Climate change: underwater forest decline

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- Ocean warming is causing a 'tropicalisation' of temperate reefs in eastern and western Australia, leading to a decline in canopy seaweeds that fulfil a role similar to trees in forests.
- Increasing temperatures have direct negative effects on cool water seaweeds and can also increase the rate at which herbivores eat them, leading to overall seaweed decline
- The disappearance of canopy seaweeds changes community structure, impacts biodiversity, and can lead to the collapse of Australia's most valuable commercial fisheries

Loss of kelp forest places commercial fisheries at risk

Rabbitfish (Siganus spp.) are one of the main warm-affinity species observed overgrazing seaweed forests in Japan, the Mediterranean and Australia. Photocredit: Adriana Vergés

Ocean warming causes physiological stress in cool water species and facilitates the expansion of warm water species onto temperate reefs. This is leading to range contractions of important cool water organisms such as canopy seaweeds, which fulfil a role similar to trees in forests. These underwater forests provide food and shelter to hundreds of species, and support Australia's most economically important fisheries, such as rock lobster and abalone.

Increased temperature impacts seaweeds directly and indirectly, e.g. via effects on species that eat them. In Tasmania, warming has been directly linked to a decline in giant kelp forest canopy cover of over 90% since the 1940s. In Western Australia, an extreme heat wave caused the disappearance of several dominant seaweeds over ~ 100 km.

The greatest *indirect* impacts of warming in seaweed forests are caused by herbivore consumers. As the distribution of warm water herbivores expands, cool water seaweeds that have evolved under low levels of herbivory face increasing herbivore diversity and grazing intensity. In Tasmania, warming has led to the range expansion of a sea urchin that has overgrazed kelp forests. Similarly, increased feeding by tropical and subtropical fishes is increasing herbivore pressure on seaweeds near the warm edge of their distribution.

The climate-mediated loss of seaweeds has reduced the biodiversity of temperate reefs in Tasmania and the Mediterranean, and has been linked to the collapse of commercial fisheries in Japan. Elsewhere in Australia, climate change is emerging as a key threat to algal forests and the species they support.

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Supporting Evidence

Title	Aim	Key Results
Basford A. J., Feary D. A., Truong G., Steinberg P. D., Marzinelli E. M. & Vergés A. (2015) Feeding habits of range-shifting herbivores: tropical surgeonfishes in a temperate environment. Mar Freshw Res.	Compare feeding habits of range-shifting tropical herbivorous surgeonfish to warm-termperate species commonly found in temperate reefs	In aquarium experiments, tropical surgeonfishes consumed more algae than temperate species, especially at high temperatures - implies overall levels of herbivory will increase if these species establish populations
Bates A. E., Barrett N. S., Stuart-Smith R. D., Holbrook N. J., Thompson P. A. & Edgar G. J. (2014) Resilience and signatures of tropicalization in protected reef fish communities. Nature Clim. Change 4, 62-7.	Analyse the species richness, diversity and functional traits of temperate reef fish communities over 20 years in a global warming hotspot and compare patterns in a marine reserve with nearby sites open to fishing	In response to 20 years warming: increasing functional trait richness and functional diversity, driven in part by a general increase in herbivores. Fished areas more susceptible to change than reserve areas
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) Defini	Clarify the processes of range contraction and extension; identify and describe different stages of each	Range extensions occur as a sequence of (1) arrival, (2) population increase, and (3) persistence. By contrast, range contractions occur progressively as (1) performance decline, (2) population decrease and (3) local extinction.
Bennett, S., T. Wernberg, E. S. Harvey, J. Santana-Garcon and B. J. Saunders (2015). Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. Ecology Letters 18(7): 714-723.	Test the effects of herbivores on maintaining a canopy-free state in a tropical-temperate transition zone after a heatwave event that led to complete seaweed canopy loss	After an intense heat-wave event in 2011 that led to complete canopy loss in a tropical-temperate transition zone, turf grazing herbivorous fishes increasedin biomass and diversity, whereas canopy-browsing herbivores retained high, but unchanged, biomass levels. These observations suggest that tropical herbivores are maintaining previously kelp-dominated temperate reefs in an alternate canopy-free state bygrazing turfs and preventing kelp reestablishment.
Booth D. J., Bond N. & Macreadie P. (2011) Detecting range shifts among Australian fishes in response to climate change. Mar Freshw Res 62, 1027-42.	Non-quantitative conceptual review of climate-mediated range shifts in freshwater, estuarine and marine fish	< 300 papers published on climate-mediated range shifts globally, 7% of these are Australian. Authors highlight conceptual difficulties associated with defining the concept of 'range shift' as fish distributions naturally fluctuateover large areas due to broad dispersal of offspring and non-climate related environmental changes (e.g. ENSO). Best available evidence of shifts comes from historical and current commercial fishery datasets related to changing water temperatures. In Australia, there is a lack of rigorous data on fish ranges and recommendations to ammend this are discussed. Increases in water temperature, reduced freshwater flows and changes in ocean currents are highlighted as the most likely drivers of climate- induced range shifts in Australian fishes.

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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, 102-14.	Document occurrence of tropical fishes within temperate reefs in the east coast of Australia and evaluate the role of the East Australian Current in facilitating their presence	A total of 47 species of tropical fishes from 11 families were observed during the summer recruitment season (January to May) in NSW. Density and species richness tended to be higher in northern NSW sites. Little evidence that individual recruitment events were correlated with local increases in water temperature inferred to be associated with East Australian Current ingresses.
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. Mar Freshw Res 63, 415-27.	Predict current species distributions for 30 tropical, sub-tropical and temperate species that occur along the coast of Western Australia	Under A1B scenario for the future ocean, the median rate of distribution shift is around 19 km/decade towards higher latitudes and 9m deeper/decade by 2055 relative to 2005; the coast of Western Australia is expected to experience a
Feary D. A., Pratchett M. S., J Emslie M., Fowler A. M., Figueira W. F., Luiz O. J., Nakamura Y. & Booth D. J. (In press) Latitudinal shifts in coral reef fishes: why some species do and others do not shift	Review of factors likely to influence latitudinal shifts in tropical fishes, including larval supply, settlement and post-settlement processes	Tropical vagrant species are more likely to originate from high-latitude populations; tropical sifhes with large body size, high swimming ability, large size at settlement and pelagic spawning behaviour are more likely to successfully settle into temperate habitats. Habitat and food limitation at settlement and within juvenile stages may constrain the incursion of tropical fish species that depend on coral resources.
Figueira W. F. & Booth D. J. (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. Global Change Biol 16, 506-16.	Quantify overwinter survival of tropical fish in SE Australia and evaluate the role of water temperature in facilitating overwintering	The probability of persistence of juvenile tropical species in temperate reefs was most strongly influenced by average winter temperature and there was no effect of recruitment strength. Current warming trajectories predict 100% of winters will be survivable by at least some tropical species in temperate reefs around Sydney by 2080.
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., Richard	Compile evidence for impacts of climate change in eastern Tasmania (Australia)	Regional decline in the extent of dense beds of giant kelp, marked changes in the distribution of nearshore fishes and range expansions of other northern warmer-water species. Over-grazing of seaweed beds by a recently established sea urchin is causing a fundamental shift in the structure and dynamics of Tasmanian rocky reef systems
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., Richard	Compile evidence for impacts of climate change in eastern Tasmania (Australia)	Regional decline in the extent of dense beds of giant kelp, marked changes in the distribution of nearshore fishes and range expansions of other northern warmer-water species. Over-grazing of seaweed beds by a recently established sea urchin is causing a fundamental shift in the structure and dynamics of Tasmanian rocky reef systems
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, 883-94.	Examine the impact of Centrostephanus rodgersii, a range-extending sea urchin, on reef habitat structure and associated biodiversity in Tasmania (Australia)	Algal communities converged to controls within 2 years of urchin removal. The faunal community of recovered with the seaweeds while the barrens habitat remained overwhelmingly impoverished with only 72 of 296 recorded taxa. C. rodgersii grazing results in an estimated minimum net loss of 150 taxa associated with seawees

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Ling S. D., Johnson C. R., Frusher S. D. & Ridgway K. R. (2009) Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc Natl Acad Sci USA 106, 22341-5.	To examine whether fishing has reduced kelp bed resilience and thus increased the risk of catastrophic overgrazing by the range-extending urchin C. rodgersii	Lobsters accounted for 92%-100% of observed predation events on urchins. In predation experiments only very large lobsters were successful predators of Centrostephanus rodgersii. Overlaying observed predation events with a physical model based on the size of the arc of the first pair of legs on lobsters, revealed that the upper theoretical limit predicted by the model was in close agreement with the ceiling of observed successful predation events. In situ only C. rodgersii >60 mm test diameter (TD) were observed to exist exposed on the reef surface and are vulnerable to lobster predation. . Given the size distribution of emergent C. rodgersii in eastern Tasmania, we estimated the minimum sized lobster capable of preying on C. rodgersii under natural conditions to be approximately 140 mm carapace length. Modelling of annual population projections using the apparent survival rates revealed significantly reduced survival for C. rodgersii inside MPAs (0.094/pop.annum) relative to the fished reefs (0.613/pop.annum). This demonstrates that fishing, by removing large predatory lobsters, has reduced the resilience of kelp beds against the climate-driven threat of the sea urchin and thus increased risk of catastrophic shift to widespread sea urchin barrens
Nakamura Y., Feary D. A., Kanda M. & Yamaoka K. (2013) Tropical fishes dominate temperate reef fish communities within western Japan. Plos One 8, e81107.	To examine the importance of resource use in structuring the distribution patterns of range shifting tropical and subtropical fishes in temperate reefs within SW Japan	Despite the temperate latitude surveyed (33 degrees N), the fish assemblage was dominated by tropical fishes numerically and in terms of richness within both coral, and rocky reef habitats. A relatively large number of tropical species are overwintering within both coral and rocky habitats, with a subset of these species being potentially reproductively active.
Sala E., Kizilkaya Z., Yildirim D. & Ballesteros E. (2011) Alien marine fishes deplete algal biomass in the eastern Mediterranean. Plos One 6, e17356.	To determine the role of herbivorous fishes on creating a shift from macroalgal dominance to barrens in the eastern Mediterranean	A well-developed algal assemblage grew in barren habitats when fish were excluded for three months. Two tropical, invasive, herbivorous fishes (Siganus luridus and S. rivulatus) are suggested to be responsible fot the creation and maintenance of barrens
Sen Gupta A., Brown J. N., Jourdain N. C., van Sebille E., Ganachaud A. & Vergés A. (In press) Episodic and non-uniform migration of thermal habitats in a warming ocean. Deep Sea Research Part II: Topical Studies in Oceanography.	To compare the rates of isotherm movement between different ocean regions and at different time scales and to examine to what extent the implied movement is uniform or sporadic.	Long-term warming implies poleward shifts of isotherms in almost all regions. At present on decadal and longer timescales changes due to low frequency natural SST variability can dominate over human-induced changes. Median isotherm shift speeds will be 7 times faster in the 21st Century compared to the 20th Century. SST warming will be greater in the summer in most oceanic regionss. Isotherms often exhibit erratic migration rates over time, even under uniform warming. Species ranges therefore also expected to undergo suddent rapid shifts rather than gradual monotonic poleward movement.
Serisawa Y., Imoto Z., Ishikawa T. & Ohno M. (2004) Decline of the Ecklonia cava population associated with increased seawater temperatures in Tosa Bay, southern Japan. Fish Sci 70, 189-91.	To assess changes in (i) abundance of the kelp Ecklonia cava, (ii) abalone catches/ generated income and seawater temperature in Tosa Bay (southern Japan) between 1991-2001	Local disappearance of Ecklonia cava after 2000. Simultaneous collapose of associated abalone fishery and rise in SST

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Smale D. A. & Wernberg T. (2013) Extreme climatic event drives range contraction of a habitat-forming species. Proceedings of the Royal Society B: Biological Sciences 280.	To document impacts of an extreme marine heat wave on the distribution and abundance of a forest-forming seaweed, and to assess potential long-term changes in reef communities	The marine heat wave eliminated Scytothalia dorycarpa at its warm distribution limit, causing a range contraction of approximately 100 km (approx. 5% of its global distribution). Seawater temperatures during the HW exceeded the seaweed's physiological threshold and caused extirpation of marginal populations.
Steneck R. S. & Johnson C. R. (2013) Kelp forests: dynamic patterns, processes and feedbacks. In: Marine Community Ecology (eds M. Bertness, B. Silliman and J. J. Stachowicz) pp. 315-36. Sinaur Associates Inc.	Review of the key patterns and processes that influence the ecosystem and functioning of kelp forest communities	Highlights the dynamic nature of kelp forests ecosystems
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., Gupt	Conceptual paper proposing a new type of phase-shift away from macroalgal dominance in temperate reefs and mediated by increased herbivory due to the range expansion and increased feeding rates of tropical/ warm-temperate species	Overgrazing of temperate macroalgae by tropical herbivorous fishes has already occurred in Japan and the Mediterranean. Emerging evidence suggests similar phenomena are occurring in other temperate reefs, with increasing occurrence of tropical fishes on temperate reefs.
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, 1518-27.	To determine how tropical rabbitfish abundance is related to sea surface temperature. To relate changes in rabbitfish abundance to benthic community composition and to quantify feeding patterns and preferences of native temperate herbivorous fish vs. invasive tropical rabbitfish.	Identification of two clearly distinct ares: a warmer group of regions with abundant tropical rabbitfish and a colder group of regions where these consumers were absent/ extremely rare. In regions with abundant rabbitfish, canopy algae were 65% less abundant, and there was a 60% reduction of overall benthic biomass (algae and invertebrates) and a 40% decrease in total species richness. Video-recorded feeding experiments showed that temperate native herbivores exhibited greater grazing rates, but tropical rabbitfish fed complementarily on both established macroalgae and on epilithic algae containing macroalgal recruits
Wernberg T., Russell B. D., Moore P. J., Ling S. D., Smale D. A., Campbell A., Coleman M. A., Steinberg P. D., Kendrick G. A. & Connell S. D. (2011) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. J Exp M	To review known changes in Australia's temperate reef ecosystems that might have been forced by climate change and variability, and to forecast future change that might be managed by policy	There are many examples of impacts that might have been forced by climate change, all of which relate to temperature and interactions with other stressors. There is a severe lack of appropriate base line data. Due to Australia's (bio)geography, further change will likely result in extinction of unique species.

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Wernberg T., Russell B. D., Thomsen M. S., Gurgel C. F. D., Bradshaw C. J. A., Poloczanska E. S. & Connell S. D. (2011) Seaweed communities in retreat from ocean warming. Curr Biol 21, 1828-32.	Test for polewards shifts in Australian temperate seaweed floras since 1940's	Poleward shift in the northern-most records of temperate species in western (0.46 degree latidtude) and eastern (1.92 degree latitude) Australia
Wernberg T., Smale D. A., Tuya F., Thomsen M. S., Langlois T. J., de Bettignies T., Bennett S. & Rousseaux C. S. (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nature Clim. Change 3, 78-82.	To test the impacts of an extreme marine heat wave on benthic and fish communities in a cool and a warm location.	The marine heat wave had substantial effects on benthic and fish communities at the northern (warm) location but not at the southern (cool) location. Forest-forming seaweeds declined (~50% loss) in abundance whereas turf seaweeds increased (~100% increase). There was an increase (~100% incraese in 'tropicalisation index') in the proportion of warm-affinity fishes.
Wernberg T., Thomsen M. S., Tuya F., Kendrick G. A., Staehr P. A. & Toohey B. D. (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecol Lett 13, 685-94.	To assess the links between physiological (photosynthesis) and ecological (abundance, recruitment and recovery) performance of the kelp Ecklonia radiata across a temperature gradient	Strong negative relationship between annual mean ocean temperature and the temperature sensitivity of both maximum net photosynthesis and dark respiration. Increasing intensity of disturbance affected photosynthetic traits, but the magnitude of the effect differed between cool and warm ocean climate with the effect being smaller under warm compared with cool conditions (F: 13% vs. 28%, ETRmax: 9% vs. 24%). There was an interaction between ocean climate and intensity of disturbance, with higher recruitment following severe compared with moderate disturbance in the cool climate, but the reverse in the warm ocean climate. An identical pattern was observed for recruit growth. In contrast to rapid recovery in the cool climate, these short-term effects on recruit performance translated into suppressed canopy recovery almost 2 years later in the warm climate.
Yamaguchi A. (2010) Biological aspects of herbivorous fishes in the coastal areas of western Japan. Bull Fish. Res. Agen. 32, 89-94.	To quantify the distribution, feeding habits, reproductive behaviour, growth, migration and population strucutre of herbivorous fishes in temperate reefs where seaweed cover has declined	Tropical/ warm-temperate herbivorous fishes overwinter in temperate reefs. The activity of rabbitfish and kyphosids markedly declines with water temperature = suggestion that recent rises in winter water temperature has extended the period of high grazing activity of herbivorous fishes. Gut content and feeding preference experiments show Kyphosus bigibbus preferentially feeds on canopy brown algae.

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