reef surfaces than in refuges within reef crevices.

5.3. Materials and Methods

Study Site

The study was carried out in the reef system near Port Gregory, Western Australia (-28.19016 S, 114.23683 W), where a series of fringing and platform rocky reefs (5-10 m depth) are located about 0.5 to 1.3 km from the coast. Some of these reefs form a protective barrier against waves, allowing the development of a sandy lagoon where meadows of the seagrasses *Posidonia* spp, *Syringodium* sp, and *Halodule* sp extend next to a backreef habitat closer to the reef crest that consists of boulders

covered in turf with sporadic foliose seaweed, *Sargassum*, coral and zoanthid colonies (Fig. 1). Reefs in the region previously had healthy populations of the kelp *Ecklonia radiata* ; however, these were eradicated (from 52.7% ± 16.6% to 0% cover; mean ± se) following an extreme marine heatwave in 2011 that caused a regime-shift to a canopy-free state, where turf cover increased from 0% to 58.7 ± 10.1% (Bennett *et al.* 2015). This was triggered by an intensification of the Leeuwin Current (Feng *et al.* 2013), that carries warm water and fish larvae from the tropics to temperate western Australia. Thus, in addition to heat, the system experienced an increase in recruitment of tropical herbivores (Bennett *et al.* 2015).

Benthic Community Structure

Mechanisms that support the recovery of a kelp dominated state (recruitment of kelp) were surveyed through GPS-tracked roving underwater visual census during two days in April and two days in December 2019. Surveys were performed in four reefs in the area of study for approximately one hour in each reef (approx. 4000 m^2). Two surveyors swam in a zig-zag pattern, following crevices and overhangs where kelp recruits could shelter (Franco *et al.* 2015). Kelp individuals found were measured in total length of thallus (cm), number of lateral blades, health condition (*i.e.* presence of bleaching, disease or epiphytes) and growth stage (1, 2 or 3) (Kirkman 1981).

Quantification of the percent cover of macrophytes in the reefs was obtained through the analyses of images from Stereo-Dive Operated Video transects of 25 x 5 m in length (S-DOV, n = 8 per reef), where a diver swam at constant pace (~20 m/min) holding the video system 0.5 m above the substratum and slightly angled downwards to record the benthos (Goetze *et al.* 2019). Videos of each transect were paused at 10 second intervals using the software TransectMeasure (SeaGIS; n = 10 per transect) to obtain information about species composition and percent cover of main morpho-functional groups of sessile biota classified as Canopy (*i.e. Ecklonia radiata* and *Sargassum* spp), Foliose Macroalgae (*e.g. Padina* sp, *Lobophora* sp, etc.; <15 cm tall) and Turf (*i.e.* epilithic algal matrix; <1cm tall) as done previously (Bennett *et al.* 2015).

Persistence of Tropical Herbivores and Herbivory

The assessment of forces that support the persistence of a canopy-free state (recruitment of tropical herbivorous fish) were surveyed by GPS-tracked roving underwater visual census during two days in April and two days in December 2019 (Beck *et al.* 2014). Recruitment of tropical herbivorous fish populations was investigated in the reef lagoon, where seagrass and backreef habitats could act as a nursery grounds (Nagelkerken *et al.* 2000). A surveyor swam at a constant pace parallel to the reef crest for 15 minutes (approx. 2000 m^2) registering the abundance and the specific habitat where individuals of adult and juvenile herbivorous fish were encountered, completing two transects parallel

to each other, ~20 meters apart, per day. Fish abundance is reported as density (fish counts 2000 m^{-2}) and as the highest school sizes (MaxS; individuals per school, ind school^{-1}) found during surveys (Zarco-Perello *et al.* 2020).

Herbivory rates and abundance of adult herbivorous fish were assessed in the reefs where baselines exist about the complete loss of kelp forest and increase of primary consumption by tropical species (Fig. 1. Bennett *et al.* 2015). To (1) estimate the current rates of browsing on kelp and (2) test if crevices in the reefs could act as natural refuges and assist in the recovery of kelp populations, we performed video-filmed herbivory assays in April and November of 2019. For this, we collected adult individuals of kelp from temperate reefs located 30 km south of Port Gregory (Horrocks) and deployed them within two hours of collection. Individuals were always maintained cool and moist, had their weight (481 ± 37 g; mean ± se) and thallus length measured (72 ± 2 cm) and were tagged and attached to dive weights by their holdfast with cable ties. 5 individuals were deployed haphazardly over exposed surfaces and 5 individuals were deployed inside adjacent crevices with approximate dimensions of 1 x 0.5 m (H x W), capable to shelter a full-grown kelp individual (n=10 per reef). To identify the species responsible for consumption, we deployed video cameras (GoPro Hero 4) recording three exposed kelps per reef (n= 6 per day) from 2 to 3.5 hrs within the typical feeding time frame of diurnal herbivorous fish (8.00–16.00 h) (Fox *et al.* 2009). Additionally, in each reef, three to six cameras were deployed randomly (>10 meters apart) in open areas without kelp to identify grazers of epilithic algal matrix, invertebrates and detritus trapped within Turf (n = 6-9 per day), which can consume and damage kelp gametophytes and sporophyte recruits. Cameras were positioned pointing straight to flat surfaces and setup up to record with medium field of view to ensure the recording of similar areas (approx. 10 m^2, based on a 2 m^2 quadrat); all bites observed were registered to calculate grazing rates at reef scale. In each day of sampling, all cameras were replaced, and all kelps were checked and retrieved only if they were completely consumed. All individuals left after 48 hrs were collected and their weight was measured to calculate the rates of biomass consumption (g h^{-1}). In total we obtained 23 videos of kelp browsing and 38 videos of turf grazing.

The abundance of fish in the reefs was calculated as MaxN (maximum number of individuals in a frame) from remote underwater videos (RUV) of the herbivory assays (Bennett *et al.* 2015) and as density (count 125 m^2) from S-DOV (as previously described). All fish were identified to species level and those found feeding were classified as grazers or browsers and temperate or tropical according to their geographic distribution (Froese & Pauly 2018). *Kyphosus sydneyanus* and *Kyphosus gladius* were grouped together given their great similarity and difficulty to differentiate in big mixed schools.

Herbivory rates were adjusted to account for the "aggregation effect" in remote underwater video sampling, where higher abundances and numbers of bites are observed by species that form schools, in contrast to species whose individuals spread across larger areas and are recorded in lower numbers by the cameras. Bite rates of each species was calculated *per capita* (bites individual h^{-1}) for each independent feeding event seen in the videos (*i.e.* the total number of bites was divided by the number of individuals feeding), which were scaled to population level by multiplying them by the highest abundance registered at each reef, in line with the mass ratio hypothesis (Grime 1998). For schooling species, we used the highest MaxN registered in each reef and for non-schooling species we used the total number of individuals observed in the S-DOV surveys or the highest MaxN if the species was not detected in the transects. In addition, we accounted for differences in bite sizes between species by multiplying their consumption according to their relative size (fork length) calculated from S-DOV using the program EventMeasure (SeaGis) (Goetze *et al.* 2019). *Kyphosus sydneyanus* and *Kyphosus biggibus* had the greatest size on average (40 cm) and was used to relativize the size of the rest of the species from 1 to 0 (Supporting Information Table S1).
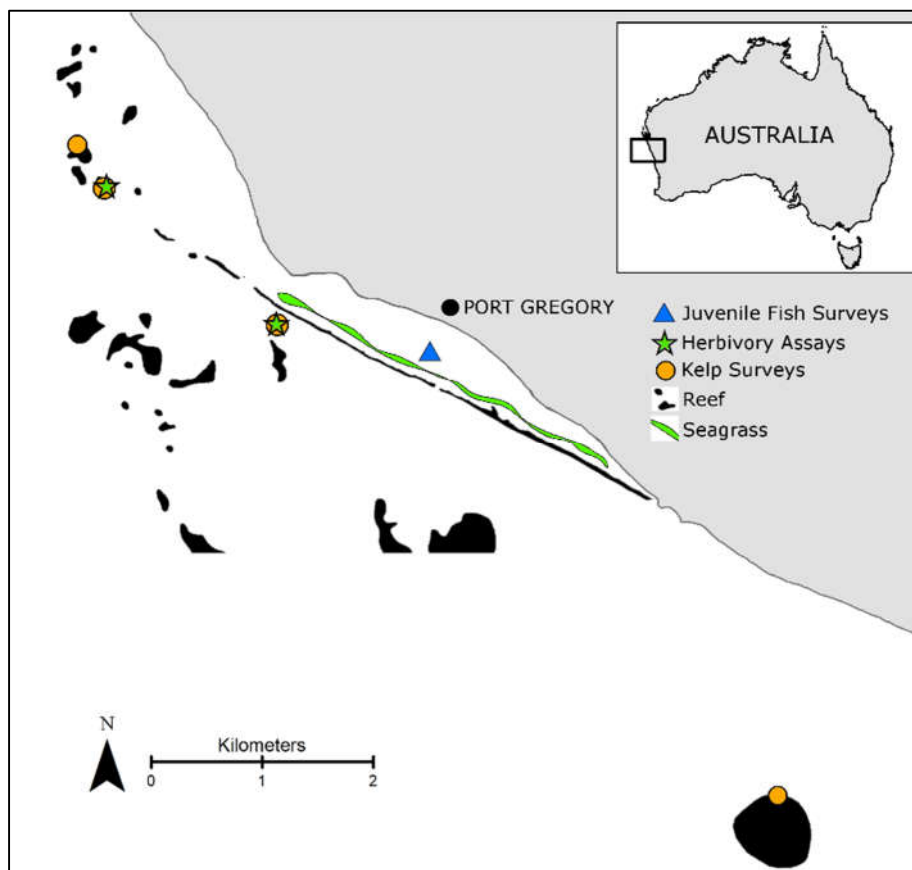
Figure 1. Map of the surveying sites of the study for juvenile fish in the lagoon, and kelp herbivory and kelp individuals in crevices in reefs of Port Gregory, Western Australia. Habitat layers obtained from www.seamapaustralia.org.

Statistical Analyses

All analyses of fish abundances and herbivory rates were done with generalized linear mixed models using the R package glmmTMB (Brooks *et al.* 2017). We tested the persistence of populations of tropical herbivorous fish by comparing the current abundance (2019) with a database collected soon after the marine heatwave (2013) using the same methodologies (Bennett *et al.* 2015). For these analyses, we only considered the sampling performed at the same time of the year as the previous study (November). Independent univariate tests were done for species of the families Siganidae, Kyphosidae, Labridae using MaxN abundances considering Day of sampling and Reef as random factors and Year as fixed factor in a crossed design, while analyses of Pomacentrid species were done using S-DOV abundances considering Reef as random factor and Year as fixed factor. Current differences in the abundances and herbivory rates of temperate versus tropical herbivorous species of grazers and browsers were done considering Day of sampling and Reef as random factors and Climatic Affinity of the fish as fixed factor in a crossed design. Differences in consumption of kelp biomass on exposed surfaces versus reef crevices were done considering Reef as random factor and Exposure as fixed factor. In all the analyses, p-values were calculated with Likelihood Ratio Tests, model fit was checked with AICc, graphical examination of predicted versus observed values, and dispersion and zero inflation tests using the R package DHARMa (Hartig 2020).

5.4. Results

Benthic Community Structure

The benthic cover of the reefs remained dominated by turf (52.8 ± 5%; mean ± se) interspersed with stands of *Sargassum* spp. (13.9 ± 4.9%) and foliose macroalgae (10.6 ± 4.4%; Fig. 2a-b). Kelp populations were not seen with S-DOV surveys; however, roaming visual census discovered kelp individuals in all four reefs surveyed only in crevices. These were very frequent in the reefs and consisted of openings in the ground, spaces between boulders or under reef overhangs. A total of 27 individuals were found, with 6.75 ± 1.8 individuals per reef on average. These ranged from 13.5 cm (stage 1) to 27 cm (stage 2) and 42.5 cm (stage 3) in length of thallus (Table 1). Most individuals were healthy, except two which were heavily overgrown by epiphytes, and four individuals had reproductive tissue. However, most kelps were short for their estimated developmental stage and showed fish bite marks in the upper blades and lamina protruding out from the crevices where they had settled (Fig. 2c-f). A big stage 3 kelp was also found drifting in one of the reefs. As this was unlikely to have originated at the local reefs, this potentially indicates connectivity with more distant or deeper kelp populations.
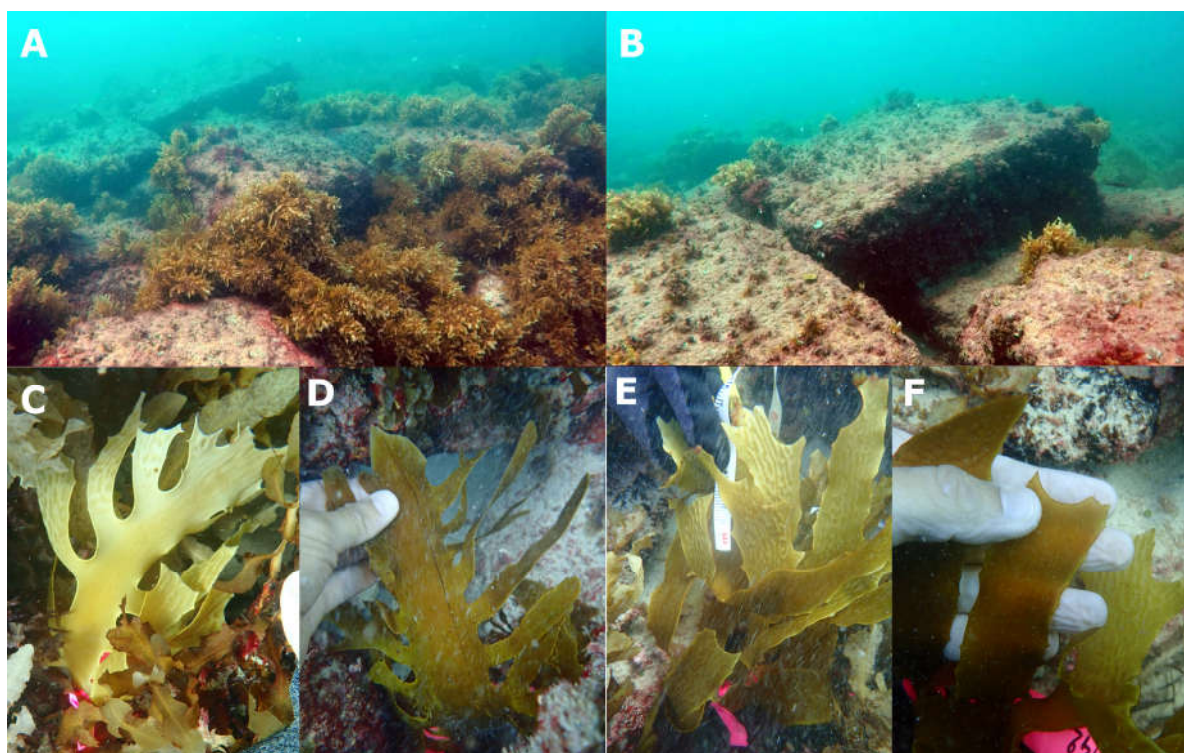
Figure 2. Seascapes dominated by *Sargassum* and turf (A, B) with kelp individuals (*Ecklonia radiata*) found in crevices with clear grazing marks (C-F) in tropicalized temperate reefs of Port Gregory, Western Australia.

Table 1. Abundance and morphological attributes of kelp individuals found in topographic shelters of tropicalized temperate reefs of Port Gregory, Western Australia. The presence of sorus tissue indicates reproductiveness.

Attribute	Stage 1	Stage 2	Stage 3
Abundance	4% (n=1)	89% (n=24)	7% (n=2)
Length	13.5 cm	27 ± 1.5 cm	31 ± 8 cm
Lateral blades		14 ± 1	28 ± 6
Sorus tissue		12% (n= 3)	50% (n=1)

Persistence of Tropical Herbivores

Aggregations of recruits and juveniles of *Siganus fuscescens* (rabbitfish) were found during visual censuses in seagrass meadows. Recently settled recruits (< 5 cm) were seen in April (MaxS: 100 ind school^{-1}), while juvenile rabbitfish (> 5cm) were seen in December (MaxS: 291). Adult rabbitfish were also seen feeding on seagrass blades (MaxS: 32), including a pair of individuals displaying courtship behaviour during April (Supporting Information Video 1). Young individuals of the tropical *Kyphosus bigibbus* and temperate *Kyphosus cornelii* (10-15 cm) were also seen close to the backreef in the lagoon during April (MaxS: 11 and 40 respectively; Fig. 3a). Juveniles of parrotfish were only seen outside of surveys close to the backreef but could not be quantified.

In the reefs we only observed adult individuals of tropical herbivores except for *Pomacentrus milleri* whose juveniles were very common. We detected differences in abundances in some herbivorous species since 2013 (GLMM, p<0.05, Supporting Information Table S2 & S3; Fig. 3b). Rabbitfish was only detected by RUV and persisted with high abundances on average (MaxN 40.7 ± 5.2 vs 18.3 ± 4.2 (2013)), while populations of *K. bigibbus* were also exclusively detected by RUV and persisted as the second most abundant tropical species (MaxN 21.7 ± 5.9 vs 27.0 ± 6.3). The parrotfish *Scarus ghobban* was a common species (MaxN 1.48 ± 0.15 vs 1.94 ± 0.1) and more frequently sighted than *Scarus schlegeli*, although the latter was more observed than in 2013 (MaxN 1.28 ± 0.2 vs 0.42 ± 0.1). The tropical damselfish *Abudefduf bengalensis* (S-DOV 2.8 ± 0.8 vs 1.0 ± 0.3; MaxN 1.2 ± 0.12 vs 0.88 ± 0.32) and *Pomacentrus milleri* (S-DOV 2.9 ± 0.1 vs 1.1 ± 0.4; MaxN 0.97 ± 0.2 vs 0.06 ± 0.04) decreased their abundances considering S-DOV but increased according to MaxN. Among temperate and subtropical species, *Kyphosus cornelii* had considerably higher abundances than in 2013 (MaxN 23.64 ± 3.94 vs 5.8 ± 2.3), while *Kyphosus sydneyanus/gladius* (MaxN 3.8 ± 1.1 vs 2.1 ± 0.5) and *Parma occidentalis* had consistent abundances between years (S-DOV 1.8 ± 0.5 vs 2.1 ± 0.52; MaxN 2 ± 0.24 vs 0.62 ± 0.11). Additionally, the tropical herbivores *Acanthurus grammoptilus* (MaxN: 1)*, Naso unicornis* (MaxN: 4) and *Kyphosus cinerascens* (MaxN: 1) were only sighted in RUV, although not observed feeding. Overall, tropical species dominated the abundance of grazers (MaxN: 50 ± 6) and browsers (MaxN: 21 ± 5) in comparison to their temperate counterparts (MaxN: 29 ± 3.5 and 3.9 ± 0.8 respectively; GLMM, p<0.05, Table S4, Fig. 3c).
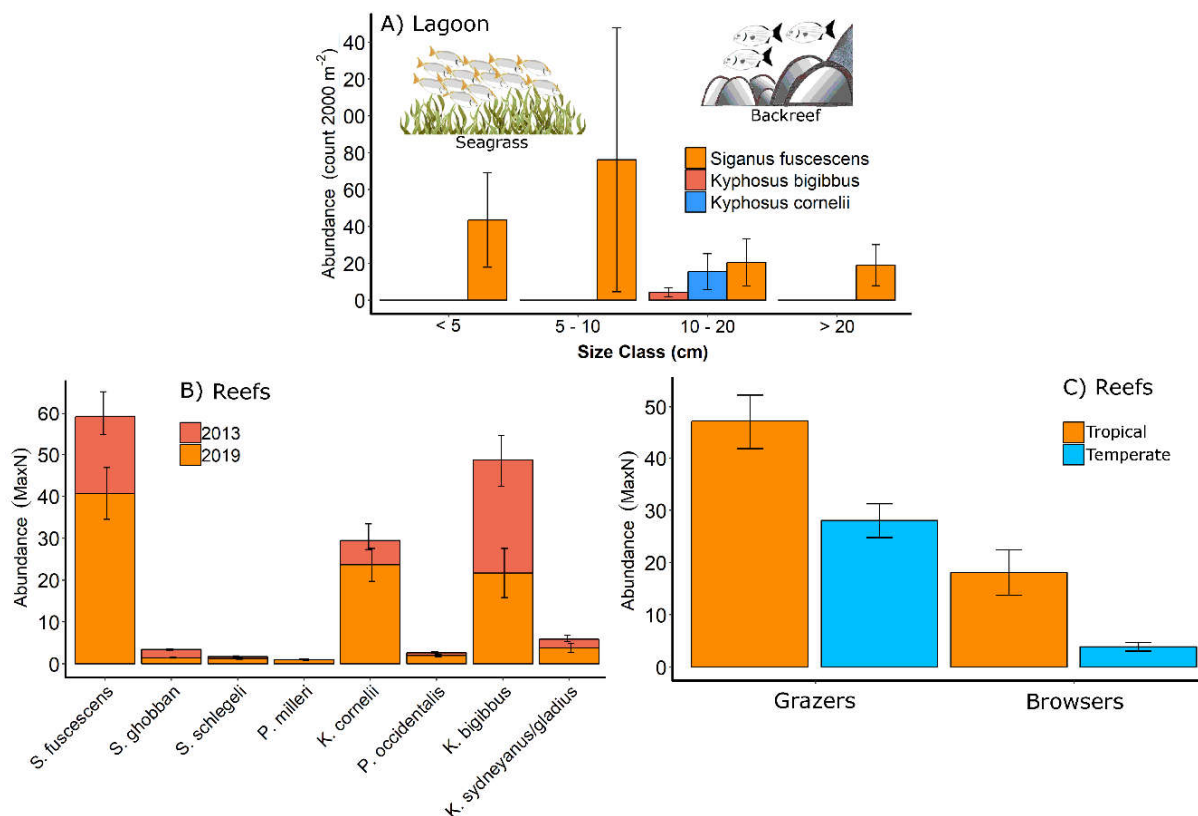
Figure 3. Abundance (mean ± se) of juvenile (fork length; <5-20 cm) and adult (>20 cm) herbivorous fish in the habitats of the lagoon (A), variation in the abundance of adult herbivorous fish from 2013 to 2019 (B) and comparison of current (2019) abundances of browsers and grazers of tropical and temperate climate affinity in reefs in Port Gregory, Western Australia (C). Juvenile *Siganus fuscescens* were found in seagrass meadows, while adults of this species and juvenile kyphosids were observed in the backreef.

Rates of Kelp Browsing and Turf Grazing

Transplanted kelps on exposed surfaces suffered high rates of herbivory, losing 80.5 ± 3.4 % of biomass on average, equivalent to 16.4 ± 1.6 g h^{-1}. In contrast, kelp individuals placed in crevices remained with 94 ± 1.2 % of their original biomass on average, with a maximum loss of 15% in one individual (GLMM, p<0.05, Table S5; Fig. 4a). Kelp browsing at individual (7.7 ± 3.6 bites h^{-1} *per capita*) and population level (308 ± 168 bites MaxN h^{-1}) was led by the tropical *K. bigibbus*, which in occasions were able to consume all lateral blades of kelp individuals in less than 5 minutes (Supporting Information Video 2). The only other species observed feeding on kelp was the temperate browser *K. sydneyanus/gladius* which consumed less in each feeding event (4.0 ± 1.3 bites h^{-1} *per capita*) and with less frequency, albeit not significantly lower bite rates at population level (43 ± 16 bites MaxN h^{-1}) than its tropical counterpart (GLMM, p>0.05; Table S5; Fig. 4b). Examination of bite marks in kelp blades after retrieval, indicated that only kyphosids consumed kelp (Fig. 4b).

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Tropical herbivores were the main consumers of turf seaweed (GLMM, $p<0.05$: Table S5). The rabbitfish *S. fuscescens* were the main grazers *per capita* (15.4 ± 4.3 bites h^{-1} ind^{-1}) and at population level (1260 ± 356 bites MaxN h^{-1}; Supporting Information Video 3), followed by the parrotfish *Scarus ghobban* (11.5 ± 2.1 bites h^{-1} ind^{-1}; 175 ± 34 bites MaxN h^{-1}), *Scarus schlegeli* (7.1 ± 4.3 bites h^{-1} ind^{-1}; 31 ± 17 bites MaxN h^{-1}), *K. biggibus* (0.5 ± 0.2 bites h^{-1} ind^{-1}; 34 ± 308 bites MaxN h^{-1}), and the damselfish *Abudefduf bengalensis* (2.0 ± 0.5 bites h^{-1} ind^{-1}; 14 ± 4 bites S-DOV h^{-1}) and *Pomacentrus milleri* (1.3 ± 0.5 bites h^{-1} ind^{-1}; 13 ± 5 bites S-DOV h^{-1}). Among the temperate species, the most important grazer was *K. cornelii* (8.4 ± 1.9 bites h^{-1} ind^{-1}; 245 ± 89 bites MaxN h^{-1}) and the damselfish *Parma occidentalis* (6.0 ± 1.3 bites h^{-1} ind^{-1}; 95 ± 22 bites S-DOV h^{-1}) (Fig. 4c). Individuals of *Arothron hispidus*, *Chaetodon lunula*, *Chelmonops curiosus*, *Cheilodactylus rubrolabiatus*, *Parupeneus spilurus*, *Plectorhinchus flavomaculatus, K. sydneyanus, Anampses geographicus, Coris auricularis, Choerodon rubescens* and the blennies *Cirripectes hutchinsi* and *Cirripectes alleni* were observed biting sporadically, accounting for 2% of total grazing rates.
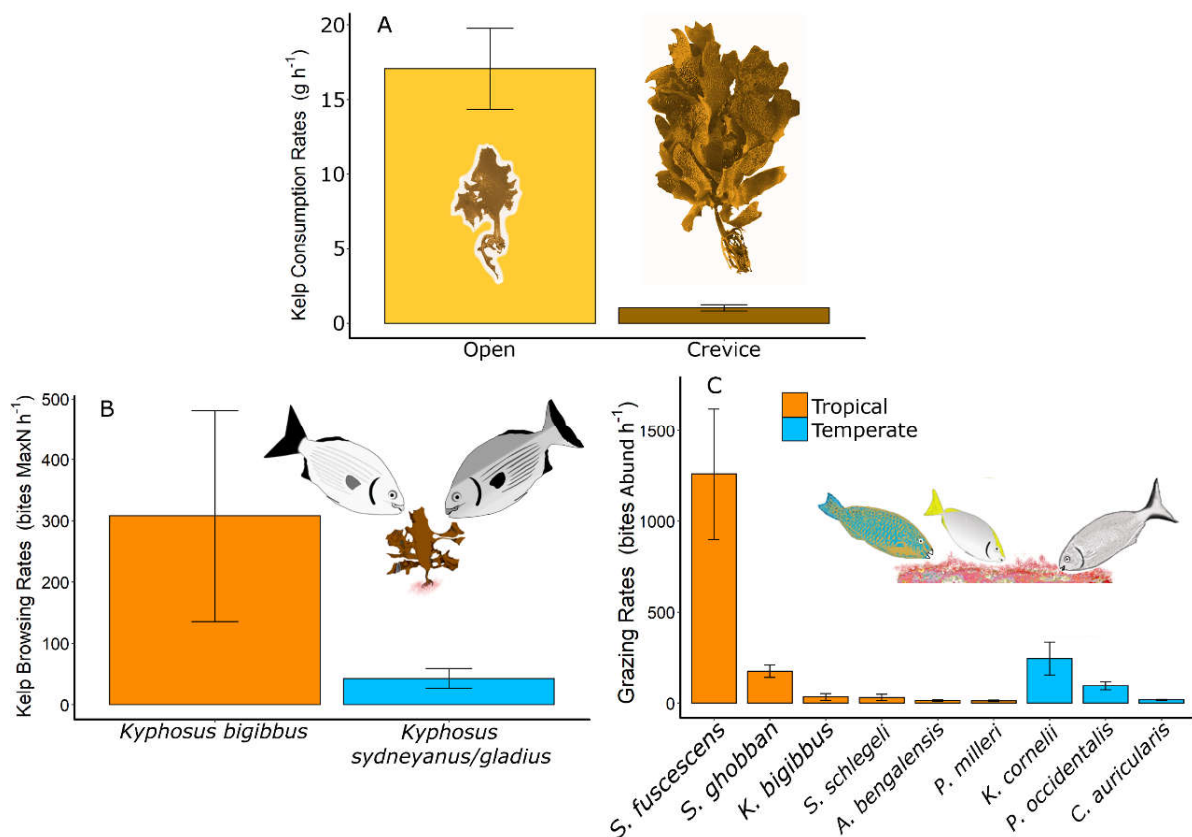
Figure 4. Consumption rates of kelp biomass in exposed surfaces versus crevices in temperate reefs (A) and rates of kelp browsing (B) and turf grazing scaled to population level (C) by temperate and tropical herbivorous fish species in Port Gregory, Western Australia. Abund: Abundance from S-DOV for Pomacentrids and MaxN for the rest of species.

5.5. Discussion

The surveyed reefs remained dominated by turf mats after 9 years of losing their kelp forest following the marine heatwave of 2011 (Wernberg *et al.* 2016). Populations of tropical herbivores are still present and there is evidence of long-term persistence from recruitment into lagoon habitats, maintaining high rates of browsing and grazing in open spaces of the reefs, constraining kelp individuals to reef crevices where they can shelter from herbivory (Fig. 5). Our results suggest that lagoon habitats are important for the demographic success of tropical herbivores expanding into temperate ecosystems. Canopy-forming seaweed and seagrass are important foraging and nursery habitats for many fish (Zarco-Perello & Enríquez 2019; Fulton *et al.* 2020). Several species of rabbitfish, including *Siganus fuscescens*, are strongly linked to tropical seagrass meadows, where they recruit in large numbers annually (Ambo-Rappe *et al.* 2013), sustaining commercial fisheries that harvest up to 170 tonnes per year in some places (Soliman & Yamaoka 2010). In the absence of seagrass, beds of *Sargassum* in lagoons have been found to shelter rabbitfish juveniles in tropical Australia (Evans *et al.* 2014). Likewise, several parrotfish species, including *Scarus ghobban*, recruit into tropical seagrass and seaweed meadows, with subsequent ontogenetic movements to adjacent reefs, transitioning between habitats during adulthood (Mellin, Kulbicki & Ponton 2007; Evans *et al.* 2014).
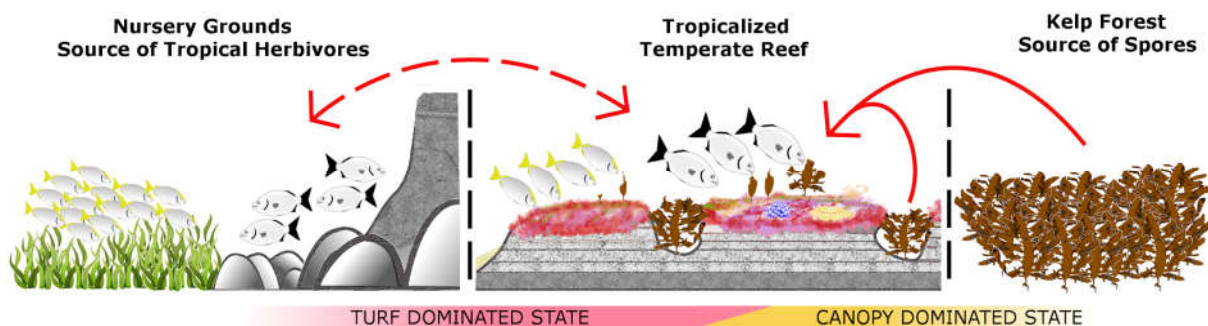
Figure 5. Conceptual model of the ecological mechanisms facilitating the persistence of canopy-free and the recovery of canopy-dominated states in tropicalized temperate reefs. Lagoonal systems serve as nursery grounds for tropical herbivores allowing them to persist at higher latitudes and suppress kelp recovery. Topographic refuges support the persistence of kelp by facilitating the settlement of kelp propagules from adjacent kelp populations and their development to reproductive maturity, where they could function as local sources of spores in the reef.

Knowledge of the recruitment of range-expanding herbivores in temperate ecosystems is limited; most of the information available relates to rabbitfish, with reports confirming the importance of seagrass and seaweed meadows as nursery grounds. The abundances of adult individuals of *S. fuscescens* remained high, surpassing the estimated abundances in 2013 and those of populations further south in western Australia (MaxN 25.8 ± 8.1; Zarco-Perello *et al.* 2019). This species forms spawning aggregations and their high abundances could be indicative of reproductive activities in our study area (Fox, Bellwood & Jennions 2015), similarly to the rabbitfish *Siganus luridus* and *Siganus rivulatus* invading the Mediterranean Sea (Azzurro *et al.* 2017), where schools of thousands of juveniles have been associated with seagrass (Kalogirou *et al.* 2010) and at a lesser extent with seaweed habitats (Bariche, Letourneur & Harmelin-Vivien 2004). *S. fuscescens* inhabiting temperate ecosystems of Japan can live up to 13 years (Katayama *et al.* 2009), spawning from 300,000 to 2.5 million of eggs per female each year (Hoque *et al.* 1999), forming aggregations of pairs which courtship consists of flank nibbling and swimming in circular motion (Hasse, Madraisau & Mcvey 1977). This courtship behaviour was observed on one occasion in the present study, providing the first record within temperate reef ecosystems to our knowledge. The abundance of juveniles we observed through roving surveys (MaxS 291) resemble that registered in the Ryukyu islands of Japan, where hundreds of individuals (MaxS 239) aggregate among seagrass meadows, suggesting that these populations are recruiting with similar order of magnitude than some subtropical environments (Nakamura & Tsuchiya 2008). In southern temperate reefs of western Australia (32°S), juvenile schools of *S. fuscescens* have been sporadically observed in seagrass but with lower abundances (MaxS 20-30; Zarco-Perello *et al.* 2019), while in Japan they have been registered among abundant kelp fronds (Beck *et al.* 2017).

We could only report the presence of parrotfish juveniles anecdotally and without species identification. The reproductive success of common parrotfish such as *S. ghobban* is open for further investigation in our study sites and at the leading edge of their current range, 400 km poleward in Rottnest Island (Zarco-Perello *et al.* 2020). Given that the appropriate habitat for parrotfish recruitment is available and species like *S. ghobban* live for up to 14 years (Grandcourt 2002; Ebisawa *et al.* 2016), some successful recruitment events are likely to occur during their lifetime in temperate reefs. Likewise, *Kyphosus bigibbus* in our study sites continue to have similar abundances than in 2013 after the marine heatwave (MaxN 156). These are lower than the abundances registered in tropical reefs in western Australia (MaxS 200 - 400) (Pillans *et al.* 2017) and temperate Japan (MaxS = 500 - 1000 individuals), where temperatures are as low as 12.6 °C during winter (Kadota *et al.* 2017). While no evidence of spawning or settlement of juveniles has been documented, *K. biggibus* has become more abundant in recent decades in Japan and can live up to 46 years (Ogino *et al.* 2020). The available

reports about the recruitment of other species of kyphosids indicate an association of juveniles with shallow reefs (Rimmer 1986; Moran & Clements 2002; Silvano & Güth 2006). This agrees with our findings of juvenile *K. biggibus* in the backreef, closer to the reef crest, suggesting that new individuals are replenishing the populations of this species, supporting their persistence in these tropicalized reefs.

Overall, our results suggest that these ecosystems still show clear signs of tropicalization 9 years after the 2011 heatwave. However, we only compared two points in time and the variations in abundance detected for some species may not represent trends of declines or increments in their populations, but natural seasonal or inter-annual oscillations. *S. fuscescens* and kyphosids seem to have relatively stable populations across seasons and years in temperate ecosystems in the absence of severe disturbances (Yatsuya, Kiyomoto & Yoshimura 2015; Zarco-Perello *et al.* 2019). Their successful recruitment in the lagoon, long life-spans and tolerance to low temperatures (Noda *et al.* 2016), indicates that their influence on kelp recovery and contributions to a positive feedback towards a turf dominated state will persist in the foreseeable future. However, for other species, such as pomacentrids, we might expect greater inter-annual variability. Tropical damselfishes have less tolerance to low temperatures (Zarco-Perello, Pratchett & Liao 2012) and are subject to high predation and interspecific competition for space and resources which can influence their abundances significantly across seasons (Doherty & Fowler 1994; Robertson 1996).

Patterns of change in abundances can be dependent on the methodologies being used, and is generally recommended to use a combination of surveying techniques to reduce biased results (Watson *et al.* 2010). Static video sampling (RUV) is generally considered to have greater power to detect changes in fish assemblages in space and time than S-DOV transects (Langlois *et al.* 2010). However, their efficacy is species-specific, in relation to particular fish behaviours (Zarco-Perello & Enríquez 2019). While S-DOV can be more adequate for bold site-attached species, RUV was better to detect schooling and rare species of ecological significance. For instance, the rabbitfish (*S. canaliculus*) responsible for 50% of *Sargassum* consumption in the Great Barrier Reef was recorded with RUV but not observed during visual census (Fox & Bellwood 2008), while during our surveys, the rare herbivores *Naso unicornis*, *Acanthurus grammoptilus* and *Kyphosus cinerascens* were only sighted with RUV, the latter representing its most southern record in western Australia.

Abundant tropical herbivores have maintained the general patterns of herbivory observed in 2013. Our video sampling showed high rates of primary consumption by tropical fish, from big schools of large (*K. bigibbus*), and medium-sized browsers and grazers (*S. fuscescens*) to small schools of medium-sized grazers (*S. ghobban* and *S. schlegeli*), small-sized detritivores (*A. geographicus*) and solitary

territorial (*A. bengalensis*, *P. milleri*) and cryptic grazers (*Cirripectes* spp). This is akin to tropicalized temperate reefs in Japan, where *K. bigibbus, S. fuscescens* and the parrotfish *Calotomus japonicus* have been linked with the deforestation of kelp forests by examination of wounds in defoliated kelps that matched bite marks of tropical herbivorous fish (Kiriyama *et al.* 1999; Kadota *et al.* 2017). However, the contribution of some temperate herbivores was important, especially *K. sydneyanus/gladius, K. cornelii* and *P. occidentalis*. Both *K. bigibbus* and *K. sydneyanus* have been documented removing large quantities of fucoid seaweed in subtropical regions (Downie *et al.* 2013; Michael *et al.* 2013). They can graze on small foliose seaweed, but select large brown algae when available in their habitats, such as *Sargassum* and kelp (Clements & Choat 1997; Salter *et al.* 2010; Yatsuya *et al.* 2015). Their consumption rates have a positive correlation with their school size (Michael *et al.* 2013), making environments with high MaxS experience significantly higher feeding intensities. We observed very high browsing rates by big schools (MaxS 50) of *K. bigibbus*, where kelp individuals were denuded of lateral blades in 5 minutes. Nonetheless, herbivory is likely to be higher than the rates calculated through diurnal static video, since tank experiments have shown that *K. bigibbus* can also feed continuously through the night (Noda *et al.* 2016), and field observations suggest that *K. sydneyanus* can feed more at dawn and dusk (Clements & Raubenheimer 2006), when our cameras were not recording.

Moreover, although we did not observe rabbitfish consuming kelp in our herbivory assays, rabbitfish are facultative herbivores that feed on seagrass, filamentous, foliose and canopy-forming seaweed (Zarco-Perello *et al.* 2020). For instance, the range-expanding rabbitfish in the Mediterranean Sea have shifted their diets completely from their original habitats in the Red Sea (Lundberg & Golani 1995; Bariche 2006), whereas *S. fuscescens* has become an important consumer of kelp and fucoids in temperate reefs of Japan (Nakayama 1999; kiriyama, Fujii & Fujita 2005) and Australia (Zarco-Perello *et al.* 2017, 2019). Consequently, it is likely that rabbitfish could contribute to kelp consumption in our study sites but we didn`t observe this due to the high consumption rates of kyphosids. This points out that we must take into account the behavioural plasticity of the species when assessing the strength of different herbivory functions in the ecosystems, distinguishing between (i) *potential herbivory*: the total capacity of the herbivorous community to perform each herbivory function under different environmental and biological conditions in the ecosystem and (ii) *effective herbivory*: primary consumption executed under current physical and biological conditions (Bellwood, Hughes & Hoey 2006).

Recovery of kelp populations depends on the recruitment of new individuals in deforested areas. To date no reports exist of kelp recovery after regime shifts to turf-dominated states through natural processes, even when the conditions that caused the perturbation have subsided (Filbee-Dexter &

Wernberg 2018). Kelp propagules are able to settle on turf and develop into sporophytes as epiphytes, and possibly endophytes, in filamentous red algae (Garbary *et al.* 1999; Bringloe *et al.* 2018); however, their mortality rates are high due to dislodgement, making the recovery process extremely slow (Feehan *et al.* 2019). Populations of kelp have been able to recover significantly only after turf carpets have been actively removed (Gorman & Connell 2009) and when artificial substrates free of sediment and turf have been provided (Terawaki *et al.* 2001) in combination with transplantations of mature kelp individuals that supply large amounts of zoospores and create intraspecific facilitation for recruitment (Layton *et al.* 2019). However, under high herbivory rates, such as tropicalized temperate reefs, the survival of any settlers is jeopardized, unless they develop in habitats inaccessible to herbivores (Lubchenco & Gaines 1981). We found that after nine years since the marine heatwave, kelp individuals are only present in topographic refuges, confirming our hypothesis that despite the return to pre-heatwave temperatures, herbivory rates by tropical herbivores remain high and still contribute to prevent the recolonization of open spaces by kelp forests. This agrees with the ecological refuge theory documented for several primary producers in land (Beschta 2005), freshwater (Bergey 2005) and some marine systems (Bennett *et al.* 2010; Brandl *et al.* 2014; Franco *et al.* 2015).

Refuges can be simulating the environment that canopy understories provide, promoting recruitment and survival (Steneck *et al.* 2002). In the absence of canopies, kelp can recruit into cavities in natural (Kirkman 1981) and artificial substrates (Terawaki *et al.* 2001). Thus, it is likely that crevices are acting as retainers of kelp spores, increasing their density and the probabilities of fertilization and development into sporophytes. The lower light conditions in shelters are likely to reduce their growth rate but in the long term this is outweighed by the protection from herbivory (Kirkman 1981). The kelp individuals we found ranged from stage 1 to stage 3, with some of them showing reproductive tissue, indicating local spores supply and recruitment in the reefs (Kirkman 1981). The origin of these kelp *pioneers* is unclear as simulations from other systems suggest that source and receptor ecosystems must be relatively close (1-3 km) to have a strong connectivity granting recruitment success (Gaylord *et al.* 2006). This suggests two possibilities, (i) that spores and drifting reproductive kelp individuals (as the one we found during our surveys) are transported by strong currents from afar, or (ii) that closer kelp populations might exist which have not been reported yet.

Our discovery of kelp individuals developing to reproductive sporophytes in topographic refuges is significant as this is the first sign of kelp resettlement on these reefs after the marine heatwave (Bennett *et al.* 2015). These habitats constitute refuges that could provide feedback towards a kelp dominated state (Sedell *et al.* 1990) by becoming sources of propagation to new areas once favourable environmental conditions are restored (Gorman & Connell 2009). Restoration of kelp forests is being attempted in multiple locations around the world (Morris *et al.* 2020), mainly through the

amelioration of disturbances and transplantation of great numbers of kelp individuals to establish interspecific feedbacks that promote self-maintenance and growth of the population in previously deforested areas (Layton *et al.* 2020). However, the impact of herbivory and its synergistic effect with warming is predicted to be increasingly important as temperatures rise and more tropical herbivorous species expand their ranges into temperate ecosystems (Vergés *et al.* 2014). Under a warming world, kelp reseeding efforts must be done in thermal refuges or with warm water-tolerant kelps (Layton *et al.* 2020; Coleman *et al.* 2020) in conjunction with strategies to reduce the impact of tropical herbivores wherever they are predicted to expand (Eger *et al.* 2020).

In the Mediteranean Sea, restoration efforts of habitat-forming macroalgae are threatened by high rates of herbivory by the local sparid fish *Sarpa salpa* (Gianni *et al.* 2018) and range-expanding rabbitfish (Azzurro *et al.* 2017), with increasing sightings of other important herbivores that could further increase consumption in the future, such as kyphosids (Mannino *et al.* 2015), scarids (Erguden *et al.* 2018) and acanthurids (Guidetti, Magnali & Navone 2015). In Japan, multiple efforts have been implemented to curb high rates of herbivory on kelp by tropical fish in transplantation experiments by setting up fences and barriers protecting seaweed from herbivores; however, such methods have proven to be expensive and complicated to implement and maintain at large spatial scales (Kuwahara 2015). Our results show that although protection by crevices was not complete, as many of the cryptic kelp individuals we found presented signs of pruning on the top of their lamina, this allowed individuals to survive up to reproductive maturity without human intervention. Transplantations into these habitats could thus be useful to create synergies that increase kelp recruitment. However, given the high herbivory rates, implementation of additional measures would be required to allow the successful propagation of kelp forests in exposed areas of the reefs (Kuwahara 2015).

The most effective strategy to reduce the impact of herbivores on seaweed has been population control. This has been well documented in temperate reefs that have suffered deforestations caused by sea urchins, where kelp has been able to recover after reductions in sea urchin abundance due to increases in predation, diseases, harvesting or culling of their populations, reducing herbivory rates and allowing kelp recruitment to resume (Ling 2008; Filbee-Dexter & Scheibling 2014). *K. biggibus* and *S. fuscescens* in temperate reefs of Nagazaki, Japan, have been caught with gill nets, with parallel efforts to increase its acceptance and value in local fish markets (Kuwahara 2015). Rabbitfish in the Mediterranean have become a common and well valued resource in several eastern countries (EastMed 2010; Cerim, Soykan & Gülşahin 2020). Similarly, in western Australia a small commercial fishery has been catching *S. fuscescens,* with diminishing landings along the years since 2012, indicating that continuous fishing could be effective to control their abundances (Lenanton *et al.* 2017). Parrotfish are not commercially fished yet in temperate regions but have great potential to

expand and become important fishery resources, as in tropical and subtropical regions (Ebisawa *et al.* 2016).

The tropicalization of temperate reefs is expected to keep advancing in the future, so it is of paramount importance to understand the interplay of processes that drive and enforce regime shifts to canopy-free states and those that help resist or reverse the ecosystems to kelp forests. We highlight the importance of considering the role of nursery grounds into the tropicalization model, indicating that lagoon habitats, such as seagrass meadows and backreef environments, are key for the settlement and subsistence of some the most important range-shifting herbivores. On the other hand, this work expands our current knowledge about the importance of refugia for the subsistence of kelp individuals subject to high rates of herbivory caused by the tropicalization of the ecosystem. Our herbivory assays in open and protected habitats, clearly indicated how tropical herbivores are contributing to the suppression of kelp recovery. The discovery of natural kelp populations surviving up to sexual maturity only in topographical shelters reinforces these findings, indicating that shelters could function as habitats from where propagules could recolonize open spaces under favourable conditions. However, our data suggest that under highly elevated consumer pressure, kelp recovery would be unlikely without the concurrent implementation of measures that reduce the abundance of herbivores (*e.g.* fishing and/or predator management) and the provision of turf-free substratum. As global warming and tropicalization of herbivory increases, these factors will become more important to consider across more regions of the world for prevention and restoration.

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Authors' Contributions

S.Z.-P. conceived the study; S.Z.-P, NB and TW acquired the funding; S.Z.-P, NB and SB collected the field data; S.Z.-P. analyzed the data. S.Z.-P. wrote the paper and all authors contributed to drafting the manuscript and gave final approval for publication.

Data availability Statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9ghx3ffgj (Zarco-Perello et al., 2021).

5.6. References

Ambo-Rappe, R., Nessa, M.N., Latuconsina, H. & Lajus, D.L. (2013) Relationship between the tropical seagrass bed characteristics and the structure of the associated fish community. *Open Journal of Ecology*, **03**, 331–342.

Andrew, N.L. & Jones, G.P. (1990) Patch formation by herbivorous fish in a temperate Australian kelp forest. *Oecologia*, **85**, 57–68.

Azzurro, E., Franzitta, G., Milazzo, M., Bariche, M. & Fanelli, E. (2017) Abundance patterns at the invasion front: the case of Siganus luridus in Linosa (Strait of Sicily, Central Mediterranean Sea). *Marine and Freshwater Research*, **68**, 697.

Bariche, M. (2006) Diet of the Lessepsian fishes, Siganus rivulatus and S. luridus (Siganidae) in the eastern Mediterranean: A bibliographic analysis. *Cybium*, **30**, 41–49.

Bariche, M., Letourneur, Y. & Harmelin-Vivien, M. (2004) Temporal fluctuations and settlement patterns of native and lessepsian herbivorous fishes on the lebanese coast (eastern mediterranean). *Environmental biology of fishes*, **70**, 81–90.

Beck, H.J., Feary, D.A., Figueira, W.F. & Booth, D.J. (2014) Assessing range shifts of tropical reef fishes: a comparison of belt transect and roaming underwater visual census methods. *Bulletin of Marine Science*, **90**, 705–721.

Beck, H.J., Feary, D.A., Nakamura, Y. & Booth, D.J. (2017) Temperate macroalgae impacts tropical fish recruitment at forefronts of range expansion. *Coral Reefs*, **36**, 639–651.

Bellwood, D.R., Hughes, T.P. & Hoey, A.S. (2006) Sleeping functional group drives coral-reef recovery. *Current Biology*, **16**, 2434–2439.

Bennett, S., Vergés, A. & Bellwood, D.R. (2010) Branching coral as a macroalgal refuge in a marginal coral reef system. *Coral reefs (Online)*, **29**, 471–480.

Bennett, S., Wernberg, T., Connell, S.D., Hobday, A.J., Johnson, C.R. & Poloczanska, E.S. (2016) The "Great Southern Reef": social, ecological and economic value of Australia's neglected kelp forests. *Marine and Freshwater Research*, **67**, 47.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J. & Saunders, B.J. (2015) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters*, **18**, 714–723.

Bergey, E.A. (2005) How protective are refuges? Quantifying algal protection in rock crevices. *Freshwater Biol*, **50**, 1163–1177.

Beschta, R.L. (2005) Reduced cottonwood recruitment following extirpation of wolves in yellowstone's northern range. *Ecology*, **86**, 391–403.

Blamey, L.K. & Bolton, J.J. (2017) The economic value of South African kelp forests and temperate reefs: Past, present and future. *Journal of Marine Systems*.

Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I.H., Winter, M., Bjorkman, A.D., Bowler, D.E., Byrnes, J.E.K., Gonzalez, A., Hines, J., Isbell, F., Jones, H.P., Navarro, L.M., Thompson, P.L., Vellend, M., Waldock, C. & Dornelas, M. (2019) The geography of biodiversity change in marine and terrestrial assemblages. *Science*, **366**, 339–345.

Brandl, S.J., Hoey, A.S. & Bellwood, D.R. (2014) Micro-topography mediates interactions between corals, algae, and herbivorous fishes on coral reefs. *Coral Reefs*, **33**, 421–430.

Breen, P.A. & Mann, K.H. (1976) Destructive grazing of kelp by sea urchins in eastern canada. *Journal of the Fisheries Research Board of Canada*, **33**, 1278–1283.

Bringloe, T.T., Bartlett, C.A.B., Bergeron, E.S., Cripps, K.S.A., Daigle, N.J., Gallagher, P.O., Gallant, A.D., Giberson, R.O.J., Greenough, S.J., Lamb, J.M., Leonard, T.W., MacKay, J.A., McKenzie, A.D., Persaud, S.M., Sheng, T., Mills, A.M.E.S., Moore, T.E. & Saunders, G.W. (2018) Detecting *Alaria esculenta* and *Laminaria digitata* (Laminariales, Phaeophyceae) gametophytes in red algae, with consideration of distribution patterns in the intertidal zone. *Phycologia*, **57**, 1–8.

Brooks, M., E., Kristensen, K., Benthem, K., J.,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M. & Bolker, B., M. (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R journal*, **9**, 378.

Cerim, H., Soykan, O. & Gülşahin, A. (2020) Mortality and exploitation of marbled spinefoot, Siganus rivulatus (Actinopterygii: Perciformes: Siganidae), from southern Aegean Sea small-scale fishery. *Acta Ichthyologica Et Piscatoria*, **50**, 183–190.

Clements, K.D. & Choat, J.H. (1997) Comparison of herbivory in the closely-related marine fish genera Girella and Kyphosus. *Marine biology*, **127**, 579–586.

Clements, K.D. & Raubenheimer, D. (2006) Feeding and nutrition. *The physiology of fishes*, 3rd ed (eds D.H. Evans & J.B. Claiborne), pp. 47–82. Taylor & Francis, Boca Raton.

Coleman, M.A., Wood, G., Filbee-Dexter, K., Minne, A.J.P., Goold, H.D., Vergés, A., Marzinelli, E.M., Steinberg, P.D. & Wernberg, T. (2020) Restore or redefine: future trajectories for restoration. *Frontiers in Marine Science*, **7**.

Connell, S.D., Foster, M.S. & Airoldi, L. (2014) What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series*, **495**, 299–307.

Doherty, P. & Fowler, A. (1994) Demographic Consequences of Variable Recruitment to Coral Reef Fish Populations: A Congeneric Comparison of Two Damselfishes. *Bulletin of Marine Science*, **54**, 297–313.

Downie, R.A., Babcock, R.C., Thomson, D.P. & Vanderklift, M.A. (2013) Density of herbivorous fish and intensity of herbivory are influenced by proximity to coral reefs. *Marine Ecology Progress Series*, **482**, 217–225.

EastMed. (2010) *Report of the Sub-Regional Technical meeting on the Lessepsian migration and its impact on Eastern Mediterranean fishery*. FAO– EastMed Project, Nicosia, Cyprus.

Ebisawa, A., Kanashiro, K., Ohta, I., Uehara, M. & Nakamura, H. (2016) Changes of group construction accompanying with growth and maturity in blue-barred parrotfish (Scarus ghobban), and influences of the fishing targeting the immature group to the stock. *Regional Studies in Marine Science*, **7**, 32–42.

Eger, A.M., Marzinelli, E., Gribben, P., Johnson, C.R., Layton, C., Steinberg, P.D., Wood, G., Silliman, B.R. & Vergés, A. (2020) Playing to the Positives: Using Synergies to Enhance Kelp Forest Restoration. *Frontiers in Marine Science*.

Erguden, D., Bayhan, Y.K., Alagöz Erguden, S. & Altun, A. (2018) Range extension of blue-barred parrotfish Scarus ghobban Forsskal, 1775 along the Mediterranean Coast of Turkey. *Acta Biologica Turcica*, **31**, 82–85.

Evans, R.D., Wilson, S.K., Field, S.N. & Moore, J.A.Y. (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. *Marine biology*, **161**, 599–607.

Feehan, C.J., Grace, S.P. & Narvaez, C.A. (2019) Ecological feedbacks stabilize a turf-dominated ecosystem at the southern extent of kelp forests in the Northwest Atlantic. *Scientific Reports*, **9**, 7078.

Feng, M., McPhaden, M.J., Xie, S.-P. & Hafner, J. (2013) La Niña forces unprecedented Leeuwin Current warming in 2011. *Scientific Reports*, **3**, 1277.

Filbee-Dexter, K. & Scheibling, R.E. (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series*, **495**, 1–25.

Filbee-Dexter, K. & Wernberg, T. (2018) Rise of turfs: A new battlefront for globally declining kelp forests. *Bioscience*.

Fox, R.J. & Bellwood, D.R. (2008) Remote video bioassays reveal the potential feeding impact of the rabbitfish Siganus canaliculatus (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs*, **27**, 605–615.

Fox, R.J., Bellwood, D.R. & Jennions, M.D. (2015) Why pair? Evidence of aggregative mating in a socially monogamous marine fish (Siganus doliatus, Siganidae). *Royal Society Open Science*, **2**, 150252.

Fox, R.J., Sunderland, T.L., Hoey, A.S. & Bellwood, D.R. (2009) Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. *Marine Ecology Progress Series*, **385**, 261–269.

Franco, J.N., Wernberg, T., Bertocci, I., Duarte, P., Jacinto, D., Vasco-Rodrigues, N. & Tuya, F. (2015) Herbivory drives kelp recruits into "hiding" in a warm ocean climate. *Marine Ecology Progress Series*, **536**, 1–9.

Froese, R. & Pauly, D. (2018) FishBase. URL http://www.fishbase.org [accessed 4 June 2018]

Fulton, C.J., Berkström, C., Wilson, S.K., Abesamis, R.A., Bradley, M., Åkerlund, C., Barrett, L.T., Bucol, A.A., Chacin, D.H., Chong-Seng, K.M., Coker, D.J., Depczynski, M., Eggertsen, L., Eggertsen, M., Ellis, D., Evans, R.D., Graham, N.A.J., Hoey, A.S., Holmes, T.H., Kulbicki, M., Leung, P.T.Y., Lam, P.K.S., Lier, J., Matis, P.A., Noble, M.M., Pérez-Matus, A., Piggott, C., Radford, B.T., Tano, S. & Tinkler, P. (2020) Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes. *Fish and Fisheries*.

Garbary, D.J., Kim, K.Y., Klinger, T. & Duggins, D. (1999) Red algae as hosts for endophytic kelp gametophytes. *Marine biology*, **135**, 35–40.

Gaylord, B., Reed, D.C., Raimondi, P.T. & Washburn, L. (2006) Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. *Ecological Monographs*, **76**, 481–502.

Gianni, F., Bartolini, F., Airoldi, L. & Mangialajo, L. (2018) Reduction of herbivorous fish pressure can facilitate focal algal species forestation on artificial structures. *Marine Environmental Research*, **138**, 102–109.

Goetze, J.S., Bond, T., McLean, D.L., Saunders, B.J., Langlois, T.J., Lindfield, S., Fullwood, L.A.F., Driessen, D., Shedrawi, G. & Harvey, E.S. (2019) A field and video analysis guide for diver operated stereo-video. *Methods in ecology and evolution / British Ecological Society*, **10**, 1083–1090.

Gorman, D. & Connell, S.D. (2009) Recovering subtidal forests in human-dominated landscapes. *Journal of Applied Ecology*, **46**, 1258–1265.

Grandcourt, E.M. (2002) Demographic characteristics of a selection of exploited reef fish from the Seychelles: preliminary study. *Marine and Freshwater Research*.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.

Guidetti, P., Magnali, L. & Navone, A. (2015) First record of the acanthurid fish Zebrasoma xanthurum (Blyth, 1852) in the Mediterranean Sea, with some considerations on the risk associated with aquarium trade. *Mediterranean Marine Science*, **17**, 147–151.

Hartig, F. (2020) *DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models*. Computer software, R package.

Hasse, J.J., Madraisau, B.B. & Mcvey, J.P. (1977) Some aspects of the life history of *Siganus canaliculatus* (Park) (Pisces: Siganidae) in Palau. *Micronesica*, **13**, 297–312.

Hoey, A.S. & Bellwood, D.R. (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology Letters*, **14**, 267–273.

Hoque, M.M., Takemura, A., Matsuyama, M., Matsuura, S. & Takano, K. (1999) Lunar spawning in Siganus canaliculatus. *Journal of Fish Biology*, **55**, 1213–1222.

Kadota, T., Kiyomoto, S., Fukuda, H. & Yoshimura, T. (2017) Temporal patterns of aggregation formation around wave-dissipating blocks in the grey sea chub *Kyphosus bigibbus*. *NIPPON SUISAN GAKKAISHI*, **83**, 74–76.

Kalogirou, S., Corsini-Foka, M., Sioulas, A., Wennhage, H. & Pihl, L. (2010) Diversity, structure and function of fish assemblages associated with Posidonia oceanica beds in an area of the eastern Mediterranean Sea and the role of non-indigenous species. *Journal of Fish Biology*, **77**, 2338–2357.

Katayama, S., Akiyama, S., Naganuma, M. & Shibata, R. (2009) Age and growth of rabbitfish Siganus fuscescens in Tateyama Bay, Japan. *Aquaculture …*, **57**, 417–422.

kiriyama, T., Fujii, A. & Fujita, Y. (2005) Feeding and Characteristic Bite Marks on Sargassum fusiforme by Several Herbivorous Fishes. *Aquaculture Science*, **53**, 355–365.

Kiriyama, T., Fujii, A., Yoshimura, T., Kiyomoto, S. & Yotsui, T. (1999) Leaf-lost Phenomenon Observed on Three Laminariaceous Species in Coastal Waters around Nagasaki Prefecture in Autumn 1998. *Aquaculture Science*, **47**, 319–323.

Kirkman, H. (1981) The first year in the life history and the survival of the juvenile marine macrophyte, Ecklonia radiata (Turn.) J. Agardh. *Journal of Experimental Marine Biology and Ecology*, **55**, 243–254.

Krumhansl, K.A., Okamoto, D.K., Rassweiler, A., Novak, M., Bolton, J.J., Cavanaugh, K.C., Connell, S.D., Johnson, C.R., Konar, B., Ling, S.D., Micheli, F., Norderhaug, K.M., Pérez-Matus, A., Sousa-Pinto, I., Reed, D.C., Salomon, A.K., Shears, N.T., Wernberg, T., Anderson, R.J., Barrett, N.S., Buschmann, A.H., Carr, M.H., Caselle, J.E., Derrien-Courtel, S., Edgar, G.J., Edwards, M., Estes, J.A., Goodwin, C., Kenner, M.C., Kushner, D.J., Moy, F.E., Nunn, J., Steneck, R.S., Vásquez, J., Watson, J., Witman, J.D. & Byrnes, J.E.K. (2016) Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 13785–13790.

Krumhansl, K.A. & Scheibling, R.E. (2012) Production and fate of kelp detritus. *Marine Ecology Progress Series*, **467**, 281–302.

Kuwahara, H. (2015) The Evaluation of Current Status for Grazing Control Techniques of Herbivorous Fish. *Fisheries Engineering*, **51**, 253–257.

Langlois, T.J., Harvey, E.S., Fitzpatrick, B., Meeuwig, J.J., Shedrawi, G. & Watson, D.L. (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. *Aquatic Biology*, **9**, 155–168.

Layton, C., Coleman, M.A., Marzinelli, E.M., Steinberg, P.D., Swearer, S.E., Vergés, A., Wernberg, T. & Johnson, C.R. (2020) Kelp forest restoration in australia. *Frontiers in Marine Science*, **7**.

Layton, C., Shelamoff, V., Cameron, M.J., Tatsumi, M., Wright, J.T. & Johnson, C.R. (2019) Resilience and stability of kelp forests: The importance of patch dynamics and environment-engineer feedbacks. *Plos One*, **14**, e0210220.

Lenanton, R.C.J., Dowling, C.E., Smith, K.A., Fairclough, D.V. & Jackson, G. (2017) Potential influence of a marine heatwave on range extensions of tropical fishes in the eastern Indian Ocean—Invaluable contributions from amateur observers. *Regional Studies in Marine Science*, **13**, 19–31.

Ling, S.D. (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia*, **156**, 883–894.

Longo, G.O., Hay, M.E., Ferreira, C.E.L. & Floeter, S.R. (2018) Trophic interactions across 61 degrees of latitude in the Western Atlantic. *Global Ecology and Biogeography*.

Lubchenco, J. & Gaines, S.D. (1981) A Unified Approach to Marine Plant-Herbivore Interactions. I. Populations and Communities. *Annual review of ecology and systematics*, **12**, 405–437.

Lundberg, B. & Golani, D. (1995) Diet Adaptations of Lessepsian Migrant Rabbitfishes, Siganus luridus and S. rivulatus, to the Algal Resources of the Mediterranean Coast of Israel. *Marine Ecology*, **16**, 73–89.

Mann, K.H. (2000) *Ecology of coastal waters: with implications for management*, 2nd ed. John Wiley & Sons, Hoboken, NJ.

Mannino, A.M., Balistreri, P., Iaciofano, D., Galil, B.S. & Brutto, S.L. (2015) An additional record of Kyphosus vaigiensis (Quoy & Gaimard, 1825) (Osteichthyes, Kyphosidae) from Sicily clarifies the confused situation of the Mediterranean kyphosids. *Zootaxa*, **3963**, 45–54.

Mellin, C., Kulbicki, M. & Ponton, D. (2007) Seasonal and ontogenetic patterns of habitat use in coral reef fish juveniles. *Estuarine, coastal and shelf science*, **75**, 481–491.

Michael, P.J., Hyndes, G.A., Vanderklift, M.A. & Vergés, A. (2013) Identity and behaviour of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef. *Marine Ecology Progress Series*, **482**, 227–240.

Moran, D. & Clements, K.D. (2002) Diet and endogenous carbohydrases in the temperate marine herbivorous fish Kyphosus sydneyanus. *Journal of Fish Biology*, **60**, 1190–1203.

Morris, R.L., Hale, R., Strain, E.M.A., Reeves, S.E., Vergés, A., Marzinelli, E.M., Layton, C., Shelamoff, V., Graham, T.D.J., Chevalier, M. & Swearer, S.E. (2020) Key Principles for Managing Recovery of Kelp Forests through Restoration. *Bioscience*.

Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., Van't Hof, T. & den Hartog, C. (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science*, **51**, 31–44.

Nakamura, Y. & Tsuchiya, M. (2008) Spatial and temporal patterns of seagrass habitat use by fishes at the Ryukyu Islands, Japan. *Estuarine, Coastal and Shelf Science*, **76**, 345–356.

Nakayama, Y. (1999) Grazing of the brown alga Ecklonia cava by three herbivorous fishes on the coast of Nakagi, South Izu, central Japan (tran S Arai). *Japanese Journal of Phycology*, 105–112.

Noda, M., Kawano, M., Okamoto, K. & Murase, N. (2016) Estimation of' ' daily feeding rate and diel feeding rhythm of herbivorous fish Kyphosus bigibbus in captivity . *Journal of National Fisheries University*, **64**, 219–225.

O'Brien, J.M. & Scheibling, R.E. (2016) Nipped in the bud: mesograzer feeding preference contributes to kelp decline. *Ecology*, **97**, 1873–1886.

O'Brien, J.M., Scheibling, R.E. & Krumhansl, K.A. (2015) Positive feedback between large-scale disturbance and density-dependent grazing decreases resilience of a kelp bed ecosystem. *Marine Ecology Progress Series*, **522**, 1–13.

Ogino, Y., Furumitsu, K., Kiriyama, T. & Yamaguchi, A. (2020) Using optimised otolith sectioning to determine the age, growth and age at sexual maturity of the herbivorous fish Kyphosus bigibbus: with a comparison to using scales. *Marine and Freshwater Research*, **71**, 855.

Pillans, R.D., Babcock, R.C., Thomson, D.P., Haywood, M.D.E., Downie, R.A., Vanderklift, M.A. & Rochester, W.A. (2017) Habitat effects on home range and schooling behaviour in a herbivorous fish (Kyphosus bigibbus) revealed by acoustic tracking. *Marine and Freshwater Research*, **68**, 1454.

Puk, L.D., Marshell, A., Dwyer, J., Evensen, N.R. & Mumby, P.J. (2020) Refuge-dependent herbivory controls a key macroalga on coral reefs. *Coral Reefs*, **39**, 953–965.

Rimmer, D.W. (1986) Changes in diet and the development of microbial digestion in juvenile buffalo bream, Kyphosus cornelii. *Marine biology*, **92**, 443–448.

Robertson, D.R. (1996) Interspecific competition controls abundance and habitat use of territorial caribbean damselfishes. *Ecology*, **77**, 885–899.

Salter, Z.T., Harvey, E.S., Kendrick, G.A. & Murray, K. (2010) The effect of kelp bed disturbance on the abundance and feeding behaviour of fishes on high-relief reefs. *Marine and freshwater behaviour and physiology*, **43**, 109–125.

Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A. & Hawkins, C.P. (1990) Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. *Environmental Management*, **14**, 711–724.

Silvano, R.A.M. & Güth, A.Z. (2006) Diet and feeding behavior of Kyphosus spp. (Kyphosidae) in a Brazilian subtropical reef. *Brazilian Archives of Biology and Technology*, **49**, 623–629.

Soliman, V.S. & Yamaoka, K. (2010) Assessment of the fishery of siganid juveniles caught by bagnet in Lagonoy Gulf, Southeastern Luzon, Philippines. *Journal of Applied Ichthyology*, **26**, 561–567.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental conservation*, **29**.

Terawaki, T., Hasegawa, H., Arai, S. & Ohno, M. (2001) Management-free techniques for restoration of Eisenia and Ecklonia beds along the central Pacific coast of Japan. *Springer Science and Business Media LLC*, **13**, 13–17.

Vásquez, J.A., Zuñiga, S., Tala, F., Piaget, N., Rodríguez, D.C. & Vega, J.M.A. (2014) Economic valuation of kelp forests in northern Chile: values of goods and services of the ecosystem. *Journal of applied phycology*, **26**, 1081–1088.

Vergés, A., Doropoulos, C., Malcolm, H.A., Skye, M., Garcia-Pizá, M., Marzinelli, E.M., Campbell, A.H., Ballesteros, E., Hoey, A.S., Vila-Concejo, A., Bozec, Y.-M. & Steinberg, P.D. (2016) Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 13791–13796.

Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M.A., Wernberg, T., Ainsworth, T. & Steinberg, P.D. (2019) Tropicalisation of temperate reefs: Implications for ecosystem functions and management actions. *Functional ecology*, **33**, 1000–1013.

Vergés, A., Steinberg, P.D., Hay, M.E., Poore, A.G.B., Campbell, A.H., Ballesteros, E., Heck, K.L., Booth, D.J., Coleman, M.A., Feary, D.A., Figueira, W., Langlois, T., Marzinelli, E.M., Mizerek, T., Mumby, P.J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A.S., Smale, D.A., Tomas, F., Wernberg, T.

& Wilson, S.K. (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings. Biological Sciences / the Royal Society*, **281**, 20140846.

Watson, D.L., Harvey, E.S., Fitzpatrick, B.M., Langlois, T.J. & Shedrawi, G. (2010) Assessing reef fish assemblage structure: how do different stereo-video techniques compare? *Marine biology*, **157**, 1237–1250.

Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C.J., Hovey, R.K., Harvey, E.S., Holmes, T.H., Kendrick, G.A., Radford, B., Santana-Garcon, J., Saunders, B.J., Smale, D.A., Thomsen, M.S., Tuckett, C.A., Tuya, F., Vanderklift, M.A. & Wilson, S. (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science*, **353**, 169–172.

Wernberg, T., Krumhansl, K., Filbee-Dexter, K. & Pedersen, M.F. (2019) Status and trends for the world's kelp forests. *World seas: an environmental evaluation* pp. 57–78. Elsevier.

Yatsuya, K., Kiyomoto, S. & Yoshimura, T. (2015) Seasonal changes in dietary composition of the herbivorous fish Kyphosus bigibbus in southwestern Japan. *Fisheries science : FS*, **81**, 1025–1033.

Zarco-Perello, S. & Enríquez, S. (2019) Remote underwater video reveals higher fish diversity and abundance in seagrass meadows, and habitat differences in trophic interactions. *Scientific Reports*, **9**, 6596.

Zarco-Perello, S., Langlois, T.J., Holmes, T., Vanderklift, M.A. & Wernberg, T. (2019) Overwintering tropical herbivores accelerate detritus production on temperate reefs. *Proceedings. Biological Sciences / the Royal Society*, **286**, 20192046.

Zarco-Perello, S., Pratchett, M. & Liao, V. (2012) Temperature-growth performance curves for a coral reef fish, *Acanthochromis polyacanthus*. *Galaxea, Journal of Coral Reef Studies*, **14**, 97–103.

Zarco-Perello, S., Wernberg, T., Langlois, T.J. & Vanderklift, M.A. (2017) Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports*, **7**, 820.

Zarco-Perello, S., Carroll, G., Vanderklift, M., Holmes, T., Langlois, T.J. & Wernberg, T. (2020) Range-extending tropical herbivores increase diversity, intensity and extent of herbivory functions in temperate marine ecosystems. *Functional ecology*.

Zarco-Perello, S., Bosch, N., & Wernberg, T. (2021) Data from: Persistence of tropical herbivores in temperate reefs constrain kelp resilience to cryptic habitats. Dryad Digital Repository. https://doi.org/10.5061/dryad.9ghx3ffgj

5.7. Supplementary Information

Table S1. Estimated sizes (fork length; cm) from stereo-dive operated videos (S-DOV; n=8 per reef), relative sizes among herbivorous fish species, and maximum abundances estimated from remote underwater video (MaxN) and S-DOV (sum of counts in all transects; Max-DOV).

Species	Estimated Size	Relative Size	Reef1 MaxN	Reef1 Max-DOV	Reef2 MaxN	Reef2 Max-DOV
Abudefduf bengalensis	17	0.42	9	10	13	6
Anampses geographicus	22	0.55	1	0	2	0
Chaetodon lunula	22	0.55	2	0	2	2
Cheilodactylus rubrolabiatus	34	0.85	1	1	1	0
Chelmonops curiosus	18	0.45	2	1	0	0
Choerodon rubescens (juvenile)	18	0.45	1	3	1	1
Coris auricularis	22	0.55	9	9	8	7
Heniochus acuminatus	22	0.55	1	0	0	0
Kyphosus cornelii	33	0.82	80	50	67	25
Kyphosus sydneyanus/gladius	40	1	25	39	30	0
Kyphosus bigibbus	40	1	46	0	150	0
Parma occidentalis	17	0.42	13	21	14	12
Parupeneus spilurus	16	0.4	6	3	5	4
Plectorhinchus flavomaculatus	38	0.95	4	0	6	1
Pomacentrus milleri	9	0.22	8	8	8	10
Scarus ghobban	30	0.75	6	19	4	11
Scarus schlegeli	30	0.75	4	0	5	0
Siganus fuscescens	27	0.67	103	0	140	0

Table S2. Abundance (MaxN) of tropical herbivorous fish species in 2013 and 2019 in the tropicalized temperate reefs of Port Gregory, Western Australia.

Family	Species	2013 (N= 35)		2019 (N=39)	
		MaxN mean ± SE	MaxN	MaxN mean ± SE	MaxN
Kyphosidae	*Kyphosus bigibbus*	27 ± 6.33	156	21.7 ± 5.9	150
	Kyphosus cornelii	5.83 ± 2.13	74	23.64 ± 3.94	80
	Kyphosus sydneyanus/gladius	2.1 ± 0.5	16	3.8 ± 1.06	30
	Kyphosus cinerascens	0	0	0.025 ± 0.025	1
Siganidae	*Siganus fuscescens*	18.31 ± 4.24	112	40.7 ± 5.52	140
Labridae	*Scarus ghobban*	1.94 ± 0.16	5	1.48 ± 0.15	3
	Scarus schlegeli	0.43 ± 0.14	3	1.28 ± 0.2	5
Acanthuridae	*Acanthurus grammoptilus*	0.057 ± 0.05	2	0.025 ± 0.025	1
	Naso unicornis	0.03 ± 0.03	1	1.18 ± 0.1	4
		DOV (N=16) mean ± SE	MaxN mean ± SE	DOV (N=16) mean ± SE	MaxN mean ± SE
Pomacentridae	*Abudefduf bengalensis*	2.8 ± 0.8	0.88 ± 0.32	1.0 ± 0.27	1.2 ± 0.12
	Pomacentrus milleri	2.9 ± 0.7	0.62 ± 0.11	1.1 ± 0.41	2 ± 0.24
	Parma occidentalis	1.8 ± 0.5	0.06 ± 0.04	2.1 ± 0.52	0.97 ± 0.2

Table S3. Results of Generalized linear mixed models (Likelihood Radio Tests for glmmTMB) for differences in fish abundance of herbivorous species between 2013 and 2019 in Port Gregory, Western Australia. * identify statistically significant differences.

Roving schooling species based on MaxN	Site attached species based on DOVs

Siganus fuscescens
`S. fuscescens ~ Year + (1|Site) + (1|Date). nbinom2`
 	
`        Df    AIC    LRT    Pr(>Chi)`
`Year   1  658.96  9.1297 0.002515 **`
	Abudefduf bengalensis
	`A.bengalensis ~ Year + (1|Site). Nbinom2`
	
	`        Df    AIC    LRT    Pr(>Chi)`
	`Year   1  124.91  5.4774  0.01926 *`

Kyphosus biggibus
`K.bigibbus ~ Year + (1|Site) + (1|Date). nbinom2`
 	
`         Df    AIC    LRT    Pr(>Chi)`
`Year   1   552.80 0.34784   0.5553`
	Pomacentrus milleri
	`P.milleri ~ Year + (1|Site). Nbinom1`
	
	`         Df    AIC    LRT    Pr(>Chi)`
	`Year   1   127.81 4.7871  0.02867 *`

Kyphosus cornelii
`K.cornelii ~ Year + (1|Site) + (1|Date). nbinom2`
 	
`        Df    AIC    LRT    Pr(>Chi)`
`Year   1   530.25 5.4183   0.01993 *`
	Parma occidentalis
	`P.occidentalis ~ Year + (1|Site). Nbinom1`
	
	`        Df    AIC    LRT    Pr(>Chi)`
	`Year   1  123.82 0.43695   0.5086`

Kyphosus sydneyanus
`K.sydneyanus ~ Year + (1|Site) + (1|Date). nbinom2`
 	
`        Df    AIC    LRT    Pr(>Chi)`
`Year   1   319.00 2.2418   0.1343`	

Scarus ghobban
`S.ghobban ~ Year + (1|Site) + (1|Date). Gaussian`
 	
`        Df    AIC    LRT    Pr(>Chi)`
`Year   1   211.09 4.2637   0.03894 *`	

Scarus schlegeli
`S.schlegeli ~ Year + (1|Site) + (1|Date). Nbinom1`
 	
`        Df    AIC    LRT    Pr(>Chi)`
`Year   1   179.18 5.5686   0.01829 *`	

Table S4. Results of Generalized linear mixed models (glmmTMB) for differences in fish abundance between tropical and temperate herbivorous fish that feed on turf seaweed (grazers) and seaweed canopy (browsers). * identify statistically significant differences.

Grazers	Browsers
Family: nbinom2 (log)	Family: nbinom2 (log)
Formula: Grazers ~ Climate affinity + (1|Reef) + (1|Date)	Formula: Browsers ~ Climate affinity + (1|Reef) + (1|Date)
Likelihood Radio Test:	Likelihood Radio Test:

Grazers:

	Df	AIC	LRT	Pr(>Chi)
<none>		1018.0		
Climate affinity	1	1026.2	10.218	0.001391 **

Browsers:

	Df	AIC	LRT	Pr(>Chi)
<none>		635.79		
Climate affinity	1	641.97	8.1752	0.004247 **

Table S5. Results of Generalized linear mixed models (glmmTMB) for differences in herbivory rates between tropical and temperate grazers (turf) and browsers (kelp) and consumption rates of exposed and cryptic kelps. * identify statistically significant differences.

Grazers	Browsers
Familiy Gaussian (identity)	Familiy Gaussian (identity)
Herbivory.log ~ Climate affinity + (1 | Site) + (1 | Date)	Herbivory.log ~ Climate affinity + (1 | Site) + (1 | Date), ziformula = ~1
Likelihood Radio Test:	Likelihood Radio Test:

Grazers:

```
        Df    AIC     LRT    Pr(>Chi)
<none>        297.27
Climate  1   302.85  7.5844  0.005888 **
```

Browsers:

```
                   Df    AIC      LRT       Pr(>Chi)
<none>                  185.09
Climate affinity  1    183.10   0.0046293  0.9458
```

Exposed vs Cryptic Kelp Consumption

Family: gaussian (identity)

Formula: Consumption Rate ~ Exposure level + (1 | Reef)

Likelihood Radio Test:

```
        Df   AIC    LRT    Pr(>Chi)
<none>       195.8
Exposure  1  217.6  23.8   1.069e-06 ***
```

Chapter 6. General Discussion

6.1. General overview of results

Herbivory can affect the abundance and composition of primary-producers, engineering the habitat structure (Bruno & Bertness 2001), the flow of energy between trophic levels and the resilience of ecosystems (Cheal *et al.* 2013; Hamilton & Caselle 2015). This thesis aimed to increase our understanding of the ability of range-expanding tropical herbivores to persist and affect the functioning of ecological processes in their receptive temperate ecosystems dominated by canopy-forming macrophytes (Fig. 6.1). For this, I quantified the phenological and phenotypic plasticity of rabbitfish across their global distribution and evaluated how this could affect their fitness and persistence at high latitudes (chapter 2). I assessed the overwintering capacity of tropical herbivores and their contribution to transform macrophytes into particulate detritus across the seasons of the year in temperate reefs (chapter 3). I then estimated the spatial overlap between populations of tropical and temperate herbivores and its consequences for the changes in diversity, intensity and extent of herbivory functions in temperate habitats (chapter 4). Finally, I analyzed the role of seagrass meadows as nursery grounds for range-expanding tropical herbivores, its link with the persistence of abundant populations across time, and the differences in their ability to suppress kelp recovery in topographical shelters and exposed surfaces in tropicalized temperate reefs devoid of kelp ten years after a marine heatwave (Chapter 5).
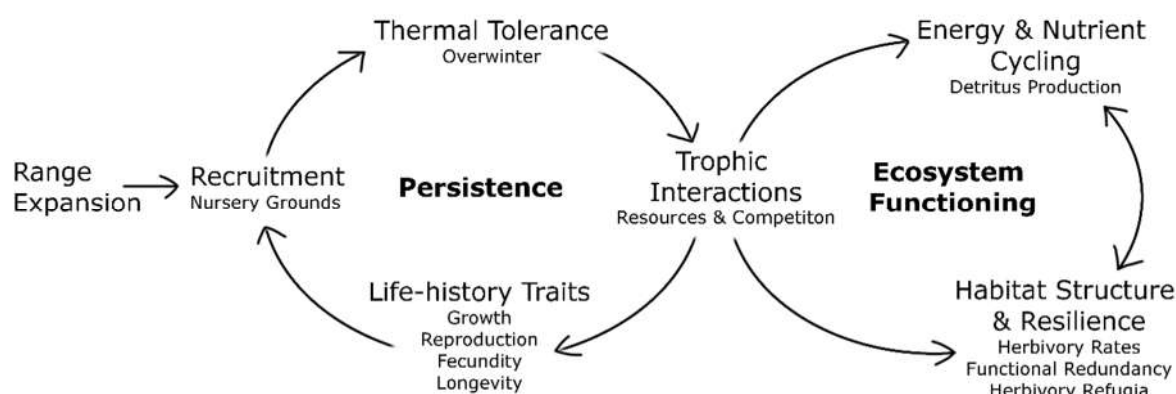

Figure 6.1. Ecological elements assessed in this thesis and its relationship with the persistence of range-expanding tropical herbivores and its effects on the functioning of temperate ecosystems.

6.2. Expansion and persistence

Persistence is a key factor that will influence the ecological impact of range-expanding tropical species in their receptive ecosystems at higher latitudes. Studies attempting to understand and predict range-expansions of tropical fishes have analyzed the importance of various environmental and biological aspects related to the success of tropical species moving poleward, such as recruitment; overwinter survival, diet requirements, habitat preferences, and certain life-history traits, such as morphological and reproductive features (Feary *et al.* 2014; Booth *et al.* 2018; Figueira, Curley & Booth 2019; Monaco *et al.* 2020). However, many of these biological and ecological aspects related to the possible range-expansion success of important tropical herbivores had not been included in the global model of tropicalization of temperate marine ecosystems (Vergés *et al.* 2014).

Recruitment - nursery grounds

Surveys across different years and locations in southwestern Australia confirmed the importance of seagrass meadows for the persistence of rabbitfish populations at higher latitudes (Chapters. One important vector of expansion to higher latitudes for marine species is the dispersal of their propagules during their pelagic larval stage (Dunstan & Bax 2007). Their success of settlement in the new environment is dependent on the suitability of their new environments for recruitment. Studies exist about the recruitment of small-sized species of damselfish (Pomacentridae), butterflyfish (Chaetodontidae) or surgeonfish (Acanthuridae), which have strong reef and coral dependencies (Feary *et al.* 2014; Beck *et al.* 2016b; Pearce *et al.* 2016). However, seagrass meadows interspersed between temperate reefs have generally been disregarded despite their recognition as important nursery grounds for many species of tropical fish (McDevitt-Irwin, Iacarella & Baum 2016). Findings in several chapters confirmed their importance for rabbitfish, where schools of juveniles of *Siganus fuscescens* roamed seagrass beds adjacent to temperate reefs around the Perth metropolitan area (Chapter 2 and 3), and in a lagoon adjacent to the tropicalized reefs of Port Gregory (Chapter 4). Their abundances were lower than those reported in tropical regions, such as Indonesia, where thousands of juveniles are collected annually by fishermen (Soliman & Yamaoka 2010; Ambo-Rappe *et al.* 2013); however, abundances were similar to those registered in some subtropical locations, such as the Ryukyu Islands, where hundreds of juveniles of *S. fuscescens* roam seagrass meadows (Nakamura & Tsuchiya 2008). This strongly suggests that the importance of seagrass meadows as nursery grounds must be considered in future predictions of the tropicalization of temperate ecosystems.

The habitat associations for the recruitment of drummers (Kyphosidae) and parrotfish (Scaridae) remain open to further investigation. Evidence of settlement of juvenile drummers at higher latitudes

is limited. Reports on the recruitment of kyphosids in general indicate an association of juveniles with shallow reefs (Rimmer 1986; Moran & Clements 2002; Silvano & Güth 2006). The sight of juvenile *K. biggibus* in the backreef of Port Gregory agrees with these previous reports; however, it is uncertain in which habitat they had settled initially, as larvae could settle first in seagrass and juveniles could then move closer to the reef once they attain bigger sizes. Evidence from studies in tropical regions suggest that seagrass meadows (Nakamura & Tsuchiya 2008; Zarco-Perello & Enríquez 2019) and seaweed fields (Evans *et al.* 2014) can be important nursery grounds for parrotfish species (Kirsch, Valentine & Heck 2002; Nakamura *et al.* 2003; Mellin, Kulbicki & Ponton 2007), suggesting that the abundant seagrass meadows and seaweed forest in temperate ecosystems could provide a similar function (Heck *et al.* 2015; Beck *et al.* 2016a). However, only adult populations of *Scarus ghobban* and *Scarus schlegelii* were observed during surveys at Rottnest Island and Port Gregory (Chapters 3 & 4). This is akin to past studies which only registered mature individuals (> 20 cm in length) in the same regions (Parker *et al.* 2021). Parrotfish juveniles were observed sporadically outside of my field surveys in backreef habitats of both sites (N. Bosch, pers. comm), indicating that these habitats could be facilitating their recruitment at higher latitudes, but these were not quantified, and further monitoring needs to be done.

Thermal tolerance - overwinter capacity

The presence of adult populations of tropical kyphosids, parrotfish and rabbitfish in many locations in southwestern Australia over successive years indicated that juveniles and adults of these species can overwinter in temperate ecosystems (Lenanton *et al.* 2017). One of the main factors limiting the persistence of range-expanding tropical species are low temperatures during winter at high latitudes. The influence of temperature on the metabolic rates and physiological processes of ectothermic organisms is very strong and extreme values above or below their critical thermal limits can lead to poor development and death (Angilletta, Niewiarowski & Navas 2002; Pörtner & Peck 2010). The importance of cold temperatures during winter as a limiting factor of the geographic distribution of species at higher latitudes has been recognized long ago (Figueira & Booth 2010; Osland *et al.* 2021). For instance, most of the juveniles of tropical fish species that settle annually at higher latitudes in southeastern Australia do not survive winter temperatures (Booth *et al.* 2018). The temperate reefs of Port Gregory experienced an increase in the abundance of parrotfish by 7-fold and rabbitfish by 6-fold following the marine heatwave of 2011 (supp. inf. (Bennett *et al.* 2015) and species of these groups, such as *S. fuscescens*, *S. ghobban* and *S. schlegeli*, have persisted with similar abundances since then (Chapter 4). Increases in tropical kyphosids after the marine heatwave were not possible to discern due to the low image resolution of diver operated stereo-videos used in this study.

However, the clearer imagery provided by stationary remote underwater videos showed that after the heatwave the relative abundance of *K. bigibbus* was 13-fold higher than the temperate *K. sydneyanus* and *K. gladius* (Bennett *et al.* 2015) and surveys in 2019 showed that *K. bigibbus* remains with similar abundances (MaxN 156 vs 150). This supports reports of their continued high abundance in temperate reefs of Japan (MaxS = 500–1,000 individuals), where winter temperatures can reach as low as 12.6°C (Kadota *et al.* 2017). *S. fuscescens* also demonstrated to have a robust tolerance to lower temperatures, as they have continually overwintered ever since their expansion in 2011 (Zarco-Perello *et al.* 2017) from Marmion Marine Park (32°S; Chapter 2) to Geographe Bay (33.5°S; Chapter 3), where they withstand winter temperatures as low as 16 and 13°C respectively (Fig. 6.2). This is similar to the winter temperatures in temperate environments of Japan (Tateyama Bay), Korea (Jeju Island) and the Mediterranean Sea (Sicily Strait) where *S fuscescens* and *Siganus luridus* have established successful reproductive populations respectively (Azzurro *et al.* 2007; Akiyama, Naganuma & Katayama 2009).

Further investigations on the thermal scope of tropical herbivores are necessary to help predict their range-expanding capabilities into temperate ecosystems. Lower temperatures at the edge of thermal tolerance limits can cause high mortality rates of adult rabbitfish under long term exposure (Hsu & Gwo 2017; Dahlke *et al.* 2020). This is particularly critical for early ontogenetic stages, since thermal tolerance is size-dependent, and the smallest individuals are more vulnerable (Hurst 2007; Dahlke *et al.* 2020). Although recently increasing, information on the thermal performance of tropical reef fish is scarce, with many important species of herbivores not being investigated regarding critical thermal limits for reproduction or growth (Zarco-Perello, Pratchett & Liao 2012; LaMonica, Fox & Donelson 2021). The only comprehensive thermal performance study for rabbitfish, shows that juveniles of *S. rivulatus* can survive temperatures of 14°C, a typical winter temperature in many temperate locations (Saoud, Mohanna & Ghanawi 2008). However, tropical juveniles can escape mortality from low temperatures if they recruit during spring and grow during the summer and autumn, quickly increasing their body size, thermal tolerance and chances to survive through winter (Hurst 2007).

Figure 6.2. Presence of *Siganus fuscescens* at the Busselton Jetty, Geographe Bay, southwestern Australia, during November 2020 (left) and April 2021 (right). Photos provided by Rachel Austin from the Busselton Jetty Underwater Observatory and Chris Dowling from the Department of Primary Industries and Regional Development.

Life-history traits

Populations of tropical herbivores at their edge of range-expansion are experiencing changes in phenological and phenotypic traits. Aside from mortality, the amplitude of seasonal changes in temperature at higher latitudes can affect the behavior and life history of ectotherms (Conover 1992), such as the onset and duration of reproduction and fecundity, growth rates, size at maturity, maximum body size and longevity (Angilletta & Dunham 2003). This can have important consequences for the persistence and further poleward expansion of tropical species; however, this remains untested for many species, including tropical herbivores. The meta-analysis analyzing changes in the life-histories of range-expanding rabbitfish indicated that *S. fuscescens* and *S. rivulatus* have shorter spawning periods restricted to spring, when temperatures are more favorable for the development of their offspring, but had higher fecundity per length class and longer life expectancy in comparison to tropical populations, which likely maximizes their life-time reproductive output and favors their persistence at higher latitudes (Conover 1992; Berrigan & Charnov 1994; Atkinson & Sibly 1997). However, life-history changes will be heterogeneous in space as a result of interactions between different environmental variables, in addition to the specific thermal reaction norms of range-shifting species (Angilletta & Dunham 2003; Audzijonyte *et al.* 2020). For instance, the only other study that

has assessed the changes in reproductive phenology in range shifting fish, showed that populations of the black sea bass (*Centropristis striata*) experienced a reduction in reproductive period, but did not change its reproductive output at higher latitudes (Slesinger, Jensen & Saba 2021). This taxonomic and spatial variation was also observed in the smaller body sizes of temperate populations of *S. rivulatus*, associated with the combined effect of lower temperatures and nutrition. In addition, other important factors could influence the magnitude and direction of life-history changes, such as interactions between range-expanding herbivores and native competitors and predators, which can affect resource acquisition, fitness and persistence in different habitats (Nash *et al.* 2012).

The persistence of rabbitfish in southwestern Australia will likely depend on the temperatures experienced during spring and summer in future years. According to the maximum longevity recorded for *S. fuscescens* (13 y/o) (Katayama *et al.* 2009), range-expanding rabbitfish in southwestern Australia that recruited after the heatwave in 2012 could live until 2025, while some of the recruits seen during 2016 and 2019 could live until 2029 and 2032 respectively. Thus, we can expect some successful events of reproduction and recruitment within their life-time, given their high fecundity (300,000 - 2.6 million eggs *per capita*) (Lee, Kim & Han 2019), the presence of adequate nursery grounds and temperatures above the thresholds related to spawning periods (> 20°C) at locations where they have established successful reproductive populations at higher latitudes in Japan and Korea (Fig. 6.3). Findings of ripe gonads in male and female rabbitfish individuals from the Perth metropolitan area by the Department of Fisheries of Western Australia (Lenanton *et al.* 2017) and further macroscopic evaluations performed by myself confirmed the reproductive activities of these herbivores in temperate ecosystems (Fig. 6.3). However, the cooler temperatures experienced during recent years (2016-2019) could have decreased the reproductive output and growth window for juveniles, particularly for populations at the higher latitudes in Geographe Bay (Feng *et al.* 2020). This could explain why juveniles have been seen infrequently during transects and roaming surveys in recent years (Chapters 3 & 4), and why they were absent in remote underwater videos carried over in Marmion during summers of 2020 and 2021, involving 10 cameras distributed across 1000 m^2 of seagrass meadows. This could suggest that recruitment success has been limited in recent years but also could be due to the smaller home ranges of juvenile fish and great spatial extent of their nursery grounds, making it difficult to find them during surveys (Chapter 3).
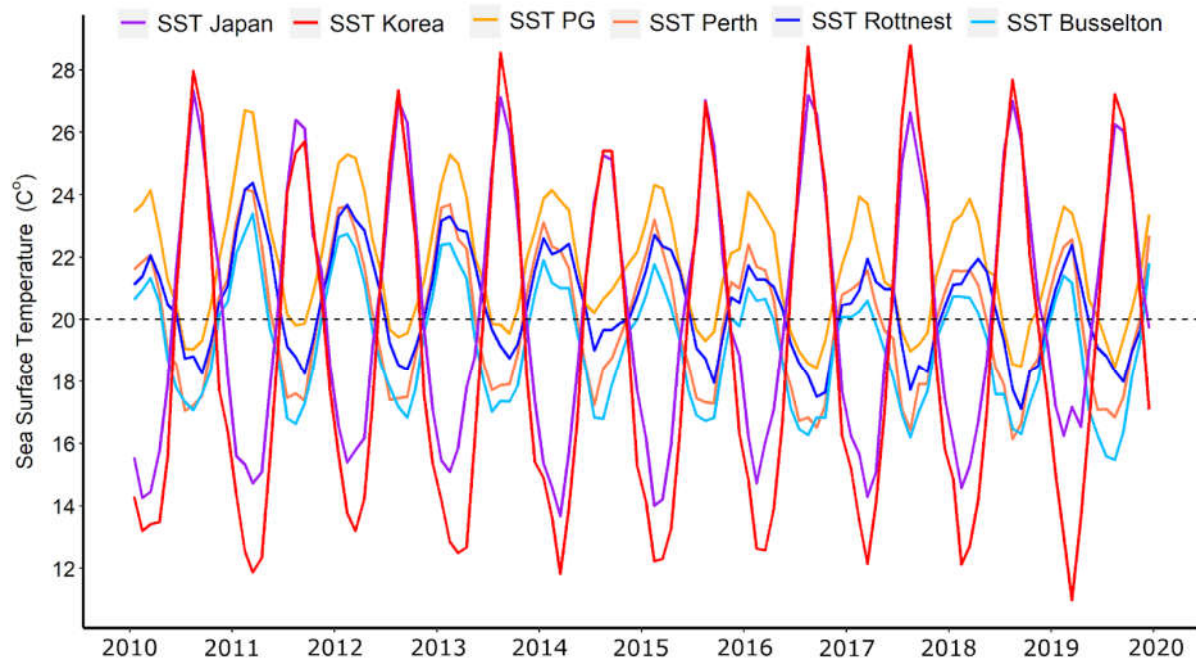
Figure 6.3. Sea surface temperature from 2010 to 2020 at locations where the rabbitfish *Siganus fuscescens* has established successful reproductive populations at higher latitudes in Japan (Takeyama Bay) and Korea (Jeju Island) and its comparison with locations in Western Australia where rabbitfish are present (Port Gregory: PG, Perth, Rottnest Island and Geographe Bay: Busselton). Below are specimens of mature female (left) and male (right) rabbitfish with ripe gonads collected in January 2017 from the temperate ecosystems of Perth. Temperature data obtained from the E. U. Copernicus Marine Service: GLORYS12V1 product).

Trophic interactions - resources & competition

The intensity of competition between tropical and temperate herbivores in southwestern Australia appears to be low. The poleward redistribution of species is creating novel species interactions in temperate ecosystems which can result in competition between functionally equivalent species. This can have three potential outcomes: (i) temperate species outcompete tropical species, hindering their

persistence, (ii) tropical species outcompete temperate species, displacing them to higher latitudes or (iii) species are able to coexist forming novel ensembles (Milazzo *et al.* 2013; Marshak & Heck 2017). Overlap analyses showed that the arrival of new species of herbivores in southwestern Australia have not caused species displacements, as there were no negative relationships between the abundances of tropical and temperate populations at any location. This indicated a low level of competition likely linked with the high abundance and diversity of macrophytes and differences in feeding behaviors and diet preferences of herbivores, aligning well with the resource partitioning and empty niche theories proposed to explain the success of many invasive species (Lowry *et al.* 2012; Streit, Cumming & Bellwood 2019).

Tropical rabbitfish and parrotfish were more associated with reefs having higher cover of turf seaweed and adjacent seagrass meadows around Perth and Rottnest Island, while most of the temperate herbivores were more associated with reefs having higher cover of canopy-forming seaweed (Chapter 4). These habitat associations correlated well with the observed feeding activities of each species. The herring cale *Olisthops cyanomelas*, and drummers *K. sydneyanus/gladius* fed primarily on kelp, *K. cornelii* consumed turf, *P. octolineatus* is a well-known seagrass consumer but also was observed consuming the brown seaweed *Cystophora* sp. (pers. obs.), while *Scarus ghobban* consumed mainly turf but also were seen biting epiphytes off seagrass blades and kelp canopies (pers. obs.). *S. fuscescens* in particular was observed in a variety of habitats, including artificial structures (*e.g.* Busselton Jetty), and consuming a high diversity of macrophytes, from filamentous to canopy-forming seaweed and seagrass, which could explain their more successful range-expansion (Monaco *et al.* 2020). Similar conclusions have been found in southeastern Australia, where the diet of range-expanding damselfish did not overlap significantly with temperate species (Kingsbury *et al.* 2019).

Diversity of diets relate to different feeding behaviours that decrease spatial overlap and resource competition among species, promoting coexistence (Michael *et al.* 2013). This includes horizontal movements between habitats with different benthic composition but also in the vertical space, as some species feed on drifting macrophytes, which reduce resource competition in the benthic space (Chapter 3). Temporal mismatches in feeding activities also can lead to reductions in competition. For instance, rabbitfish switched from drifting herbivory when their abundance was low and benthic herbivory when their school size was high during daytime. Some species can be crepuscular (*e.g. K. sydneyanus*; (Clements & Raubenheimer 2006)) or nighttime feeders (*e.g. K. bigibbus; (Noda et al. 2016)*), avoiding trophic interactions with daytime feeders, which can affect their feeding rates or the spatial shape and size of foraging ranges (Nash *et al.* 2012). Antagonistic interactions were observed between temperate and tropical fish during herbivory assays in Port Gregory and Perth, where the

damselfish *Parma occidentalis* and *Parma maccullochi* and the drummer *Kyphosus cornelii* defended their territories against parrotfish and rabbitfish, disrupting their foraging activities and reducing their feeding rates (Barrientos, Zarco-Perello *et al.*, *in review*), similar to interactions in tropical reef systems (Francini-Filho *et al.* 2010). Although significant negative impacts were not evident, as tropical herbivores quickly regrouped to feed in adjacent areas, this could have long-term effects on growth, body condition or reproductive output (White & Warner 2007). Abundant resources and low diversity and abundance of competitors will likely facilitate the persistence of tropical herbivores under favorable physical environmental conditions (Marras *et al.* 2015); however, further tropicalization is expected to increase competition among herbivorous species and more research on novel species interactions would be useful to predict outcomes of winners and losers among expanding and native herbivores, as well as their effect on other trophic groups and ecological processes of temperate ecosystems.

6.3. Effects on ecosystem functioning

Herbivory is a key ecological function which regulates the energy flow and habitat structure of marine ecosystems through the consumption of macrophytes (Nowicki, Fourqurean, & Heithaus, 2018; Poore et al., 2012). Increases in the abundance and diversity of tropical herbivores in temperate reefs and seagrass meadows are predicted to intensify the consumption rates on primary producers, potentially affecting habitat structure, flow of energy and nutrients between trophic levels and their ecological resilience (Vergés *et al.* 2014; Hyndes *et al.* 2016). However, there is a scarcity of quantitative information about the spatial and temporal changes in herbivory rates on different macrophytes, hindering our ability to corroborate these predicted effects.

Energy and nutrient cycling

Range-expanding herbivores can increase primary consumption rates and detritus production throughout the year in temperate reefs (Chapter 2). Macrophytes contribute to sustain up to 40% of the biomass of the fish communities in temperate reefs (Truong *et al.* 2017); however, up to 82% of the primary productivity is transported away from its origin, subsidizing trophic resources in adjacent ecosystems, such as seagrass meadows or sandy beaches (Krumhansl & Scheibling 2012; de Bettignies *et al.* 2013). Increased primary consumption could lead to a higher retention of primary production in its place of origin, affecting the flow of energy and nutrients in the local and interconnected trophic chains. Seasonal surveys demonstrated that herbivory rates increased as a factor of abundance of herbivores and temperature, where populations of rabbitfish accelerated the consumption of

macrophytes by five-fold in comparison with their temperate competitor *K. sydneyanus* (Chapter 2). This included the consumption of kelp but also a diversity of other seaweed and seagrass that were attached to the substrate or drifting in the water column. The observed higher herbivory rates were concomitant with the rates of shredding and excretion of macrophytes as particulate organic matter, essentially transforming the function of canopy-forming macrophytes from habitat providers to sources of nutrition for other organisms that otherwise would not be able to access these resources (Rothans & Miller 1991; Sauchyn & Scheibling 2009; Yorke, Page & Miller 2019). Detritus is a trophic resource with high nutrient content and is a key dietary component for many grazing fishes which constitute an important percentage of the overall biomass of fish assemblages in tropical reefs (McMahon *et al.* 2016). Higher availability of this resource would benefit the populations of organisms that feed on it in temperate reefs, which in turn could contribute to accelerate the energy flow to higher trophic levels (Depczynski *et al.* 2007).

The increase in the abundance and richness of tropical species in temperate ecosystems will encompass all trophic levels (Blowes *et al.* 2019). This can lead to the intensification of herbivory but also predation rates, increasing secondary productivity (Friedland *et al.* 2020; Whalen *et al.* 2020). Contributions to this energy pathway will be different among species, with smaller body sizes and solitary behavior having higher predation mortality rates (Mihalitsis *et al.* 2021). Increases in the abundances of cryptic species of fish, such as blennies and gobies, could be important in this process as they are important benthic feeders and can sustain up to 60% of total fish productivity in coral reefs (Brandl *et al.* 2019). Roaming herbivorous fish that tend to form schools, a hypothesized antipredator behavior (Ward *et al.* 2011), will probably contribute more directly to secondary production through suffering predation on eggs, larvae and juveniles stages, when they are more vulnerable. These trophic effects have been described in the Mediterranean Sea, where the rabbitfish *S. rivulatus*, *S. luridus* accelerated the flow of energy from primary producers to detritivores and higher trophic levels from months to hours through the ingestion and excretion of seaweed, and by predation from groupers (Serranidae), constituting up to 68% of their stomach content (Goren & Galil 2005).

These patterns agree with the theoretical predictions on the modifications of energy transfer in temperate ecosystems due to the advent of range-extending tropical herbivores (Hyndes *et al.* 2016; Vergés *et al.* 2019). However, further research aimed at identifying the specific trophic pathways of energy transfer associated with herbivory-derived detritus and novel prey-predator interactions in tropicalized ecosystems is necessary to calculate the magnitude of its effect in the food webs.

Habitat structure and resilience

The addition of tropical herbivorous fish to temperate ecosystems lead to increases in functional diversity and intensity of grazing on turf and browsing on canopy-seaweed and seagrass. Functional redundancy only occurred in some sites because of the low number of temperate species for each herbivory function. In particular, seagrass browsing increased the most in locations where the rabbitfish *S. fuscescens* has established abundant populations. This resembled the importance of other rabbitfish species for this herbivory function, such as *Siganus lineatus* which is an important seagrass consumer in northwestern Australia (Vanderklift *et al*. 2021). Further tropicalization at higher latitudes and increases of seagrass browsing could affect the function of seagrass meadows as refuge and feeding grounds for some permanent and transient species of fish and invertebrates, as this depends on the density and length of the leaf blades (McCloskey & Unsworth 2015); however, a major impact is predicted to be exerted by the potential range-expansion of megafauna such as marine turtles and sirenia (Hyndes *et al.* 2016).

Kelp browsing by range-extending rabbitfish has not surpassed productivity rates in southwestern Australia (Steneck *et al.* 2002; Bellwood, Hughes & Hoey 2006; Eklöf *et al.* 2008). Assessments of increases in the intensity of herbivory functions across the region using community weighted mean of trait values showed that tropicalized locations have experienced increases of canopy browsing; nonetheless, average values were like non-tropicalized regions further south which are dominated by canopy seaweed, indicating that consumption rates have not surpassed productivity rates. This is not entirely surprising, as in contrast to sea urchins which consume kelp individuals from the stipe, causing their detachment (Leighton, Jones & North 1966; Ling *et al.* 2015), roving herbivorous fish forage across multiple kelp canopies as they move within their home-range, diluting the net intensity of their consumption per unit of kelp (Semmler *et al.* 2021). This was supported by assessments of *per capita* bite rates of *S. fuscescens* by following individuals for 5 minutes counting the number of bites taken on different macrophytes during April and May 2019 in Marmion Marine Park (n=9), Cottesloe Fish Habitat Protection Area (n=16), Rottnest Island (n = 19) and Port Gregory (n=16). These calculations showed that total herbivory rates varied widely depending on their school size and location, but in all cases consumption was partitioned among a wide variety of macrophytes available in their habitat (Figure 6.4a, b). Kelp consumption accounted only for a quarter of the total number of bites (24.5 ± 5.1 %), being higher than seagrass (17 ± 5.4 %) but equal to sargassum (24.3 ± 4.9 %) and lower than turf (36 ± 5.9 %). The diet flexibility of rabbitfish among different macrophytes lessens their impact on kelp populations but these still can be ecologically relevant. According to *per capita* bite rates and calculations of biomass ingested per bite (0.3 g) based on a linear regression (biomass=0.0696*area), kelp consumption per day (12 hrs) by rabbitfish could approach production rates (g m^2 day^{-1}) within a

core home-range of 8000 m^2 (Green *et al.* 2015; Weeks *et al.* 2017; Pickholtz *et al.* 2018), only at high abundances of rabbitfish and low densities of kelp, considering a kelp productivity in the region of 1.5 g day^{-1} ind^{-1} (Vanderklift, Lavery & Waddington 2009) (Figure 6.4c).

Important increases in herbivory rates can be concerning even if they fall below production rates, since the resilience of seaweed forests against environmental disturbances can be weakened (McClanahan 1992; Steneck *et al.* 2002). Eutrophication, pollution, storms and high temperatures can cause significant mortality rates in kelp populations, reducing their densities and increasing their vulnerability to regime-shifts (Filbee-Dexter & Wernberg 2018; Wernberg *et al.* 2019b). Lower densities of kelp reduce productivity and weaken positive feedbacks that maintain the stability of their populations through high spore supply and the facilitation of recruitment (Layton *et al.* 2019). Thus, a strong disturbance could push the system over the tipping point where herbivory surpasses production leading to a canopy-free state (Boada *et al.* 2017). The calculated consumption-production balance presented earlier is only a general approximation, and more assessments of both processes are needed as they vary greatly at finer scales of space and time (Catano *et al.* 2016; Ruttenberg *et al.* 2019; Wernberg *et al.* 2019a). However, the general trends illustrate the empirical observations in Australia and other studies in Japan. Many reefs in southwestern Australia have high densities of kelp, despite having abundant rabbitfish populations, such as several sites in Rottnest Island and northern Perth (top of heatmap Fig. 6.4). On the other hand, the reefs in Port Gregory suffered a decline in density and productivity of kelp, leading to an increase in herbivory *per capita*, where high abundances of tropical herbivores quickly consumed isolated kelp individuals (bottom right of heatmap Fig. 6.4). This is akin to the "isoyake" phenomenon experienced by the kelp populations of southern Japan, where is likely that a combination of thermal stress lead to high mortality rates of kelp, lowering density and production below the herbivory rates of tropical herbivores (Tanaka *et al.* 2012; Kumagai *et al.* 2018).

The natural recovery of kelp populations from a shift to a tropicalized turf-dominated state is uncertain. The finding of kelp individuals successfully settling and surviving to maturity in herbivory refugia at the tropicalized reefs of Port Gregory, indicated that they are receiving propagules from external sources; however, the extensive cover of turf and the high abundances of grazers and browsers are preventing kelp survival in exposed areas of the reefs. Turf mats hinder a great proportion of the settlement and survival of juvenile kelp individuals (Gorman & Connell 2009), while fish species that feed on the benthos can consume or damage recruits that had managed to settle (Vergés *et al.* 2014). Assessments of the fish communities and feeding rates in Port Gregory, indicated that grazing species are likely to experience major increases in abundance, diversity and redundancy

during an ongoing process of tropicalization. These include roving grazing herbivores (*e.g.* parrotfish, rabbitfish and surgeonfish) and seaweed farmers (*i.e.* damselfish), but also detritivores and invertivores that "brush" and dig within the turf, which will likely damage and detach any kelp sporophytes, hindering their survival (Feehan, Grace & Narvaez 2019). Grazing herbivores specialized in biting deeper in the substratum, clearing the reef surfaces from turf (functionally known as scrapers and excavators), could facilitate the settlement of kelp propagules into hard ground (Francini-Filho *et al.* 2008). However, this potential beneficial effect is uncertain, as turf seaweed quickly recolonize available substrates, and under high grazing rates, consumption of recruits can exceed its benefit, as has been shown for the recruitment of scleractinian corals in certain tropical reefs (Trapon, Pratchett & Hoey 2013). Moreover, the preferences of tropical species for habitats with less canopy (Hoey & Bellwood 2011) may strengthen the persistence of turf mats by intensifying grazing pressure in these habitats while promoting their productivity through high excretion rates of nutrients (Burkepile *et al.* 2013; Shantz *et al.* 2015). Overall, this indicates that a reversal to a canopy-dominated state would require important reductions of turf seaweed and benthic consumers. Whether or not this could happen naturally remains unknown. Evidence from Port Gregory suggests this is unlikely in marginal locations, since both factors have remained stable a decade after the heatwave event and their regime-shift, despite that temperature has decreased back to pre-heatwave levels for several years (Feng *et al.* 2020).

Recovery of kelp may require the implementation of restoration strategies in certain situations. Restoration management will be challenging for regions where the synergistic effect of higher temperatures and increases in herbivory will be increasingly important in the future (Vergés *et al.* 2019). Efforts of kelp restoration are increasing around the world through the amelioration of disturbances and translocation of kelp individuals (Layton *et al.* 2020). Under favorable environmental conditions, simple transfer of kelps from other locations could be effective; however, considering a warming world, transplants will likely die off if they lack resistant genotypes for gradual increases of temperatures and marine heatwaves (Coleman *et al.* 2020) or if abundant herbivores are present in the ecosystem (Kuwahara 2015). Thus, an effective long-term investment in restoration would need to consider multifaceted strategies that strengthen the productivity of macrophyte populations (Gianni *et al.* 2018; Morris *et al.* 2020), similar to terrestrial forests (Löf *et al.* 2019). Assuming the existence of heat-resistant kelps, designs should include enhanced techniques that increase recruitment (Fredriksen *et al.* 2020) and reduce mortality, such as reseeding kelp within refuges from herbivory or among other benthic species that are less palatable (Ling, Reeves & Kriegisch 2020; Guignabert *et al.* 2020) and controlling herbivore populations through natural predators (Hamilton & Caselle 2015; Eisaguirre *et al.* 2020) or by developing new fisheries (Kuwahara 2015; Cerim, Soykan &

Gülşahin 2020). In the absence of heat-resistant kelps, it is important to consider that in some cases restoration will not be feasible and ecosystems likely will not recover to their original state because local-scale resource and conservation management can`t control a warming environment or the immigration of all range-shifting species. In these instances, hybrid and novel communities of species will be created (Hobbs, Higgs & Harris 2009), and perhaps restoration aims should aim for the substitution of foundation species that restore or approximate important ecosystem services, such as habitat complexity and nutrient cycling that can support biodiverse and productive ecosystems (Teagle & Smale 2018; Pessarrodona, Foggo & Smale 2019; Vergés *et al.* 2019).
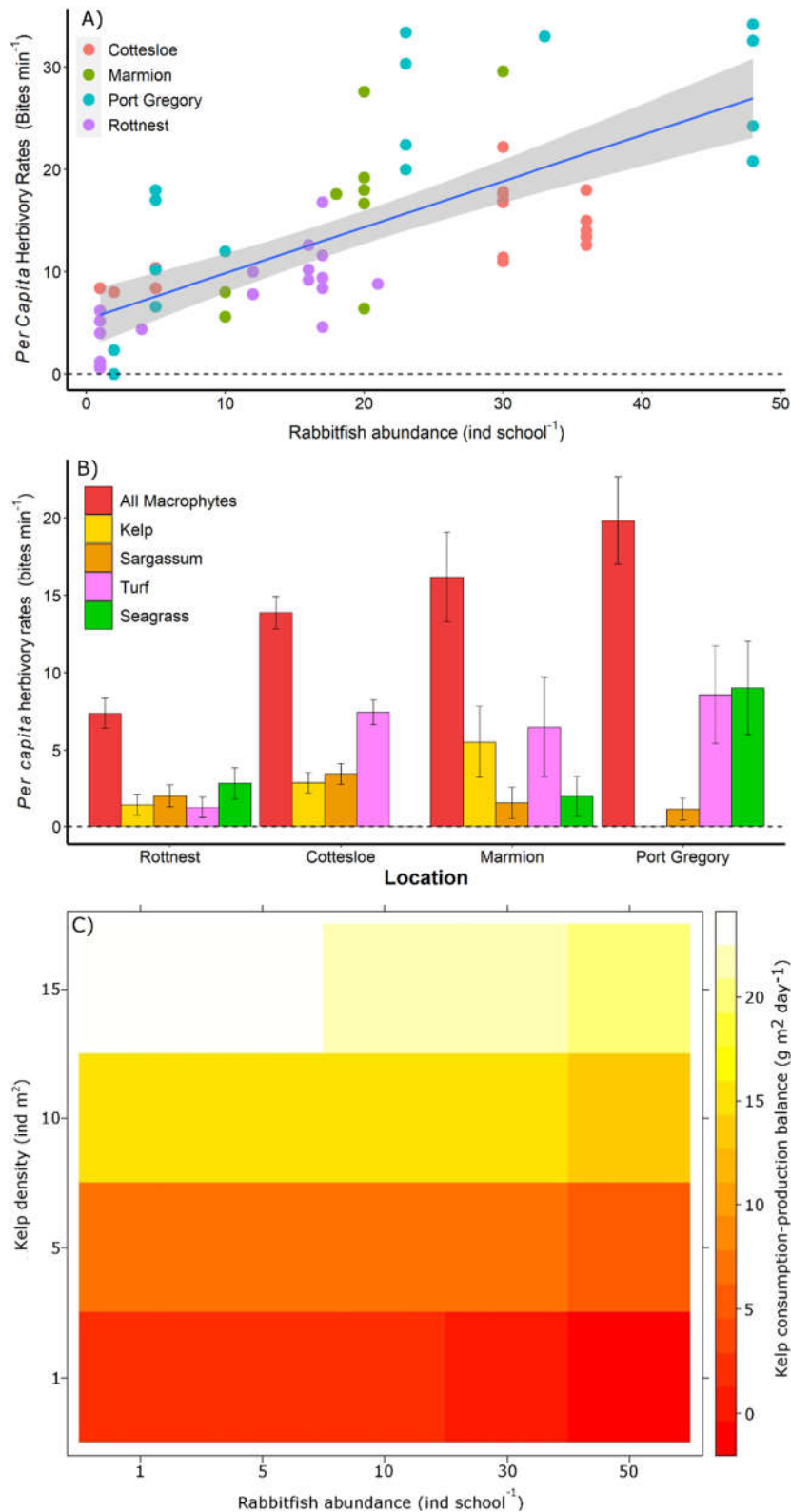
Figure 6.4. Total *per capita* bite rates (bites min^{-1}) of the rabbitfish *S. fuscescens* as a function of their abundance in different locations of southwestern Australia (A), its average partitioning among different macrophyte groups present in their habitats (B) and the balance between rates of biomass of kelp consumed by the tropical rabbitfish *Siganus fuscescens* and productivity of the kelp *Ecklonia radiata* (g m^2 day^{-1}) according to their abundances in temperate reefs of southwestern Australia (C).

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6.4. Conclusions

Range-expanding rabbitfish can maximize their fitness and persistence at high latitudes through changes in their reproductive phenology and phenotype (Chapter 2) in combination with their overwintering capacity, feeding flexibility and low interspecific competition and adequate nursery grounds in their receptive ecosystems (Chapter 3 & 4). Their establishment has increased the diversity and redundancy of herbivory functions, accelerating the consumption of different macrophytes and the production of detritus, but this was heterogeneous in space and time as a factor of the environmental temperature, their abundances and the spatial overlap with temperate competitors (Chapter 3 & 4). Regional comparisons of overlapped community weighted means of herbivory trait values indicated that herbivory intensity had not surpassed rates of primary production in dense kelp forests. However, these increases could be reducing the resilience of kelp forests in the face of severe disturbances. Kelp individuals were only able to survive high consumption rates by tropical herbivores in topographical refugia within reefs which had lost their kelp forests due to the marine heatwave in 2011 (Chapter 5). As the range-expansion of tropical species is dependent on the advancement of climate change, their effects will be in synergy and this needs to be considered in resource management and conservation programs. Regions of the world experiencing strong warming will need to implement monitoring programs and strategies of mitigation, restoration and adaptation for the conservation of the ecosystem services in the face of future climate change. However, there is a great need to do more research at the individual level of multiple species, in terms of physiological performance under future warming, its responses in phenology, phenotype and biogeography, adaptation and phenotypic plasticity, it's consequences at community level regarding species interactions and its effects on the balance between consumption and production at finer spatio-temporal scales to calculate regime-shift thresholds under different scenarios of tropicalization.

6.5. References

Akiyama, S., Naganuma, M. & Katayama, S. (2009) Annual life cycle of rabbitfish Siganus fuscescens in Tateyama Bay, Chiba prefecture. *Fisheries Engineering*, **46**, 107–115.

Ambo-Rappe, R., Nessa, M.N., Latuconsina, H. & Lajus, D.L. (2013) Relationship between the tropical seagrass bed characteristics and the structure of the associated fish community. *Open Journal of Ecology*, **03**, 331–342.

Angilletta, M.J. & Dunham, A.E. (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *The American Naturalist*, **162**, 332–342.

Angilletta, M.J., Niewiarowski, P.H. & Navas, C.A. (2002) The evolution of thermal physiology in ectotherms. *Journal of thermal biology*, **27**, 249–268.

Atkinson, D. & Sibly, R.M. (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*, **12**, 235–239.

Audzijonyte, A., Richards, S.A., Stuart-Smith, R.D., Pecl, G., Edgar, G.J., Barrett, N.S., Payne, N. & Blanchard, J.L. (2020) Fish body sizes change with temperature but not all species shrink with warming. *Nature Ecology & Evolution*.

Azzurro, E., Carnevali, O., Bariche, M. & Andaloro, F. (2007) Reproductive features of the non-native Siganus luridus (Teleostei, Siganidae) during early colonization at Linosa Island (Sicily Strait, Mediterranean Sea). *Zeitschrift fur angewandte Ichthyologie = Journal of applied ichthyology*, **23**, 640–645.

Beck, H.J., Feary, D.A., Fowler, A.M., Madin, E.M.P. & Booth, D.J. (2016a) Temperate predators and seasonal water temperatures impact feeding of a range expanding tropical fish. *Marine Biology*, **163**, 70.

Beck, H.J., Feary, D.A., Nakamura, Y. & Booth, D.J. (2016b) Wave-sheltered embayments are recruitment hotspots for tropical fishes on temperate reefs. *Marine Ecology Progress Series*, **546**, 197–212.

Bellwood, D.R., Hughes, T.P. & Hoey, A.S. (2006) Sleeping functional group drives coral-reef recovery. *Current Biology*, **16**, 2434–2439.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J. & Saunders, B.J. (2015) Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters*, **18**, 714–723.

Berrigan, D. & Charnov, E.L. (1994) Reaction norms for age and size at maturity in response to temperature: A puzzle for life historians. *Oikos*, **70**, 474.

de Bettignies, T., Wernberg, T., Lavery, P.S., Vanderklift, M.A. & Mohring, M.B. (2013) Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus. *Limnology and Oceanography Letters*, **58**, 1680–1688.

Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I.H., Winter, M., Bjorkman, A.D., Bowler, D.E., Byrnes, J.E.K., Gonzalez, A., Hines, J., Isbell, F., Jones, H.P., Navarro, L.M., Thompson, P.L. & Dornelas, M. (2019) The geography of biodiversity change in marine and terrestrial assemblages. *Science*, **366**, 339–345.

Boada, J., Arthur, R., Alonso, D., Pagès, J.F., Pessarrodona, A., Oliva, S., Ceccherelli, G., Piazzi, L., Romero, J. & Alcoverro, T. (2017) Immanent conditions determine imminent collapses: nutrient regimes define the resilience of macroalgal communities. *Proceedings. Biological Sciences / the Royal Society*, **284**.

Booth, D.J., Beretta, G.A., Brown, L. & Figueira, W.F. (2018) Predicting Success of Range-Expanding Coral Reef Fish in Temperate Habitats Using Temperature-Abundance Relationships. *Frontiers in Marine Science*, **5**.

Brandl, S.J., Tornabene, L., Goatley, C.H.R., Casey, J.M., Morais, R.A., Côté, I.M., Baldwin, C.C., Parravicini, V., Schiettekatte, N.M.D. & Bellwood, D.R. (2019) Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. *Science*, **364**, 1189–1192.

Burkepile, D.E., Allgeier, J.E., Shantz, A.A., Pritchard, C.E., Lemoine, N.P., Bhatti, L.H. & Layman, C.A. (2013) Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. *Scientific Reports*, **3**, 1493.

Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W. & Burkepile, D.E. (2016) Reefscapes of fear: predation risk and reef hetero-geneity interact to shape herbivore foraging behaviour. *The Journal of Animal Ecology*, **85**, 146–156.

Cerim, H., Soykan, O. & Gülşahin, A. (2020) Mortality and exploitation of marbled spinefoot, Siganus rivulatus (Actinopterygii: Perciformes: Siganidae), from southern Aegean Sea small-scale fishery. *Acta Ichthyologica Et Piscatoria*, **50**, 183–190.

Cheal, A.J., Emslie, M., Aaron, M.M., Miller, I. & Sweatman, H. (2013) Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. *Ecological Applications*, **23**, 174–188.

Clements, K.D. & Raubenheimer, D. (2006) Feeding and nutrition. *The physiology of fishes*, 3rd ed (eds D.H. Evans), & J.B. Claiborne), pp. 47–82. Taylor & Francis, Boca Raton.

Coleman, M.A., Wood, G., Filbee-Dexter, K., Minne, A.J.P., Goold, H.D., Vergés, A., Marzinelli, E.M., Steinberg, P.D. & Wernberg, T. (2020) Restore or redefine: future trajectories for restoration. *Frontiers in Marine Science*, **7**.

Conover, D.O. (1992) Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology*, **41**, 161–178.

Dahlke, F.T., Wohlrab, S., Butzin, M. & Pörtner, H.-O. (2020) Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, **369**, 65–70.

Depczynski, M., Fulton, C.J., Marnane, M.J. & Bellwood, D.R. (2007) Life history patterns shape energy allocation among fishes on coral reefs. *Oecologia*, **153**, 111–120.

Dunstan, P.K. & Bax, N.J. (2007) How far can marine species go? Influence of population biology and larval movement on future range limits. *Marine Ecology Progress Series*, **344**, 15–28.

Eisaguirre, J.H., Eisaguirre, J.M., Davis, K., Carlson, P.M., Gaines, S.D. & Caselle, J.E. (2020) Trophic redundancy and predator size class structure drive differences in kelp forest ecosystem dynamics. *Ecology*.

Eklöf, J.S., de la Torre-Castro, M., Gullström, M., Uku, J., Muthiga, N., Lyimo, T. & Bandeira, S.O. (2008) Sea urchin overgrazing of seagrasses: A review of current knowledge on causes, consequences, and management. *Estuarine, Coastal and Shelf Science*, **79**, 569–580.

Evans, R.D., Wilson, S.K., Field, S.N. & Moore, J.A.Y. (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. *Marine Biology*, **161**, 599–607.

Feary, D.A., Pratchett, M.S., J Emslie, M., Fowler, A.M., Figueira, W.F., Luiz, O.J., Nakamura, Y. & Booth, D.J. (2014) Latitudinal shifts in coral reef fishes: why some species do and others do not shift. , **15**, 593–615.

Feehan, C.J., Grace, S.P. & Narvaez, C.A. (2019) Ecological feedbacks stabilize a turf-dominated ecosystem at the southern extent of kelp forests in the Northwest Atlantic. *Scientific Reports*, **9**, 7078.

Feng, M., Caputi, N., Chandrapavan, A., Chen, M., Hart, A. & Kangas, M. (2020) Multi-year marine cold-spells off the west coast of Australia and effects on fisheries. *Journal of Marine Systems*, 103473.

Figueira, W.F. & Booth, D.J. (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Global Change Biology*, **16**, 506–516.

Figueira, W.F., Curley, B. & Booth, D.J. (2019) Can temperature-dependent predation rates regulate range expansion potential of tropical vagrant fishes? *Marine Biology*, **166**, 73.

Filbee-Dexter, K. & Wernberg, T. (2018) Rise of turfs: A new battlefront for globally declining kelp forests. *Bioscience*.

Francini-Filho, R.B., Ferreira, C.M., Coni, E.O.C., De Moura, R.L. & Kaufman, L. (2010) Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: influence of resource availability and interference competition. *Journal of the Marine Biological Association of the UK*, **90**, 481–492.

Francini-Filho, R.B., Moura, R.L., Ferreira, C.M. & Coni, E.O.C. (2008) Live coral predation by parrotfishes (Perciformes: Scaridae) in the Abrolhos Bank, eastern Brazil, with comments on the classification of species into functional groups. *Neotropical Ichthyology*, **6**, 191–200.

Fredriksen, S., Filbee-Dexter, K., Norderhaug, K.M., Steen, H., Bodvin, T., Coleman, M.A., Moy, F. & Wernberg, T. (2020) Green gravel: a novel restoration tool to combat kelp forest decline. *Scientific Reports*, **10**, 3983.

Friedland, K.D., Langan, J.A., Large, S.I., Selden, R.L., Link, J.S., Watson, R.A. & Collie, J.S. (2020) Changes in higher trophic level productivity, diversity and niche space in a rapidly warming continental shelf ecosystem. *The Science of the Total Environment*, **704**, 135270.

Gianni, F., Bartolini, F., Airoldi, L. & Mangialajo, L. (2018) Reduction of herbivorous fish pressure can facilitate focal algal species forestation on artificial structures. *Marine Environmental Research*, **138**, 102–109.

Goren, M. & Galil, B.S. (2005) A review of changes in the fish assemblages of Levantine inland and marine ecosystems following the introduction of non-native fishes. *Zeitschrift fur angewandte Ichthyologie = Journal of applied ichthyology*, **21**, 364–370.

Gorman, D. & Connell, S.D. (2009) Recovering subtidal forests in human-dominated landscapes. *Journal of Applied Ecology*, **46**, 1258–1265.

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J. & White, A.T. (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews of the Cambridge Philosophical Society*, **90**, 1215–1247.

Guignabert, A., Augusto, L., Gonzalez, M., Chipeaux, C. & Delerue, F. (2020) Complex biotic interactions mediated by shrubs: Revisiting the stress-gradient hypothesis and consequences for tree seedling survival. *Journal of Applied Ecology*.

Hamilton, S.L. & Caselle, J.E. (2015) Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proceedings. Biological Sciences / the Royal Society*, **282**, 20141817.

Heck, K.L., Fodrie, F.J., Madsen, S., Baillie, C.J. & Byron, D.A. (2015) Seagrass consumption by native and a tropically associated fish species: potential impacts of the tropicalization of the northern Gulf of Mexico. *Marine Ecology Progress Series*, **520**, 165–173.

Hobbs, R.J., Higgs, E. & Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, **24**, 599–605.

Hoey, A.S. & Bellwood, D.R. (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology Letters*, **14**, 267–273.

Hsu, T.-H. & Gwo, J.-C. (2017) Fine-scale genetic structure of rabbitfish, Siganus fuscescens, in Penghu Archipelago following a mass mortality event caused by extreme cold winter weather. *Genes & genomics*, **39**, 645–652.

Hurst, T.P. (2007) Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, **71**, 315–345.

Hyndes, G.A., Heck, K.L., Vergés, A., Harvey, E.S., Kendrick, G.A., Lavery, P.S., McMahon, K., Orth, R.J., Pearce, A., Vanderklift, M., Wernberg, T., Whiting, S. & Wilson, S. (2016) Accelerating tropicalization and the transformation of temperate seagrass meadows. *Bioscience*, **66**, 938–948.

Kadota, T., Kiyomoto, S., Fukuda, H. & Yoshimura, T. (2017) Temporal patterns of aggregation formation around wave-dissipating blocks in the grey sea chub *Kyphosus bigibbus*. *NIPPON SUISAN GAKKAISHI*, **83**, 74–76.

Katayama, S., Akiyama, S., Naganuma, M. & Shibata, R. (2009) Age and growth of rabbitfish Siganus fuscescens in Tateyama Bay, Japan. *Aquaculture …*, **57**, 417–422.

Kingsbury, K.M., Gillanders, B.M., Booth, D.J. & Nagelkerken, I. (2019) Trophic niche segregation allows range-extending coral reef fishes to co-exist with temperate species under climate change. *Global Change Biology*.

Kirsch, K.D., Valentine, J.F. & Heck, K.L. (2002) Parrotfish grazing on turtlegrass Thalassia testudinum: evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. *Marine Ecology Progress Series*, **227**, 71–85.

Krumhansl, K.A. & Scheibling, R.E. (2012) Production and fate of kelp detritus. *Marine Ecology Progress Series*, **467**, 281–302.

Kumagai, N.H., García Molinos, J., Yamano, H., Takao, S., Fujii, M. & Yamanaka, Y. (2018) Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **115**, 8990–8995.

Kuwahara, H. (2015) The Evaluation of Current Status for Grazing Control Techniques of Herbivorous Fish. *Fisheries Engineering*, **51**, 253–257.

LaMonica, L.E., Fox, R.J. & Donelson, J.M. (2021) Thermal sensitivity of juvenile rabbitfishes Siganus doliatus and S. lineatus (Siganidae): a key role for habitat? *Coral Reefs*.

Layton, C., Coleman, M.A., Marzinelli, E.M., Steinberg, P.D., Swearer, S.E., Vergés, A., Wernberg, T. & Johnson, C.R. (2020) Kelp forest restoration in australia. *Frontiers in Marine Science*, **7**.

Layton, C., Shelamoff, V., Cameron, M.J., Tatsumi, M., Wright, J.T. & Johnson, C.R. (2019) Resilience and stability of kelp forests: The importance of patch dynamics and environment-engineer feedbacks. *Plos One*, **14**, e0210220.

Lee, S.J., Kim, M.J. & Han, S.H. (2019) Reproductive ecology of rabbit fish, Siganus fuscescens in the coastal waters off Jeju Island of Korea. *Journal of the Korean Society of Fisheries Ocean Technology*, **55**, 349–355.

Leighton, D.L., Jones, L.G. & North, W.J. (1966) Ecological relationships between giant kelp and sea urchins in southern california. *Proceedings of the fifth international seaweed symposium, halifax, august 25–28, 1965* pp. 141–153. Elsevier.

Lenanton, R.C.J., Dowling, C.E., Smith, K.A., Fairclough, D.V. & Jackson, G. (2017) Potential influence of a marine heatwave on range extensions of tropical fishes in the eastern Indian Ocean—Invaluable contributions from amateur observers. *Regional Studies in Marine Science*, **13**, 19–31.

Ling, S.D., Reeves, S.E. & Kriegisch, N. (2020) Octocoral barrier to grazing sea urchins allows macroalgal recovery on barrens ground. *Journal of Experimental Marine Biology and Ecology*, **524**, 151292.

Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon, A.K., Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., Blamey, L.K., Hereu, B., Ballesteros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M., Fujita, D. & Johnson, L.E. (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **370**, 20130269.

Löf, M., Madsen, P., Metslaid, M., Witzell, J. & Jacobs, D.F. (2019) Restoring forests: regeneration and ecosystem function for the future. *New Forests*, **50**, 139–151.

Lowry, E., Rollinson, E.J., Laybourn, A.J., Scott, T.E., Aiello-Lammens, M.E., Gray, S.M., Mickley, J. & Gurevitch, J. (2012) Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and Evolution*, **3**, 182–196.

Marras, S., Cucco, A., Antognarelli, F., Azzurro, E., Milazzo, M., Bariche, M., Butenschön, M., Kay, S., Di Bitetto, M., Quattrocchi, G., Sinerchia, M. & Domenici, P. (2015) Predicting future thermal habitat

suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. *Conservation Physiology*, **3**, cou059.

Marshak, A.R. & Heck, K.L. (2017) Interactions between range-expanding tropical fishes and the northern Gulf of Mexico red snapper Lutjanus campechanus. *Journal of Fish Biology*, **91**, 1139–1165.

McClanahan, T.R. (1992) Resource utilization, competition, and predation: a model and example from coral reef grazers. *Ecological Modelling*, **61**, 195–215.

McCloskey, R.M. & Unsworth, R.K.F. (2015) Decreasing seagrass density negatively influences associated fauna. *PeerJ*, **3**, e1053.

McDevitt-Irwin, J.M., Iacarella, J.C. & Baum, J.K. (2016) Reassessing the nursery role of seagrass habitats from temperate to tropical regions: A meta-analysis. *Marine Ecology Progress Series*, **557**, 133–143.

McMahon, K.W., Thorrold, S.R., Houghton, L.A. & Berumen, M.L. (2016) Tracing carbon flow through coral reef food webs using a compound-specific stable isotope approach. *Oecologia*, **180**, 809–821.

Mellin, C., Kulbicki, M. & Ponton, D. (2007) Seasonal and ontogenetic patterns of habitat use in coral reef fish juveniles. *Estuarine, coastal and shelf science*, **75**, 481–491.

Michael, P.J., Hyndes, G.A., Vanderklift, M.A. & Vergés, A. (2013) Identity and behaviour of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef. *Marine Ecology Progress Series*, **482**, 227–240.

Mihalitsis, M., Hemingson, C.R., Goatley, C.H.R. & Bellwood, D.R. (2021) The role of fishes as food: A functional perspective on predator–prey interactions. *Functional ecology*.

Milazzo, M., Mirto, S., Domenici, P. & Gristina, M. (2013) Climate change exacerbates interspecific interactions in sympatric coastal fishes. *The Journal of Animal Ecology*, **82**, 468–477.

Monaco, C.J., Bradshaw, C.J.A., Booth, D.J., Gillanders, B.M., Schoeman, D.S. & Nagelkerken, I. (2020) Dietary generalism accelerates arrival and persistence of coral-reef fishes in their novel ranges under climate change. *Global Change Biology*.

Moran, D. & Clements, K.D. (2002) Diet and endogenous carbohydrases in the temperate marine herbivorous fish Kyphosus sydneyanus. *Journal of Fish Biology*, **60**, 1190–1203.

Morris, R.L., Hale, R., Strain, E.M.A., Reeves, S.E., Vergés, A., Marzinelli, E.M., Layton, C., Shelamoff, V., Graham, T.D.J., Chevalier, M. & Swearer, S.E. (2020) Key Principles for Managing Recovery of Kelp Forests through Restoration. *Bioscience*.

Nakamura, Y., Horinouchi, M., Nakai, T. & Sano, M. (2003) Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. *Ichthyological research*, **50**, 15–22.

Nakamura, Y. & Tsuchiya, M. (2008) Spatial and temporal patterns of seagrass habitat use by fishes at the Ryukyu Islands, Japan. *Estuarine, Coastal and Shelf Science*, **76**, 345–356.

Nash, K.L., Graham, N.A.J., Januchowski-Hartley, F.A. & Bellwood, D.R. (2012) Influence of habitat condition and competition on foraging behaviour of parrotfishes. *Marine Ecology Progress Series*, **457**, 113–124.

Noda, M., Kawano, M., Okamoto, K. & Murase, N. (2016) Estimation of daily feeding rate and diel feeding rhythm of herbivorous fish Kyphosus bigibbus in captivity . *Journal of National Fisheries University*, **64**, 219–225.

Osland, M.J., Stevens, P.W., Lamont, M.M., Brusca, R.C., Hart, K.M., Waddle, J.H., Langtimm, C.A., Williams, C.M., Keim, B.D., Terando, A.J., Reyier, E.A., Marshall, K.E., Loik, M.E., Boucek, R.E., Lewis, A.B. & Seminoff, J.A. (2021) Tropicalization of temperate ecosystems in North America: The

northward range expansion of tropical organisms in response to warming winter temperatures. *Global Change Biology*.

Parker, J.R.C., Saunders, B.J., Bennett, S. & Harvey, E.S. (2021) Successful establishment of range-shifting, warm water Labridae in temperate South Western Australia. *Marine Ecology Progress Series*.

Pearce, A., Hutchins, B., Hoschke, A. & Fearns, P. (2016) Record high damselfish recruitment at Rottnest Island, Western Australia, and the potential for climate-induced range extension. *Regional Studies in Marine Science*, **8**, 77–88.

Pessarrodona, A., Foggo, A. & Smale, D.A. (2019) Can ecosystem functioning be maintained despite climate-driven shifts in species composition? Insights from novel marine forests. *The Journal of Ecology*, **107**, 91–104.

Pickholtz, R.S.M., Kiflawi, M., Friedlander, A.M. & Belmaker, J. (2018) Habitat utilization by an invasive herbivorous fish (Siganus rivulatus) in its native and invaded range. *Biological invasions*, **20**, 3499–3512.

Pörtner, H.O. & Peck, M.A. (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*, **77**, 1745–1779.

Rimmer, D.W. (1986) Changes in diet and the development of microbial digestion in juvenile buffalo bream, Kyphosus cornelii. *Marine Biology*, **92**, 443–448.

Rothans, T.C. & Miller, A.C. (1991) A link between biologically imported particulate organic nutrients and the detritus food web in reef communities. *Marine Biology*, **110**, 145–150.

Ruttenberg, B.I., Adam, T.C., Duran, A. & Burkepile, D.E. (2019) Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales. *Ecological Applications*, **29**, e01893.

Saoud, I.P., Mohanna, C. & Ghanawi, J. (2008) Effects of temperature on survival and growth of juvenile spinefoot rabbitfish (Siganus rivulatus). *Aquaculture research*, **39**, 491–497.

Sauchyn, L.K. & Scheibling, R.E. (2009) Degradation of sea urchin feces in a rocky subtidal ecosystem: implications for nutrient cycling and energy flow. *Aquatic Biology*, **6**, 99–108.

Semmler, R.F., Brandl, S.J., Keith, S.A. & Bellwood, D.R. (2021) Fine-scale foraging behavior reveals differences in the functional roles of herbivorous reef fishes. *Ecology and Evolution*.

Shantz, A.A., Ladd, M.C., Schrack, E. & Burkepile, D.E. (2015) Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecological Applications*, **25**, 2142–2152.

Silvano, R.A.M. & Güth, A.Z. (2006) Diet and feeding behavior of Kyphosus spp. (Kyphosidae) in a Brazilian subtropical reef. *Brazilian Archives of Biology and Technology*, **49**, 623–629.

Slesinger, E., Jensen, O.P. & Saba, G. (2021) Spawning phenology of a rapidly shifting marine fish species throughout its range. *ICES Journal of Marine Science*.

Soliman, V.S. & Yamaoka, K. (2010) Assessment of the fishery of siganid juveniles caught by bagnet in Lagonoy Gulf, Southeastern Luzon, Philippines. *Journal of Applied Ichthyology*, **26**, 561–567.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental conservation*, **29**.

Streit, R.P., Cumming, G.S. & Bellwood, D.R. (2019) Patchy delivery of functions undermines functional redundancy in a high diversity system. *Functional ecology*.

Tanaka, K., Taino, S., Haraguchi, H., Prendergast, G. & Hiraoka, M. (2012) Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. *Ecology and Evolution*, **2**, 2854–2865.

Teagle, H. & Smale, D.A. (2018) Climate-driven substitution of habitat-forming species leads to reduced biodiversity within a temperate marine community. *Diversity & Distributions*.

Trapon, M.L., Pratchett, M.S. & Hoey, A.S. (2013) Spatial variation in abundance, size and orientation of juvenile corals related to the biomass of parrotfishes on the Great Barrier Reef, Australia. *Plos One*, **8**, e57788.

Truong, L., Suthers, I.M., Cruz, D.O. & Smith, J.A. (2017) Plankton supports the majority of fish biomass on temperate rocky reefs. *Marine Biology*, **164**, 73.

Vanderklift, M.A., Lavery, P.S. & Waddington, K.I. (2009) Intensity of herbivory on kelp by fish and sea urchins differs between inshore and offshore reefs. *Marine Ecology Progress Series*, **376**, 203–211.

Vanderklift, M.A., Pillans, R.D., Hutton, M., De Wever, L., Kendrick, G.A., Zavala-Perez, A., Vergés, A., Garthwin, R., Oades, D., McCarthy, P., George, K., Sampi, T., George, D., Sampi, C., Edgar, Z., Dougal, K. & Howard, A. (2021) High rates of herbivory in remote northwest Australian seagrass meadows by rabbitfish and green turtles. *Marine Ecology Progress Series*, **665**, 63–73.

Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M.A., Wernberg, T., Ainsworth, T. & Steinberg, P.D. (2019) Tropicalisation of temperate reefs: Implications for ecosystem functions and management actions. *Functional ecology*, **33**, 1000–1013.

Vergés, A., Steinberg, P.D., Hay, M.E., Poore, A.G.B., Campbell, A.H., Ballesteros, E., Heck, K.L., Booth, D.J., Coleman, M.A., Feary, D.A., Figueira, W., Langlois, T., Marzinelli, E.M., Mizerek, T., Mumby, P.J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A.S., Smale, D.A. & Wilson, S.K. (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings. Biological Sciences / the Royal Society*, **281**, 20140846.

Ward, A.J.W., Herbert-Read, J.E., Sumpter, D.J.T. & Krause, J. (2011) Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 2312–2315.

Weeks, R., Green, A.L., Joseph, E., Peterson, N. & Terk, E. (2017) Using reef fish movement to inform marine reserve design. *Journal of Applied Ecology*, **54**, 145–152.

Wernberg, T., Coleman, M.A., Babcock, R.C., Bell, S.Y., Bolton, J.J., Connell, S.D., Hurd, C.L., Johnson, C.R., Marzinelli, E.M., Shears, N.T., Steinberg, P.D., Thomsen, M.S., Vanderklift, M.A., Vergés, A. & Wright, J.T. (2019a) Biology and Ecology of the Globally Significant Kelp Ecklonia radiata. *Oceanography and marine biology: an annual review* (eds S.J. Hawkins),, A.L. Allcock),, A.E. Bates),, L.B. Firth),, I.P. Smith),, S.E. Swearer), & P.A. Todd), pp. 265–323. CRC Press.

Wernberg, T., Krumhansl, K., Filbee-Dexter, K. & Pedersen, M.F. (2019b) Status and trends for the world's kelp forests. *World seas: an environmental evaluation* pp. 57–78. Elsevier.

Whalen, M.A., Whippo, R.D.B., Stachowicz, J.J., York, P.H., Aiello, E., Alcoverro, T., Altieri, A.H., Benedetti-Cecchi, L., Bertolini, C., Bresch, M., Bulleri, F., Carnell, P.E., Cimon, S., Connolly, R.M., Cusson, M., Diskin, M.S., D'Souza, E., Flores, A.A.V., Fodrie, F.J., Galloway, A.W.E. & Duffy, J.E. (2020) Climate drives the geography of marine consumption by changing predator communities. *Proceedings of the National Academy of Sciences of the United States of America*.

White, J.W. & Warner, R.R. (2007) Behavioral and energetic costs of group membership in a coral reef fish. *Oecologia*, **154**, 423–433.

Yorke, C.E., Page, H.M. & Miller, R.J. (2019) Sea urchins mediate the availability of kelp detritus to benthic consumers. *Proceedings. Biological Sciences / the Royal Society*, **286**, 20190846.

Zarco-Perello, S. & Enríquez, S. (2019) Remote underwater video reveals higher fish diversity and abundance in seagrass meadows, and habitat differences in trophic interactions. *Scientific Reports*, **9**, 6596.

Zarco-Perello, S., Pratchett, M. & Liao, V. (2012) Temperature-growth performance curves for a coral reef fish, *Acanthochromis polyacanthus*. *Galaxea, Journal of Coral Reef Studies*, **14**, 97–103.

Zarco-Perello, S., Wernberg, T., Langlois, T.J. & Vanderklift, M.A. (2017) Tropicalization strengthens consumer pressure on habitat-forming seaweeds. *Scientific Reports*, **7**, 820.