Climate driven regime shift of a temperate marine ecosystem

Thomas Wernberg[1*†], Scott Bennett[1,2,3†], Russell C. Babcock[1,4], Thibaut de Bettignies[1,5], Katherine Cure[1], Martial Depczynski[6], Francois Dufois[7], Jane Fromont[8], Christopher J. Fulton[9], Renae K. Hovey[1], Euan S. Harvey[2], Thomas H. Holmes[1,10], Gary A. Kendrick[1], Ben Radford[6], Julia Santana-Garcon[1,2,3], Benjamin J. Saunders[2], Dan A. Smale[1,11], Mads S. Thomsen[1,12], Chenae A. Tuckett[1], Fernando Tuya[13], Mathew A. Vanderklift[7], Shaun Wilson[1,10]

[1] School of Plant Biology & UWA Oceans Institute, University of Western Australia, 39 Fairway, Crawley, WA 6009 Australia

[2] Department of Environment and Agriculture, School of Science, Curtin University, Bentley, WA 6102 Australia

[3] Department of Global Change Research, Institut Mediterrani d'Estudis Avançats (Universitat de les Illes Balears - Consejo Superior de Investigaciones Científicas), Esporles, Spain.

[4] CSIRO Oceans and Atmosphere, GPO Box 2583, Brisbane, QLD 4001 Australia

[5] Service du Patrimoine Naturel, Muséum National d'Histoire Naturelle, 36 rue Geoffroy Saint-Hilaire CP41, Paris 75005, France

[6] Australian Institute of Marine Science, 39 Fairway, Crawley, WA 6009 Australia

[7] CSIRO Oceans & Atmosphere Flagship, Private Bag 5, Wembley, WA 6913 Australia

[8] Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986 Australia

[9] Research School of Biology, Australian National University, Canberra, ACT 2601 Australia

[10] Marine Science Program, Science Division, Department of Parks and Wildlife, Kensington, WA 6151 Australia

[11] Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB United Kingdom

[12] Marine Ecology Group, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch New Zealand

[13] IU-ECOAQUA, Universidad de Las Palmas de Gran Canaria, 35017, Canary Islands Spain

*Correspondence to: thomas.wernberg@uwa.edu.au.

† Shared lead authorship. Other authors arranged alphabetically.

One Sentence Summary:

Rapid collapse of extensive kelp forests and a regime shift to tropicalized temperate reefs followed extreme heatwaves and decades of gradual warming.

Abstract:

Ecosystem reconfigurations arising from climate driven changes in species distributions are expected to have profound ecological, social and economic implications. Here, we reveal a rapid climate driven regime shift of Australian temperate reef communities, which lost their defining kelp forests and became dominated by persistent seaweed turfs. Following decades of ocean warming, extreme marine heatwaves forced a 100 km range contraction of extensive kelp forests, and saw temperate species replaced by seaweeds, invertebrates, corals and fishes characteristic of subtropical and tropical waters. This community wide tropicalization fundamentally altered key ecological processes, suppressing the recovery of kelp forests.

Main Text:

Broad scale losses of species which provide the foundations for habitats cause dramatic shifts in ecosystem structure because they support core ecological processes (*1-3*). Such habitat loss can lead to a regime shift where reinforcing feedback mechanisms intensify to provide resilience to an alternate community configuration, often with profound ecological, social and economic consequences (*4-6*). Benthic marine regime shifts have been associated with the erosion of ecological resilience through overfishing or eutrophication, altering the balance between consumers and resources, rendering ecosystems vulnerable to major disturbances (*1, 2, 6, 7*). Now, climate change is also contributing to the erosion of resilience (*8, 9*), where increasing temperatures are modifying key physiological, demographic and community scale processes (*8, 10*), driving species redistribution at a global scale and rapidly breaking down long-standing biogeographic boundaries (*11, 12*). These processes culminate in novel ecosystems where tropical and temperate species interact with unknown implications (*13*). Here we document how a marine heatwave caused the loss of kelp forests across ~2,300 km^2 of Australia's Great Southern Reef, forcing a regime shift to seaweed turfs. We demonstrate a rapid 100 km range-contraction of kelp forests and a community-wide shift toward tropical species with ecological processes suppressing kelp forest recovery.

To document ecosystem changes we surveyed kelp forests, seaweeds, fish, mobile invertebrates and corals at 65 reefs across a ~2,000 km tropical to temperate transition zone in western Australia (*14*). Surveys were conducted between 2001 to 2015, covering the years before and after an extreme marine heatwave impacted the region.

The Indian Ocean adjacent to western Australia is a 'hotspot' where the rate of ocean warming is in the top 10% globally (*15*), and isotherms are shifting poleward at a rate of 20 – 50 km per decade (*16*). Until recently, kelp forests were dominant along >800 km of the west coast (*8*), covering 2,266 km^2 of rocky reefs between 0 – 30 m depth south of 27.7°S (Fig. 1). Kelp forests along the midwest section of this coast (27.7 – 30.3°S) have experienced steadily increasing ocean temperatures since the 1970s, recently punctuated by three of the warmest summers in the last 215 years (Fig. 2, *17, 18, 19*). In December 2010, immediately prior to an extreme marine 'heatwave', kelp forests covered over ~70% of shallow rocky reefs in the

midwest (Figs. 2, S1), with no differences in kelp cover or biomass among reefs along the west coast (Figs. 1, S1, S2, *8*). During this time, seaweed and fish communities in the midwest were similar to the temperate southwest (~500 km farther south), and clearly distinct from those of tropical reefs in the northwest (~500 km farther north) (Figs. 3A, B, S3, *17*).

By early 2013, only two years later, our extensive surveys found a 43% (963 km^2) loss of kelp forests on the west coast (Fig. 1). Previously dense kelp forests north of 29°S had disappeared (Figs. 2, S1) or been severely decimated (>90% loss, Fig. 1), representing a ~120 km range contraction and functional extinction (reduction in abundance sever enough to delete ecological function) from 370 km^2 of reef. In their place we found a dramatic increase in the cover of turf forming seaweeds (Fig. 2) and a community wide shift from species characteristic of temperate waters, to species and functional groups characteristic of subtropical and tropical waters (Figs. 3, 4, S3, $\varphi_{2,52} = -0.70$, $p < 0.001$). Compared to the composition of the highly impacted midwest reef communities in Kalbarri before the 2011 marine heatwave, differences in community structure (Bray-Curtis dissimilarity) to Perth in the temperate southwest increased by 91% and 28% for seaweeds and fishes, respectively, whereas differences to Ningaloo Reef in the tropical northwest decreased by 32% and 16%, respectively. This broad scale community wide reef transformation reflected consistent decreases in the abundance of taxa characteristic of temperate reefs, coinciding with increases in the abundance of species characteristic of subtropical and tropical reefs - for both seaweeds (Fig. 3C, Table S2, $\varphi_{2,20} = -0.81$, $p < 0.001$) and fishes (Fig. 3D, Table S3, $\varphi_{2,20} = -0.64$, $p = 0.008$). Similar changes were seen for sessile and mobile invertebrates in the southern part of the midwest region, where small hermatypic coral colonies increased almost 6-fold in abundance, and doubled in species richness (Table S5), while abundances of sea urchins and gastropods also increased and decreased in accordance with their thermal affinities (Fig. 4, Tables S4, S5, $\varphi_{2,12} = -0.68$, $p < 0.045$).

Even though the acute climate stressor has abated (Figs. 2, S1), as of late 2015, almost five years after the heatwave, we have observed no signs of kelp forest recovery on the heavily impacted reefs north of 29°S. Instead, concurrent with an 80% reduction in standing seaweed biomass (Fig. S2), we have recorded subtropical and tropical fish feeding rates on canopy seaweeds that are three times higher than on comparable coral reef systems. Similarly, we have found a 400% increase in biomass of scraping and grazing fishes, a functional group characteristic of coral reefs, which now display grazing rates on seaweed turfs that are comparable to those observed on healthy coral reefs worldwide (Table S6, *10*). High herbivore pressure now suppresses the recovery of kelp forests by cropping turfs and kelp recruits (*10*).

We deduce that extreme temperatures beginning in 2011 exceeded a physiological tipping point for kelp forests north of 29°S, and now reinforcing feedback mechanisms have established, supporting the new kelp-free state. Similar ecosystem changes have not been observed in the southwest, where heatwave temperatures remained within the thermal tolerance of kelps (*17*) and the greater distance to tropical bioregions limited the incursion of tropical species. Threshold temperatures for kelp forests appear close to 2.5ºC above long term summer maximum temperatures, consistent with other seaweeds in the region (*20*). However, the partial loss of kelp forests on reefs between 29 – 32ºS suggests there is variation in threshold temperatures within and between kelp populations.

The consistent responses of both cool and warm water species clearly illustrate the important role of temperature. However, the transition in community structure and subsequent

persistence of the new regime would have been augmented by the low and high availability of temperate and tropical propagules and immigrants, respectively, as well as changes in competitive interactions following the loss of kelp canopies (*21*). The oceanography of the region is dominated by the poleward flowing Leeuwin Current, which delivers warm nutrient poor water and tropical species into the temperate region, while limiting the supply of propagules including kelp zoospores from higher latitude kelp forests (*22, 23*). Indeed, healthy coral reefs already occur at the Houtman-Abrolhos Islands, 60 km offshore from Kalbarri directly in the path of the Leeuwin Current. Until now, however, cooler coastal waters have enabled kelp forests to dominate nearshore reefs.

The Leeuwin Current is strongly influenced by the El Niño Southern Oscillation (*24*). The strength of the Leeuwin Current and the flow of warm tropical water down the west coast of Australia increase during the La Niña phase of this cycle. These La Niña conditions drive warming anomalies such as the 2011 marine heatwave (*24*) and are predicted to double in frequency and intensity in the near future (*25*). Moreover, the southeast Indian Ocean has gradually warmed at least 0.65 °C over the past five decades, and will continue to warm until the end of the century and beyond (*19*). Kelp forest recovery from disturbances can be slow in the nutrient poor west coast waters, even in the cool southwest (*8, 26*), providing time for populations of herbivorous fish to become established and seaweed turfs to proliferate. Consequently, the probability of prolonged cool conditions that could reset community structure and ecological processes to facilitate the recovery of kelp forests, is becoming increasingly unlikely, while the risk of more heatwaves that will exacerbate and expand the new tropicalized ecosystem state is increasing (*25*).

Short term climate variability has previously precipitated large scale destruction of kelp forests (*27, 28*), which have mostly recovered as environmental conditions returned to normal. The future of kelp forest communities in western Australia is, however, grim. Warming, increasing heatwaves and intrusion of tropical species into temperate habitats are unequivocal (*13, 19, 25*). The current velocity of ocean warming is pushing kelp forests towards the southern edge of the Australian continent (*29*), where they are at risk of rapid local extinction over thousands of kilometers due to the east-west orientation of the continent's poleward coastline and west to east flow of surface currents (*12*). This would devastate lucrative fishing and tourism industries worth more than A\$10 billion per year (*30*) and have catastrophic consequences for the thousands of endemic species (*30*) supported by the kelp forests of Australia's Great Southern Reef.

References and Notes:

1.   T. P. Hughes, Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547-1551 (1994).
2.   R. S. Steneck *et al.*, Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* **29**, 436-459 (2002).
3.   M. S. Thomsen *et al.*, Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. *Integr. Comp. Biol.* **50**, 158-175 (2010).
4.   M. Scheffer, S. Carpenter, J. A. Foley, C. Folke, B. Walker, Catastrophic shifts in ecosystems. *Nature* **413**, 591-596 (2001).
5.   N. A. J. Graham *et al.*, Managing resilience to reverse phase shifts in coral reefs. *Frontiers Ecol. Env.* **11**, 541-548 (2013).

6. R. S. Steneck, A. Leland, D. C. McNaught, J. Vavrinec, Ecosystem flips, locks, and feedbacks: the lasting effects of fisheries on Maine's kelp forest ecosystem. *Bull. Mar. Sci.* **89**, 31-55 (2013).

7. S. D. Ling, C. R. Johnson, S. D. Frusher, K. R. Ridgway, Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proc. Nat. Acad. Sci. U.S.A.* **106**, 22341-22345 (2009).

8. T. Wernberg *et al.*, Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. *Ecol. Lett.* **13**, 685-694 (2010).

9. N. A. J. Graham, S. Jennings, M. A. MacNeil, D. Mouillot, S. K. Wilson, Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**, 94-97 (2015).

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

11. E. S. Poloczanska *et al.*, Global imprint of climate change on marine life. *Nat. Clim. Change* **3**, 919-925 (2013).

12. T. Wernberg *et al.*, Seaweed communities in retreat from ocean warming. *Curr. Biol.* **21**, 1828-1832 (2011).

13. A. Vergés *et al.*, The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proc. Roy. Soc. B.* **281**, 20140846 (2014).

14. Materials and methods are available as supplementary materials on Science Online.

15. A. Hobday, G. Pecl, Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. *Rev. Fish Biol. Fisheries*, 1-11 (2013).

16. M. T. Burrows *et al.*, The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652-655 (2011).

17. T. Wernberg *et al.*, An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat. Clim. Change* **3**, 78–82 (2013).

18. J. Zinke *et al.*, Corals record long-term Leeuwin current variability including Ningaloo Nino/Nina since 1795. *Nat. Commun.* **5**, 3607 (2014).

19. J. Lough, A. Sen Gupta, A. J. Hobday, in *Report Card of Marine Climate Change for Australia: detailed scientific assessment,* E. S. Poloczanska, A. J. Hobday, A. J. Richardson, Eds. (Hobart, 2012), pp. Retrieved from www.oceanclimatechange.org.au 30/38/15.

20. S. Bennett, T. Wernberg, B. Arackal Joy, T. de Bettignies, A. H. Campbell, Central and rear-edge populations can be equally vulnerable to warming. *Nat. Commun.* **6**, 10280 (2015).

21. D. P. Thomson, R. C. Babcock, M. A. Vanderklift, G. Symonds, J. R. Gunson, Evidence for persistent patch structure on temperate reefs and multiple hypotheses for their creation and maintenance. *Estuar. Coas. Shelf Sci.* **96**, 105-113 (2012).

22. M. Feng, D. Slawinski, L. E. Beckley, J. K. Keesing, Retention and dispersal of shelf waters influenced by interactions of ocean boundary current and coastal geography. *Mar. Freshw. Res.* **61**, 1259-1267 (2010).

23. M. A. Coleman *et al.*, Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp. *J. Ecol.* **99**, 1026–1032 (2011).

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

25. W. Cai *et al.*, Increased frequency of extreme La Nina events under greenhouse warming. *Nat. Clim. Change* **5**, 132-137 (2015).

26. B. D. Toohey, G. A. Kendrick, E. S. Harvey, Disturbance and reef topography maintain high local diversity in *Ecklonia radiata* kelp forests. *Oikos* **116**, 1618-1630 (2007).

27. P. K. Dayton, M. J. Tegner, Catastrophic storms, El Nino, and patch stability in a southern California kelp community. *Science* **224**, 283-285 (1984).

28. E. A. Martinez, L. Cardenas, R. Pinto, Recovery and genetic diversity of the intertidal kelp *Lessonia nigrescens* (Phaeophyceae) 20 years after El Nino 1982/83. *J. Phycol.* **39**, 504-508 (2003).

29. M. T. Burrows *et al.*, Geographical limits to species-range shifts are suggested by climate velocity. *Nature*, (2014).

30. S. Bennett *et al.*, The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. *Mar. Freshw. Res.* **67**, 47-56 (2016).

31. T. Wernberg, M. S. Thomsen, F. Tuya, G. A. Kendrick, Biogenic habitat structure of seaweeds change along a latitudinal gradient in ocean temperature. *J. Exp. Mar. Biol. Ecol.* **400**, 264-271 (2011).

32. R. K. Hovey, K. P. Van Niel, L. M. Bellchambers, M. B. Pember, Modelling deep water habitats to develop a spatially explicit, fine scale understanding of the distribution of the western rock lobster, *Panulirus cygnus*. *PLoS ONE* **7**, e34476 (2012).

33. T. G. Whiteway, Australian bathymetry and topography grid, June 2009. *Geoscience Australia Record 2009/21*, 46pp. (2009).

34. L. M. Bellchambers, S. N. Evans, J. J. Meeuwig, Abundance and size of western rock lobster (*Panulirus cygnus*) as a function of benthic habitat: implications for ecosystem-based fisheries management. *Mar. Freshw. Res.* **61**, 279-287 (2010).

35. B. Radford, K. P. Van Niel, K. Holmes, WA marine futures: benthic modelling and mapping, final report, June 2008 (2008).

36. T. Wernberg, M. Coleman, A. Fairhead, S. Miller, M. Thomsen, Morphology of *Ecklonia radiata* (Phaeophyta: Laminarales) along its geographic distribution in south-western Australia and Australasia. *Mar. Biol.* **143**, 47-55 (2003).

37. T. Wernberg, G. A. Kendrick, J. C. Phillips, Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. *Divers. Distrib.* **9**, 427-441 (2003).

38. F. Tuya, T. Wernberg, M. S. Thomsen, The relative influence of local to regional drivers of variation in reef fishes. *J. Fish Biol.* **79**, 217-234 (2011).

39. C. J. Fulton *et al.*, Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem. *Limnol. Oceanogr.* **59**, 156-166 (2014).

40. T. H. Holmes *et al.*, A comparison of visual- and stereo-video based fish community assessment methods in tropical and temperate marine waters of Western Australia. *Limnol. Oceanogr. Methods*, (2013).

41. R. B. Taylor, T. J. Willis, Relationships amongst length, weight and growth of north-eastern New Zealand reef fishes. *Mar. Freshw. Res.* **49**, 255-260 (1998).

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

43. R. Froese, D. Pauly, FishBase. *World Wide Web electronic publication.* www.fishbase.org (2015).

44. E. Harvey, M. Shortis, A system for stereo-video measurement of sub-tidal organisms. *Mar. Tech. Soc. J.* **29**, 10-22 (1995).

45. B. J. Saunders, E. S. Harvey, G. A. Kendrick, Factors influencing distribution and habitat associations in an endemic group of temperate Western Australian reef fishes over a latitudinal gradient. *Mar. Ecol. Prog. Ser.* **517**, 193-208 (2014).

46. M. J. Anderson, R. N. Gorley, K. R. Clarke, PERMANOVA+ for PRIMER: Guide to software and statistical methods. *PRIMER-E Ltd, Plymouth, UK, ed. 2nd edition*, pp. 214 (2008).

47. M. A. Vanderklift, G. A. Kendrick, Variation in abundances of herbivorous invertebrates in temperate subtidal rocky reef habitats. *Mar. Freshw. Res.* **55**, 93-103 (2004).

48. T. Wernberg, M. White, M. A. Vanderklift, Population structure of turbinid gastropods on wave-exposed subtidal reefs: effects of density, body size and algae on grazing behaviour. *Mar. Ecol. Progr. Ser.* **362**, 169-179 (2008).

49. J. Fromont *et al.*, Strategic research fund for the marine environment collaborative research project: biodiversity of marine fauna on the central west coast. (Western Australian Museum, Perth, 2006).

50. J. M. Huisman, *Marine plants of Australia.* (University of Western Australia Press, Perth, 2000), pp. 300.

51. S. D. Connell, A. D. Irving, Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. *J. Biogeogr.* **35**, 1608-1621 (2008).

52. R. H. Kuiter, *Guide to Sea Fishes of Australia - a comprehensive reference for divers and fishermen.* (New Holland Publishers, Pty Ltd, 1999).

53. M. B. Westera *et al.*, Sea surface temperatures of the Leeuwin Current in the Capes region of Western Australia: potential effects on the marine biota of shallow reefs. *J. Roy. Soc. W.A.* **92**, 197–210 (2009).

54. S. W. Knudsen, K. D. Clements, *Kyphosus gladius*, a new species of sea chub from Western Australia (Teleostei: Kyphosidae), with comments on *Segutilum klunzingeri* Whitley. *Zootaxa* **3599**, 1–18 (2013).

55. K. Clements, J. Choat, Comparison of herbivory in the closely-related marine fish genera *Girella* and *Kyphosus*. *Mar. Biol.* **127**, 579-586 (1997).

56. G. J. Edgar, *Australian marine life - the plants and animals of temperate waters.* (Reed Books, Melbourne, Victoria, 1997), pp. 544.

57. A. S. Hoey, D. R. Bellwood, Cross-shelf variation in browsing intensity on the Great Barrier Reef. *Coral Reefs* **29**, 499-508 (2010).

58. R. M. Bonaldo, D. R. Bellwood, Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. *Mar. Ecol. Progr. Ser.* **360**, 237-244 (2008).

59. A. S. Hoey, D. R. Bellwood, Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* **12**, 1316-1328 (2009).

60.   A. S. Hoey, D. R. Bellwood, Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecol. Lett.* **14**, 267-273 (2011).

61.   S. Bennett, D. R. Bellwood, Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Mar. Ecol. Progr. Ser.* **426**, 241-U269 (2011).

62.   R. Fox, D. Bellwood, 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 (2008).

63.   P. J. Michael, G. A. Hyndes, M. A. Vanderklift, A. Vergés, Identity and behaviour of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef. *Mar. Ecol. Progr. Ser.* **482**, 227-240 (2013).

64.   D. B. Rasher, A. S. Hoey, M. E. Hay, Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* **94**, 1347-1358 (2013).

65.   K. Chong-Seng, K. Nash, D. Bellwood, N. Graham, Macroalgal herbivory on recovering versus degrading coral reefs. *Coral Reefs*, **33**, 409-419 (2014).

66.   A. Hoey, D. Bellwood, Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* **27**, 37-47 (2008).

67.   R. J. Fox, D. R. Bellwood, Direct versus indirect methods of quantifying herbivore grazing impact on a coral reef. *Mar. Biol.* **154**, 325-334 (2008).

68.   D. R. Bellwood, C. J. Fulton, Sediment-mediated suppression of herbivory on coral reefs: Decreasing resilience to rising sea levels and climate change? *Limnol. Oceanogr.* **53**, 2695-2701 (2008).

69.   G. Longo, S. Floeter, Comparison of remote video and diver's direct observations to quantify reef fishes feeding on benthos in coral and rocky reefs. *J. Fish Biol.* **81**, 1773-1780 (2012).

70.   D. E. Burkepile, M. E. Hay, Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* **30**, 351-362 (2011).

Fig. 1. Extent of kelp forests in western Australia before and after the 2011 marine heatwave. Extent of kelp forests from 0-30 m depth prior to 2011 (map, left), with color heat indicating proportion lost by 2013. Area of kelp forests before 2011 in 0.5° bins (full bars, right). Before 2011 kelp forests covered 2,266 km^2 along the >800 km of coastline. However, by 2013, 43% of these kelp forests had disappeared (red bars, right). Grey squares (southwest region) and black circles (midwest region) mark locations where reefs were surveyed to establish proportional kelp loss (Table S1).

Fig. 2. Regime shift from kelp forests to seaweed turfs following the 2011 marine heatwave. Kelp forests were dense in Kalbarri until 2011 (A), when they disappeared from ~100 km of coastline (Fig. 1) and were replaced by seaweed turfs (B). The habitat transition (C, lines)

coincided with exceptionally warm summers in 2011, 2012 and 2013 (C, red bars) punctuating gradually increasing mean ocean temperatures over the past decades (*17*). Mean (± SE, n = 3 reefs) kelp forest (dark blue circles/line) and seaweed turf (dark red circles/line) cover chronologically aligned with monthly SST anomalies (blue/red bars) relative to monthly climatological means for 1981-2015 (Table S1).

Fig. 3. Changes in seaweed and fish communities on impacted reefs following the 2011 marine heatwave. Ordinations (nMDS) of seaweed (A) and fish (B) communities show how community structure on reefs north of 29˚S shifted from a close resemblance to temperate reefs farther south to greater resemblance of tropical reefs to the north. Dark blue = Perth (2005-07), light blue = Kalbarri before (2005-07), pink = Kalbarri after (2013-15), red = Ningaloo Reef (2010) (Table S1). Each symbol represents an individual reef. Ordinations based on Bray-Curtis dissimilarities calculated from Ln[x+1] transformed data. Change in Ln[x+1] transformed abundance of seaweeds (C; grams fresh weight per 1.5 m^2) and fish (D; individuals per 2500 m^2) in Kalbarri (2005-07 vs. 2013-2015) clearly show the decline in cool water species (blue bars) and concurrent increase in warm water species (red bars), with several species not previously recorded (+) or now absent from the samples (-). Each bar represents an average across six reefs for an individual species. White bars indicate taxa with ambiguous distributions. Species are listed in Tables S2 and S3.

Fig. 4. Changes in benthic invertebrate abundances in the midwest following the 2011 marine heatwave. Change in Ln[x+1] transformed abundance of common mobile invertebrates (A; individuals per 30 m^2) and hermatypic corals (B; colonies per 1000 m^2). Colours and symbols as in Fig. 3. Each bar represents an average across 6 and 23 reefs for an individual species of mobile invertebrates and corals, respectively. Mobile invertebrates were counted in Jurien Bay (2005, 2011 vs. 2013, 2014) and corals between Cervantes and Dongara (30.6 - 29.3°S) (2005-2006 vs 2013) (Table S1). Species are listed in Tables S4 and S5.

Supplementary Materials:

Materials and Methods

Figures S1-S3

Tables S1-S6

Supplementary References (*31-70*)
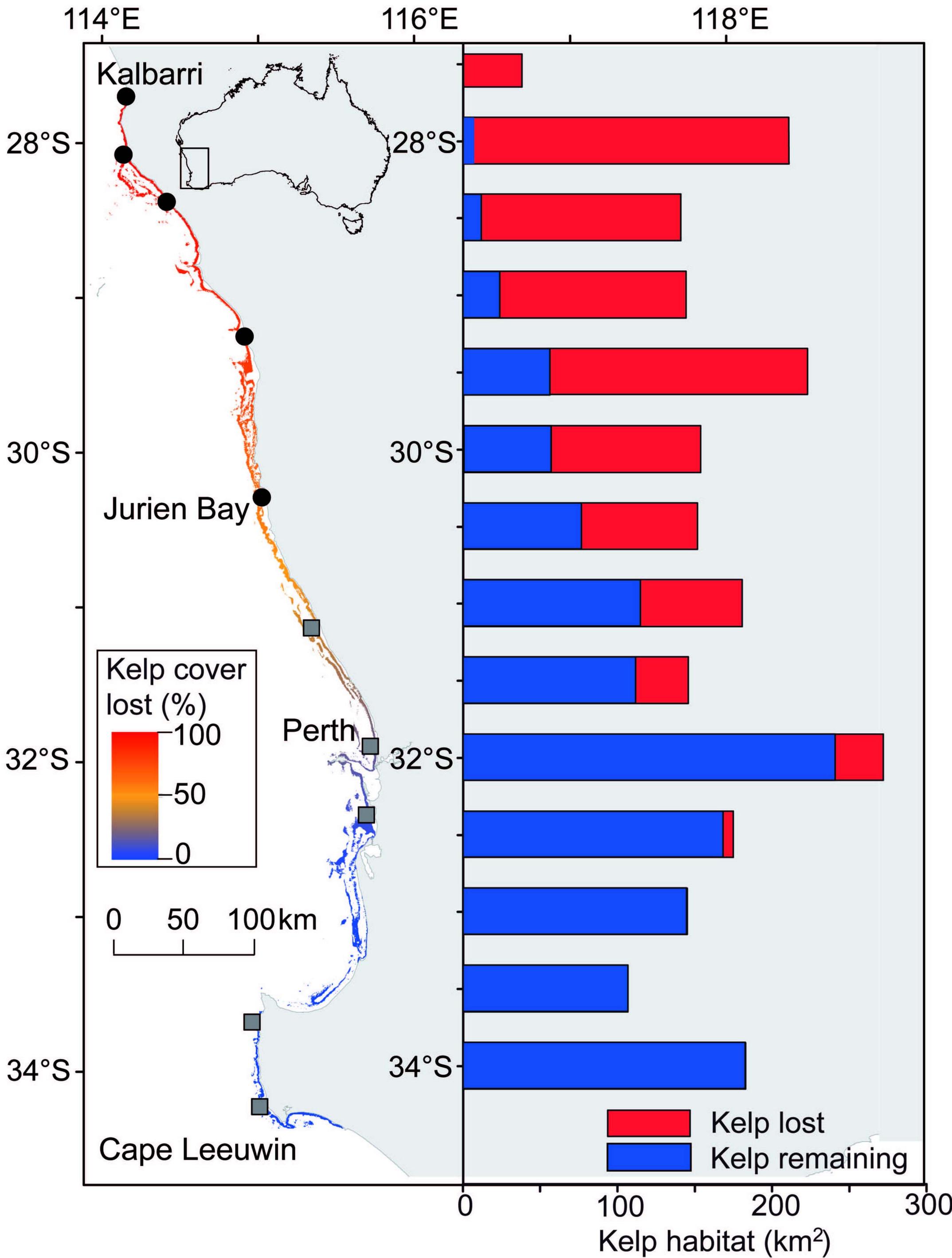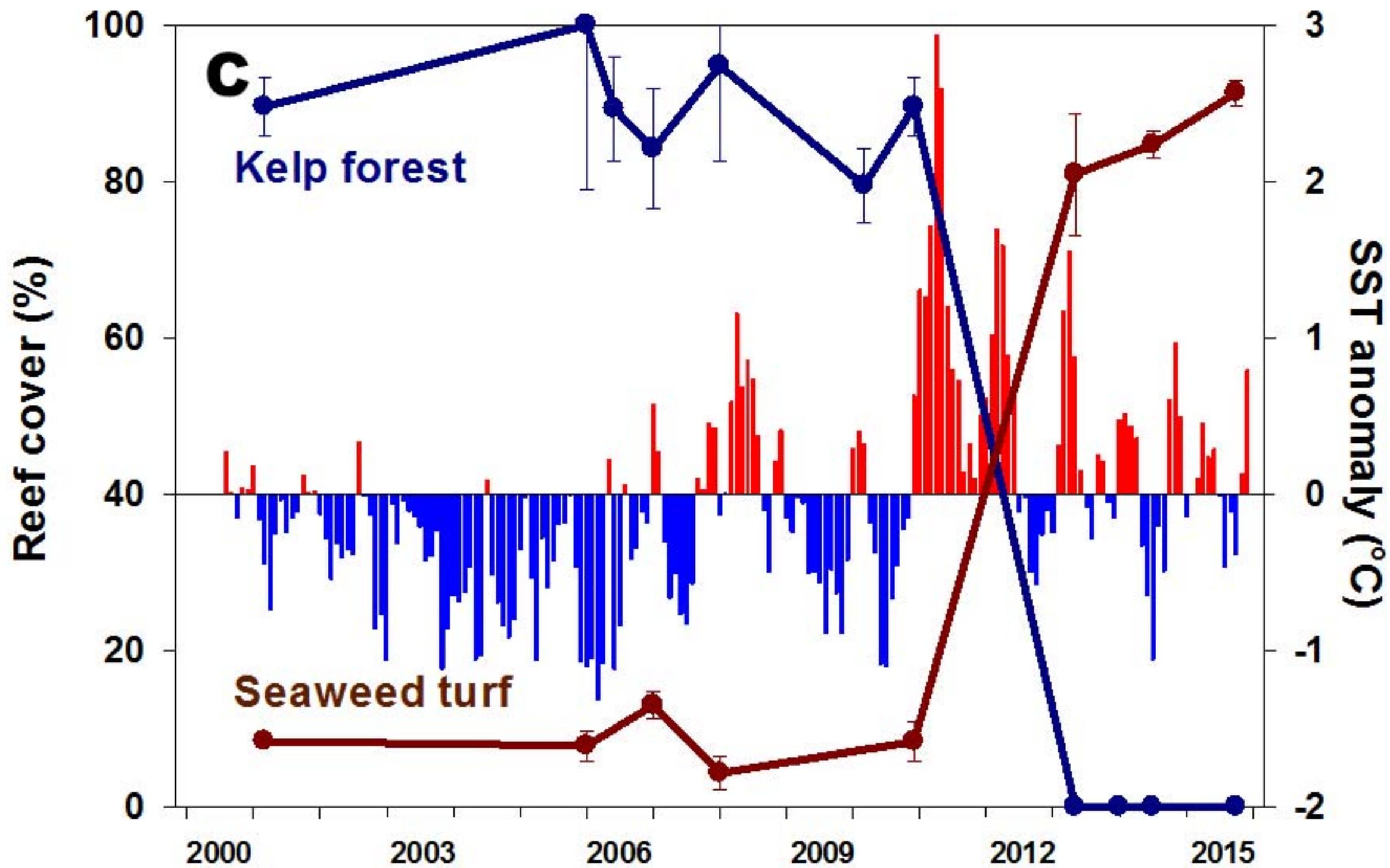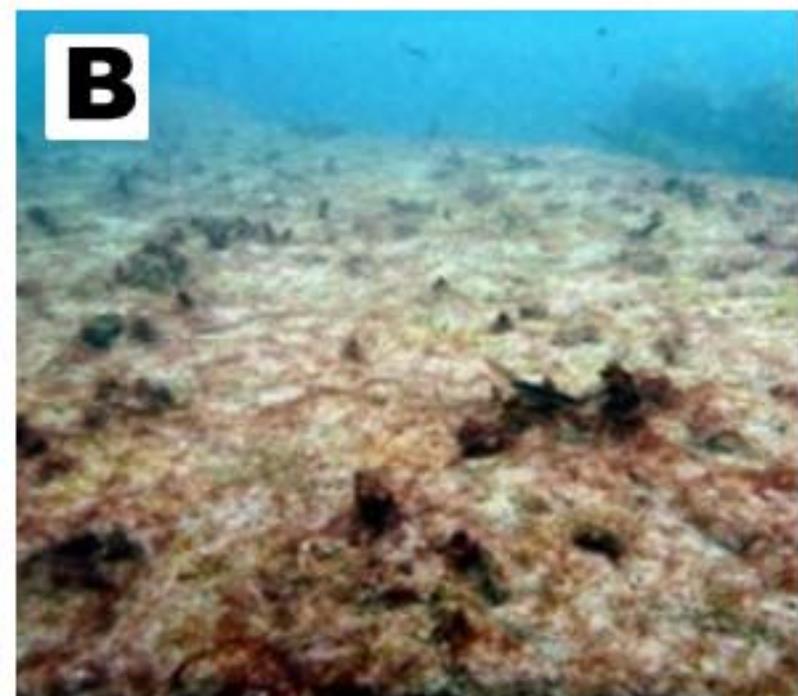
Southwest temperate · Midwest before · Midwest after · Northwest tropical

Seaweeds

Fish

A — Stress = 0.10

B — Stress = 0.05

C

D

Abundance change

Abundance change

Mobile inverts

A

+

Abundance change

Corals

B

+

+

+

+

-

Abundance change
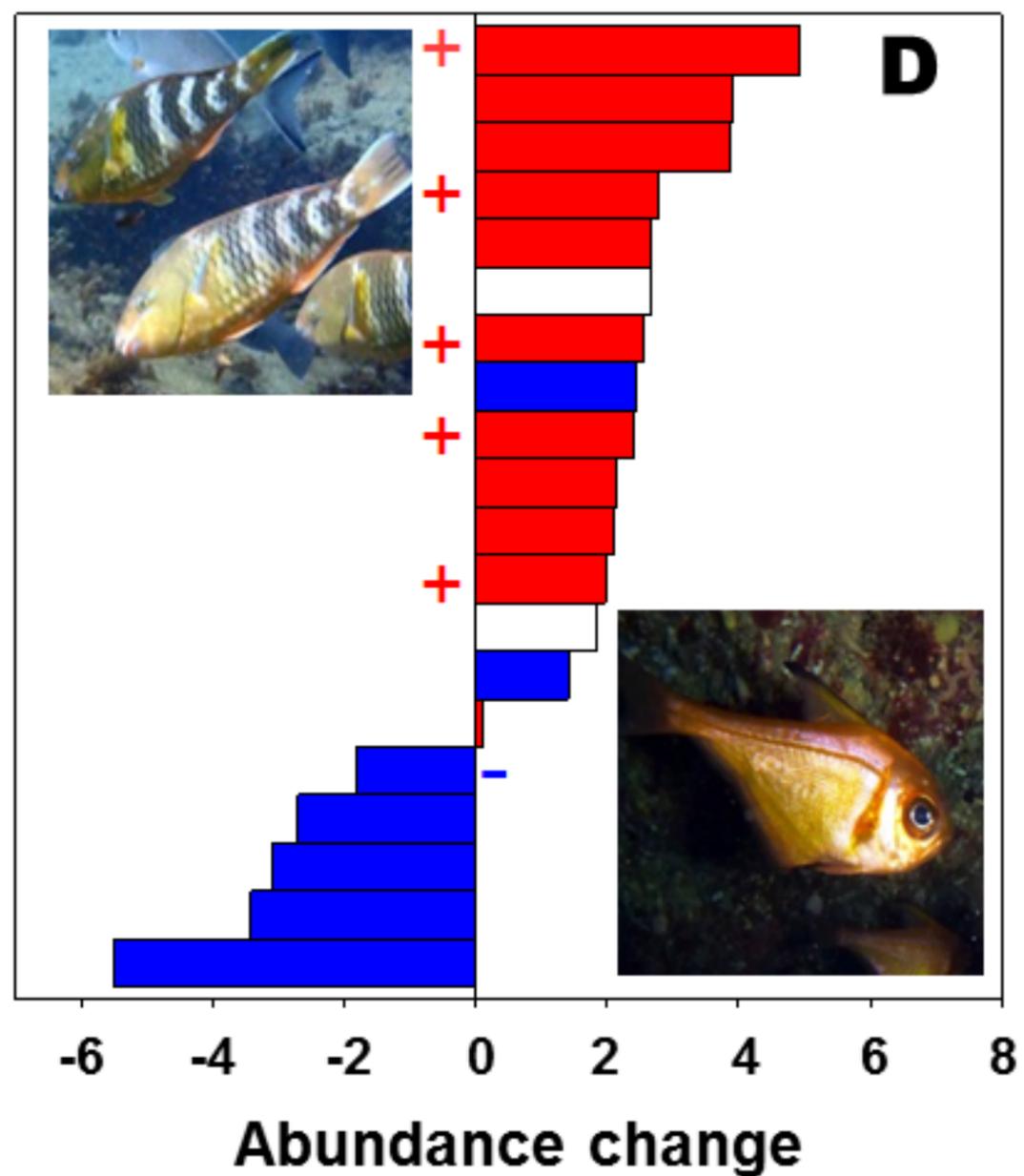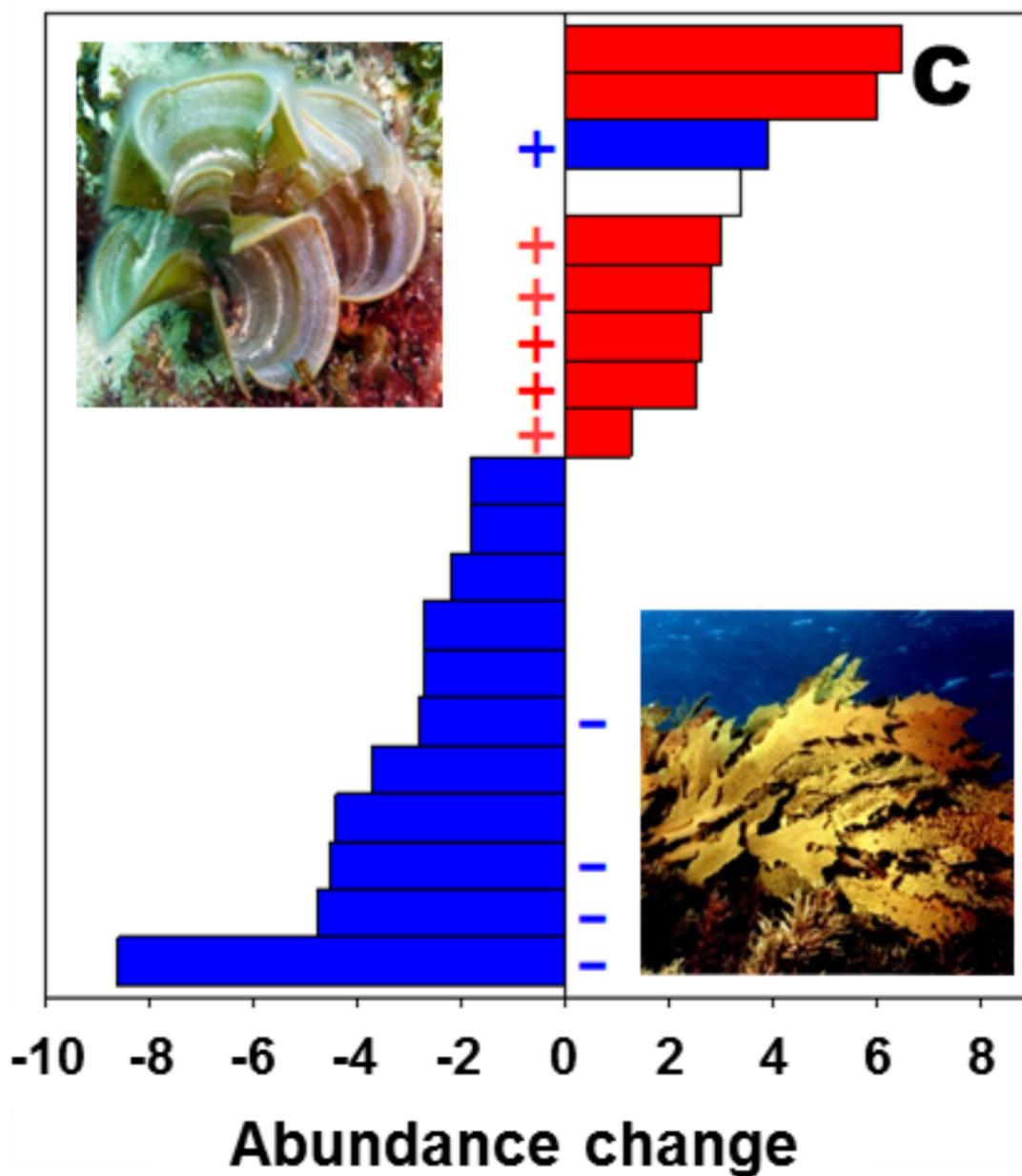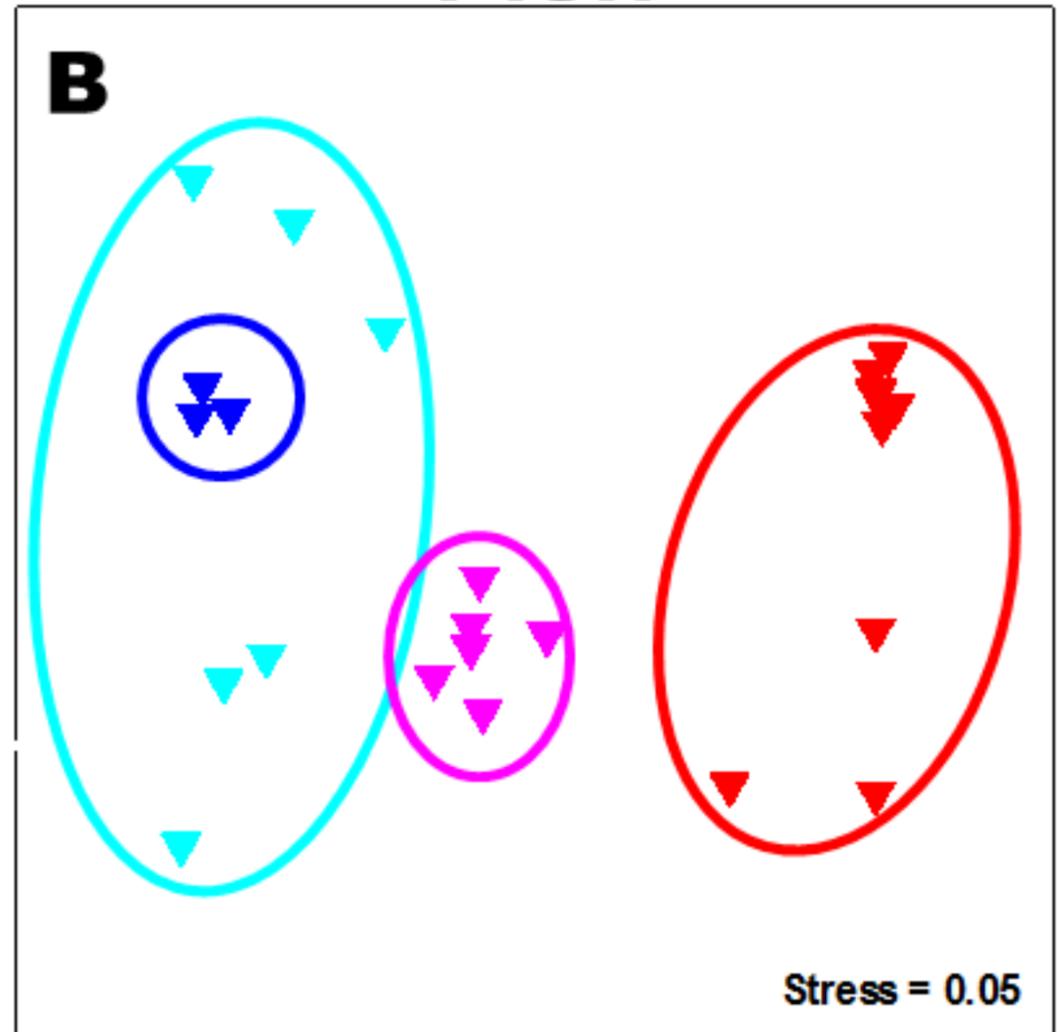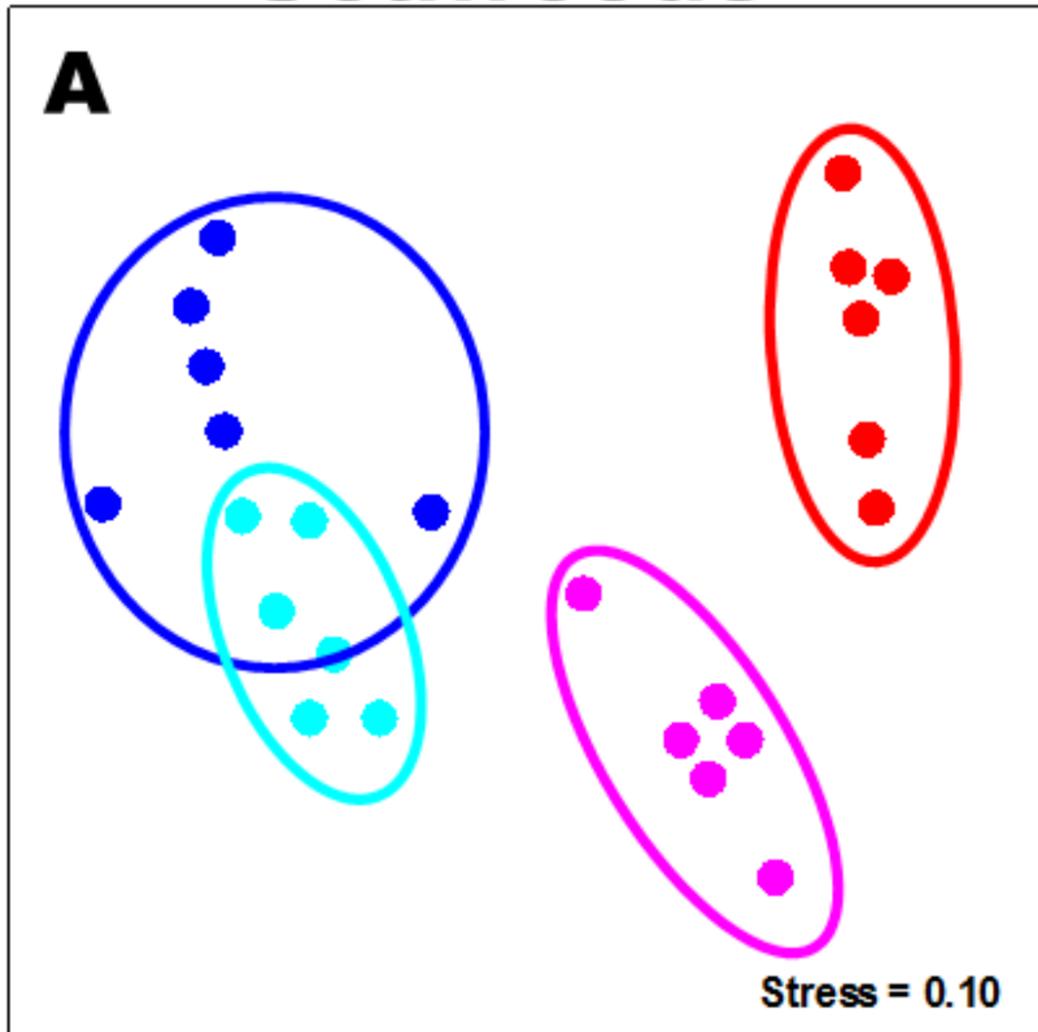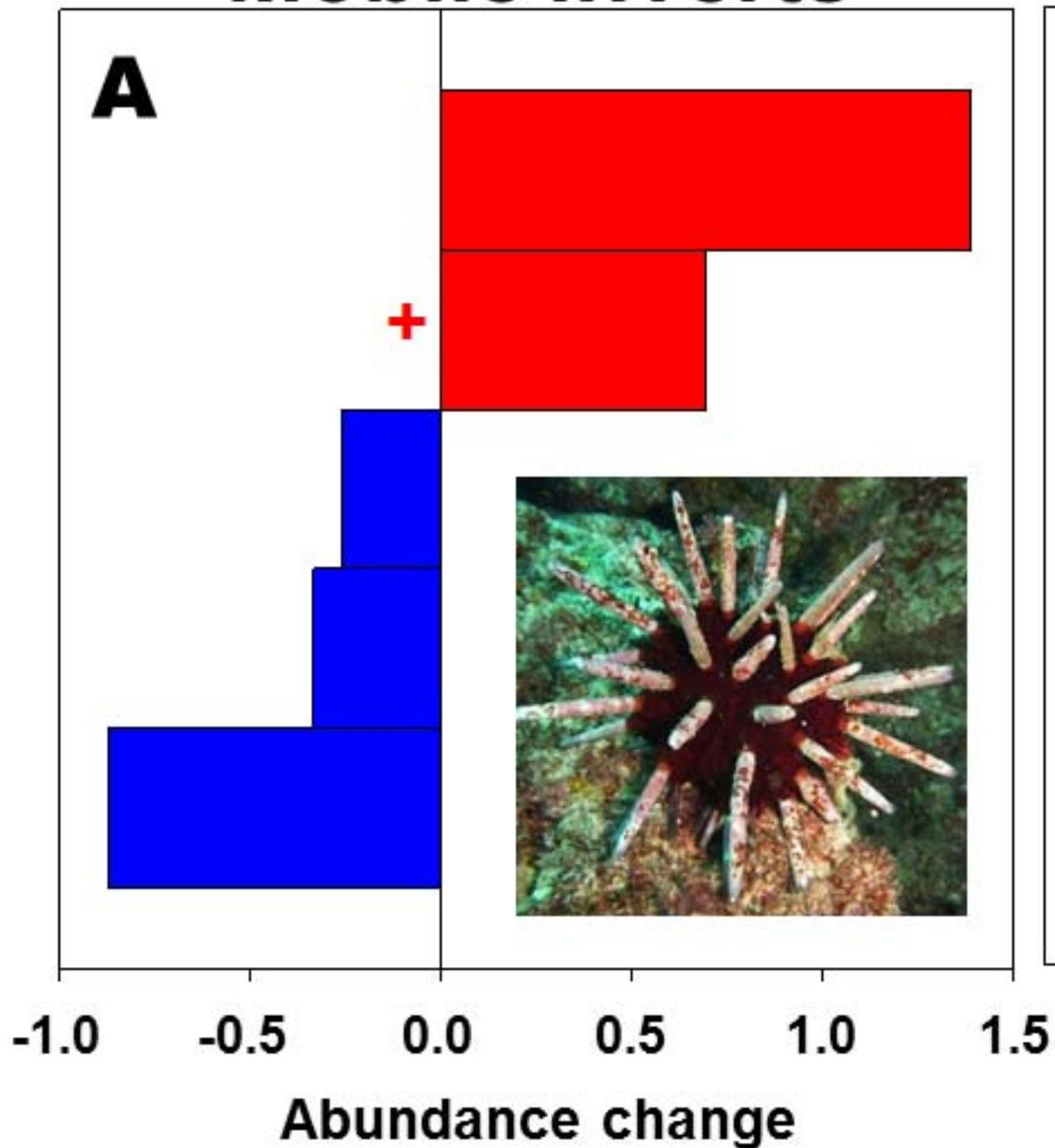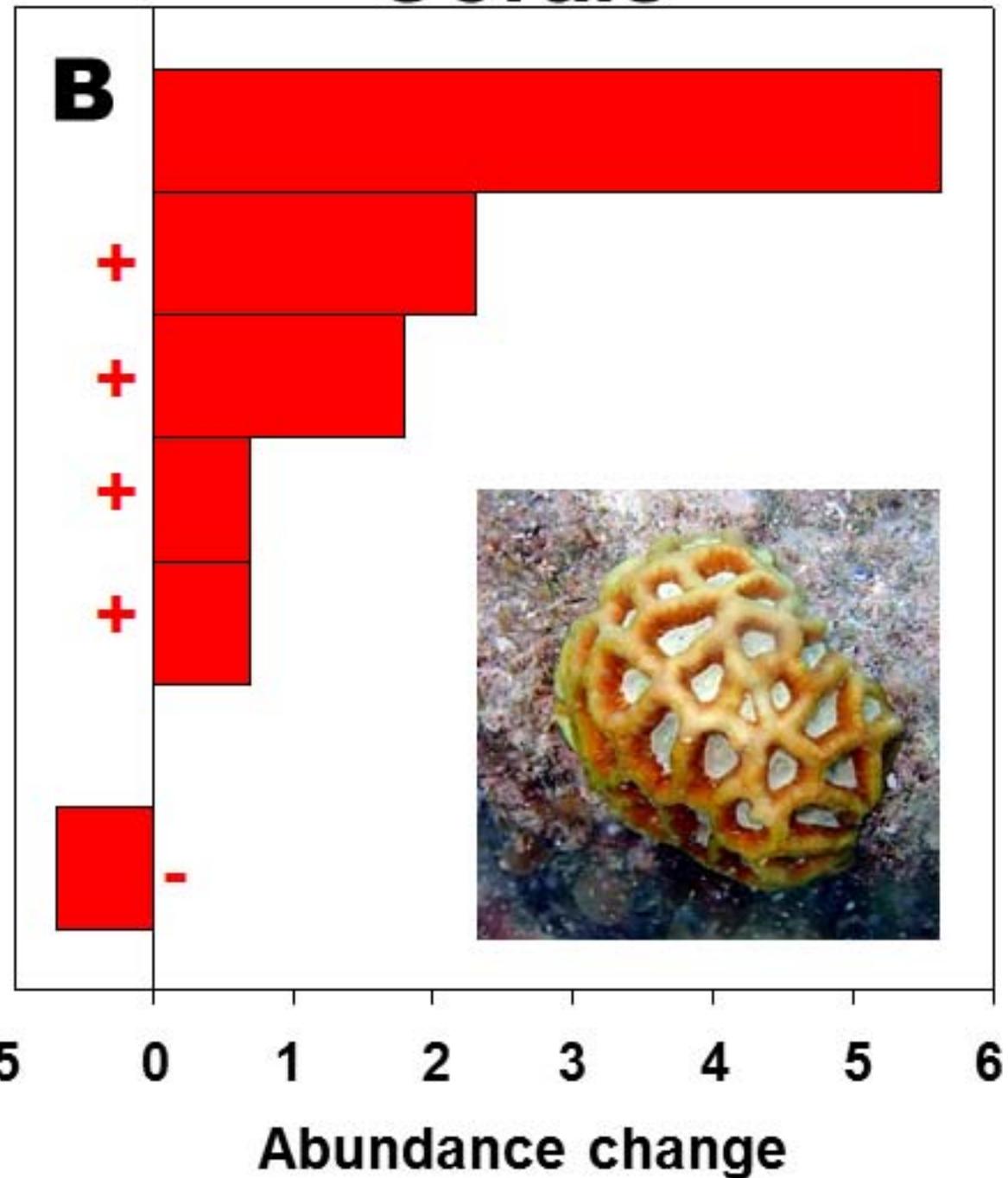
Supplementary Materials for

Climate Driven Regime Shift of a Temperate Marine Ecosystem

Thomas Wernberg, Scott Bennett, Russell C. Babcock, Thibaut de Bettignies, Katherine Cure, Martial Depczynski, Francois Dufois, Jane Fromont, Christopher J. Fulton, Renae K. Hovey, Euan S. Harvey, Thomas H. Holmes, Gary A. Kendrick, Ben Radford, Julia Santana-Garcon, Benjamin J. Saunders, Dan A. Smale, Mads S. Thomsen, Chenae A. Tuckett, Fernando Tuya, Mathew A. Vanderklift, Shaun Wilson

correspondence to: thomas.wernberg@uwa.edu.au

This PDF file includes:

Materials and Methods

Study Area

This study took place in Western Australia, where the Leeuwin Current carries warm water down the coast from the tropical Ningaloo Reef (23°S) to the temperate kelp forests of Australia's south coast. Here, we focus on changes in the abundance and composition of reef associated marine life in the midwest region (approx. 27.7-30.3°S) since 2001. The midwest region has experienced significant warming over the past 4 – 6 decades, at an average rate of 0.013°C year-1 (*19*). In addition to the gradually increasing mean temperatures, summer ocean temperatures from 2011 – 2013 were the warmest on record. The hottest of these years, 2011, resulted in an unprecedented marine heatwave, where ocean temperatures along >2,000 km coastline soared to >2 °C above the long term mean temperature for >10 weeks, exceeding anything recorded in the previous 215 years (*17, 18, 24*).

Kelp Loss

The extent of kelp loss (Fig. 1) was determined by combining measurements of kelp (*Ecklonia radiata*) cover at different latitudes before and after the 2011 marine heatwave with detailed spatial modeling of kelp distribution (Table S1). Latitudinal patterns in kelp cover were determined by conducting extensive benthic surveys at 36 reefs across 4 evenly spaced locations in 2005 (*8, 31*) and 52 reefs across 10 locations (*cf.* Fig. 1) in 2012/13, from Kalbarri (27.7 ºS) to Cape Leeuwin (34.2 ºS). The 52 reefs sampled in 2012/13 included the original 36 reefs. To best characterize latitudinal patterns, physically similar, wave exposed reefs at similar depth (8 – 12 m) were randomly selected >1 km apart. A scuba diver swam six 25×1 m non-overlapping transects at each reef (following *31*), recording the benthic cover (%) of kelp. In 2005, there were no differences in kelp cover across the 4 locations (p > 0.05, *8, 31*). Relative kelp loss was calculated as the change in cover between surveys. Extensive searches were undertaken on each reef in Kalbarri (n=6), Port Gregory (80 km south, n=6) and Horrocks (110 km south, n=6) where no kelp was recorded in 2012/13, with 3 – 4 divers additionally swimming specifically to search for kelps for >30 minutes. Latitudinal kelp loss patterns were modelled using a 3rd order polynomial regression (proportion kelp remaining = $0.0062 \, x^3 + 0.5618 \, x^2 + 16.815 \, x + 166$, $r^2 = 0.962$, n = 10, x = latitude).

A full coverage map of kelp distribution for Australia's west coast was developed through species distribution modelling (see *32*), using the Australian national bathymetry grid (approximately 250 m $\times 250$ m resolution, *33*), bathymetry derived terrain variables and geo-referenced towed video data collected along the west coast between 2000 and 2009 (*32, 34, 35*). Kelp distribution between Kalbarri and Cape Leeuwin out to 30 m water depth was extracted from the kelp distribution raster in ArcGIS (Esri ® ArcGIS TM 10.2) to produce a new raster specifically for the area of study. A raster of the 3rd order polynomial relationship between kelp loss and latitude was created for the study area and then multiplied by the kelp distribution raster, generating a spatially explicit representation of predicted kelp loss along the west coast of Australia. The number of pixels with kelp present at each latitudinal interval was calculated and multiplied by the predicted kelp loss at that same latitude and size of the pixel, to give an estimate of the

potential area loss of kelp forest. These estimates were summed within each half a degree of latitude.

Time series of kelp forest and turf seaweed cover (Fig. 2C) were constructed from 15 years of observations and sampling at the same three reefs in Kalbarri between 2001 to 2015. These reefs were a subset of those visited to assess proportional kelp loss (see above) and community changes (see below). In 2005, abundances were estimated within 6×1 m^2 quadrats per reef. In 2006 – 2009, abundances were estimated within 4×3.14 m^2 circular plots per reef and after 2011 within 10×0.25 m^2 quadrats per reef. All reefs were visited in December 2001, where the kelp forests were 'extensive and dense' (*36*, Fig. 2A) and December 2010, but no kelp data collected; nothing unusual about the canopy cover was noted and, consequently, these dates are represented by the mean ($\pm$ SE) across all other pre-2011 sampling dates. Reefs in Cape Leeuwin, Perth, Jurien Bay, Port Gregory and Kalbarri were revisited several times each year for additional surveys in 2014 and 2015.

Community Changes

We contrasted changes to fish and seaweed communities in the midwest region with tropical northwest (Ningaloo Reef) and temperate southwest (Perth) regions, these being 500 – 600 km farther north and south, respectively. In each region, we sampled 3 – 6 distinct reefs >1 km apart. In the southwest and midwest, these were 8 – 12 m depth rocky reefs. In the northwest, reefs were 3 – 5 m deep coral reef lagoon (dominated by limestone pavement) sites, as these are extensive and the main seaweed habitats for fish in the region. Sampling, as described below, was undertaken between late austral spring and early autumn (October to May) by experienced researchers. Seasonal differences in sampling time are unlikely to have influenced the observed patterns as previous studies have shown seasonal changes in both seaweed (*37*) and fish communities (*38*) to be subtle compared to those occurring across this latitudinal gradient. Similarly, observer and depth biases are unlikely to have influenced the observed changes in fish communities, as demonstrated by the highly consistent results obtained by Underwater Visual Censuses (UVC) and Diver Operated stereo Videography (stereo DOV) (Fig. 3B *vs.* Fig. S3).

To determine changes in seaweed community structure (Fig. 3), we collected all foliose seaweeds within 6×0.25 m^2 quadrats, a standard protocol previously used in both temperate (*37*) and tropical (*39*) habitats. This was done in November 2005 (southwest, midwest before, Kalbarri), November 2010 (northwest), (*39*) and in May 2013 (midwest after, Kalbarri). All seaweeds were harvested and then identified in the laboratory. Fishes were quantified using UVC's, following Holmes et al. (*40*). A SCUBA diver counted and identified all fishes along three 25×5 m belt transects (*38*). In the southwest (Perth) and midwest (Kalbarri) fishes were sampled in October 2006, March 2007, June 2007 and October 2007 (38), and in the northwest (Ningaloo) in February 2008. In the midwest (Kalbarri), fishes were resampled again ('after' the 2011 marine heatwave) in March and November 2013, and August 2015. In addition, fish abundance and biomass changes (using known length-weight relationships, *41, 42, 43*) were also determined independently using stereo DOVs following standardized methods in all three regions (*40*). Stereo DOVs used two underwater video cameras, separated by 700 mm on a base bar, facing inward at an angle of 8 degrees to enable accurate measurement of fish

lengths (*44*). Twelve 25 × 5m transects were performed on each of six reefs in the midwest (Port Gregory) in July 2006 on exposed reefs between 6 – 10 m depth (*cf. 45*). These transects were repeated in June 2013 at the exact same coordinates using the same methodology. In 2013, an additional six reefs from the northwest region (Ningaloo) and six reefs from the southwest (Perth) were sampled at similar depth and wave exposure to act as tropical and temperate reference regions respectively. Video footage obtained by stereo DOVs was analysed using the software 'EventMeasure (Stereo)' (SeaGIS Pty Ltd). All fish observed were identified to the lowest taxonomic level possible, and counted. *Kyphosus bigibbus*, *K. sydneyanus* and *K. gladius* were not distinguishable on all transects, and therefore the three species were conservatively pooled for the analysis of community structure (Fig. S3). Feeding assays were however filmed at closer range and distinguished between these species (*10*). Initial phase (IP) *Scarus ghobban* and *S. schlegeli* were also not distinguishable on all transects and were, therefore, pooled, as IP individuals constituted the majority of the parrotfish abundance. Non-metric Multidimensional Scaling (nMDS) based on Bray-Curtis dissimilarities calculated from Ln[x+1] transformed data was used to illustrate multivariate patterns of seaweed and fish community structure. Analyses of similarity percentages (SIMPER) identified which species were driving differences in community structure in the midwest before and after the warm summers of 2011 – 2013 (see *46* for technical details on these methods).

Changes in mobile and sessile invertebrate communities over the past decade, before and after the 2011 heatwave, were quantified within the midwest region only as no data prior to 2011 were available for the northwest and southwest (Fig. 4). Mobile invertebrates (large gastropods and sea urchins) were sampled at six reefs in Jurien Bay (30.3 °S) by counting all individuals along six 1 × 5m belt transects in summer 2004 and 2005 (before) (*47, 48*) and again in 2012 and 2013 (after). Transects were pooled for each sampling year and averaged for each reef and time period. We restricted the analyses to common species, defined as those with an average abundance of more than one individual recorded per reef per time period. Hermatypic corals were sampled at 23 reefs distributed across four midwest locations (Cervantes, Jurien Bay, Green Head and Dongara, 30.6 – 29.3°S) by counting and measuring (maximum linear length) all individual colonies along three 1 × 5m belt transects in 2005/06 (before) (*49*) and again in 2013 (after). All transects were pooled for each sampling period and location, standardized for total sampling area and averaged across locations for each sampling period. We restricted analyses to small colonies (< 6 cm maximum linear length) which would have recruited and/or grown during the census period. For both mobile invertebrates and hermatypic corals, data were Ln[x+1] transformed for calculation of changes in abundances in order to match the SIMPER outputs for seaweeds and fishes.

Seaweeds, fishes and invertebrates were classified according to their affinity for either cool or warm water, based on their predominant distribution south (cool) or north (warm) relative to the midwest coast region or their functional ecology (e.g., *Sargassum* spp., Table S2). A third category, 'ambiguous', was used to describe cosmopolitan species and unresolved taxa with species representatives in opposite climes. Sources for all classifications can be found in Tables S2, S3, S4 and S5. To test if the direction of change in abundance (decrease vs increase) of taxa in the community was related to their temperature affinity (cool vs warm) all observations (Fig. 3C,D and Fig. 4) were categorized and their frequency of association tested in 2 × 2 contingency tables using

Fisher's exact method for each taxon and all combined. To be conservative we included ambiguous species, and species with no change, as responding opposite to expectation. Due to the low number of observed taxa for mobile invertebrates and corals (n = 5 and n = 7, respectively) we pooled these into one test of responses of 'invertebrates'.
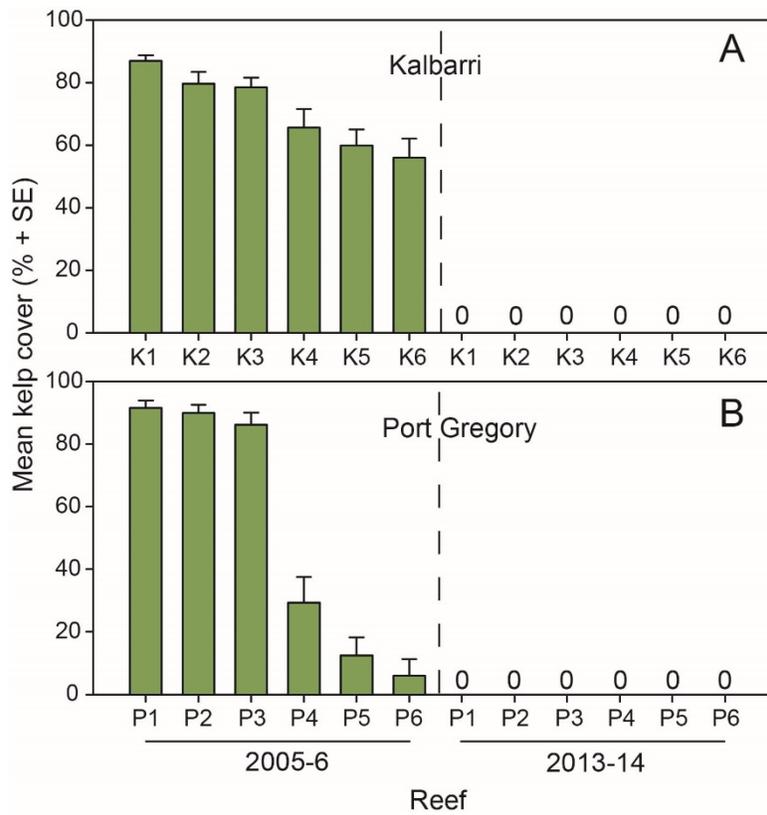
Fig. S1.

Landscape-scale cover of kelp forests (*Ecklonia radiata*) at two locations in the midwest before and after the 2011 marine heatwave. In Kalbarri (27.7 ºS, A), kelp forests covered 71% (mean ± 5 SE, n = 6 reefs) of reefs in 2005, and were not different (p > 0.05) to similar reefs in Jurien Bay (30.3 ºS), Perth (31.8 ºS) and Cape Leeuwin (34.2 ºS) sampled at the same time (8, 31). In Port Gregory (28.2 ºS, B), kelp forests covered 52% (mean ± 16 SE, n = 6 reefs) in 2006. Bars represent reefs >1 km apart, sampled along 25 m transects (n = 10 and 12, respectively). No kelps were seen in either region, at any of the 12 reefs (or elsewhere) during extensive searching in 2013, 2014 and 2015.
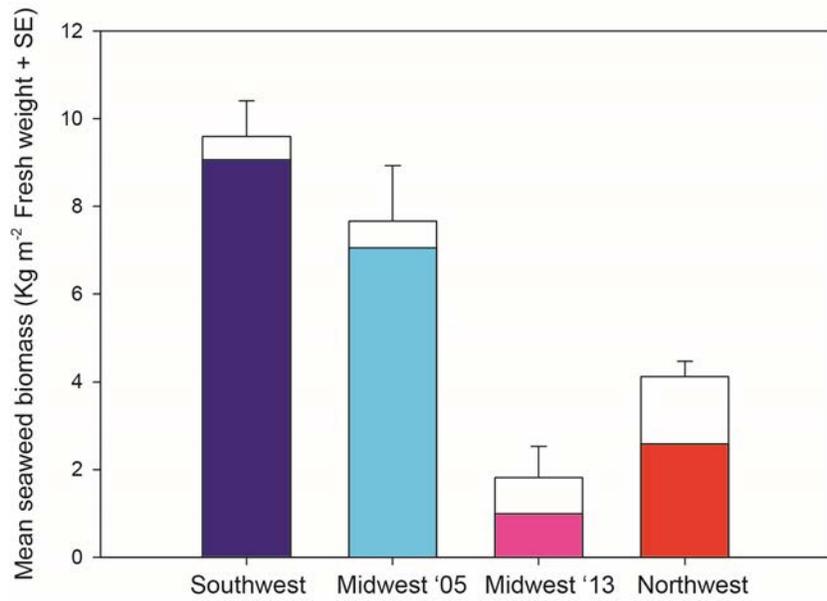
Fig. S2

Total standing seaweed canopy (colored bars) and understory (open bars) biomass in the southwest (Perth, 2005), northwest (Ningaloo, 2010) and midwest (Kalbarri, 2005, 2013) regions before and after the 2011 marine heatwave. Each bar represents an average of six reefs >1 km apart, where seaweeds were harvested by scuba divers within six 0.25 m^2 quadrats. Canopy seaweeds are kelps and fucoids larger than ~25 cm.
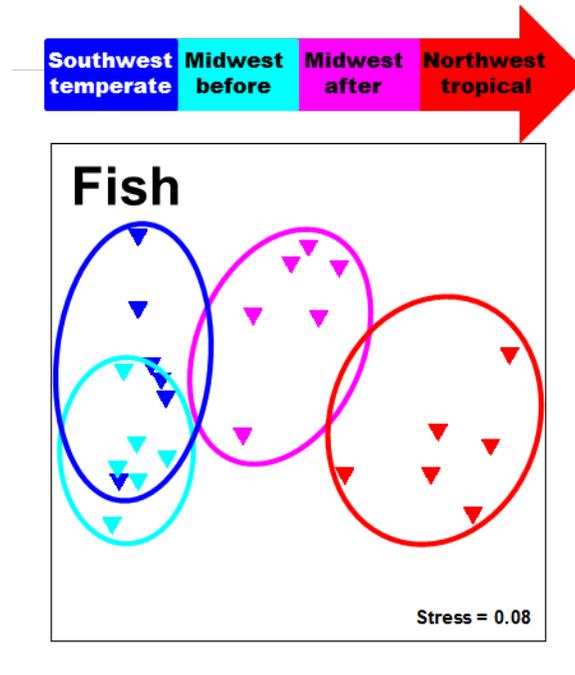
Fig. S3

Ordination (nMDS) based on diver operated video analysis showing changes in fish communities in the midwest (Port Gregory, 28.1 – 28.3ºS) between 2006 (light blue) and 2013 (pink) relative to the southwest (Perth, 2006, dark blue) and the northwest (Ningaloo, 2013, red). The video-captured data clearly shows a shift in community structure from strong resemblance of the temperate communities farther south towards a greater similarity to the tropical communities farther north. Points represent reefs >1 km apart, sampled by twelve 25 m transects where species abundances were converted to biomass using known length-weight relationships (*10*). Transects were averaged for each reef and data Ln[x+1]-transformed for analysis.

Table S1.

Summary of sampling methods, locations and sites. Details on analyses are provided in the Materials and methods section.

| Data	Location(s)	Years	Basic sampling design
Kelp extent and loss (Fig, 1)			
	Map of kelp distribution, west coast	2000 – 2009	Species distribution modelling, using bathymetry derived terrain variables and geo-referenced towed video data (*32-35*). Color heat (proportion kelp forest lost) generated by applying the 3rd order polynomial relationship between kelp loss and latitude obtained from surveys in 2005 and 2012 – 13.
	Proportion kelp loss,		4 – 12 reefs surveyed per location. 6 – 10 replicate 25×1 m belt transects per reef recording kelp cover. Reefs selected to be >1 km apart, physically similar: 8-12m depth, wave exposed, initially (2005) dominated by kelps (>50% cover) (*8, 31*). Proportional kelp loss with latitude fitted by polynomial regression.
	Kalbarri (27.7ºS)	2005, 2013	
	Port Gregory (28.2ºS)	2013	
	Horrocks (28.4ºS)	2013	
	Dongara (29.3 ºS)	2013	
	Jurien Bay (30.3ºS)	2005, 2013	
	Lancelin (31.0ºS)	2013	
	Perth (31.8ºS)	2005, 2013	
	Warnbro Sound (32.3ºS)	2012	
	Cape Naturaliste (33.5ºS)	2012	
	Cape Leeuwin (34.2ºS)	2005, 2013	
	Area of kelp loss, west coast	2005 to 2013	There were no differences in reef kelp cover or biomass between locations in 2005 (*8, 31*). The number of pixels with kelp was calculated for each latitudinal interval and multiplied by proportional loss to give an estimate of the area loss of kelp forest
Kelps and turf (Figs. 2, S1)			
	Kelp and turf abundance (Fig. 2), Kalbarri (27.7ºS)	2001 to 2015	Abundances quantified at the same three reefs (a subset of those described above) each time, within randomly positioned sampling units: 6×1 m^2 quadrats (2005), 4×3.14 m^2 circular plots (2006 – 2009) or 10×0.25 m^2 quadrats per reef (post 2011). Values for 2001 and 2010 were estimated from *in situ* observations and the mean of all other pre-2011 measurements.
	Kelp loss (Fig. S1),		Landscape-scale cover of kelp forests measured along 25 m transects at six reefs in each location. In Kalbarri (n = 10 transects per reef) a scuba diver recorded cover in situ (*8, 31*). In Port Gregory (n = 12 transects per reef) transects were filmed by DOV (*40*) and cover estimated subsequently. No kelps were seen in either region, at any of the surveyed reefs (or elsewhere) during extensive searching in 2013, 2014 and 2015.
	Kalbarri (27.7ºS)	2005, 2013, 2014, 2015	
	Port Gregory (28.2ºS)	2006, 2013, 2014, 2015	

Continued next page...

Data	Location(s)	Years	Basic sampling design
Community change (Figs. 3, 4, S2, S3)			
	Seaweeds (Figs. 3A, C, S2), Ningaloo (23 – 21°S, northwest)	2010	All foliose seaweeds were collected within 6 x 0.25 m^2 quadrats at each of six reefs, and identified and weighed in the laboratory (*37, 39*).
	Kalbarri (27.7ºS, midwest)	2005, 2013	
	Perth (31.8ºS, southwest)	2005	
	Fishes (Figs. 3B, D), Ningaloo (23 – 21°S, northwest)	2008	Underwater Visual Censuses (UVCs, *40*), where a SCUBA diver counted and identified all fishes *in situ* along three 25×5 m belt transects at each reef, were undertaken. Eight reefs were sampled in Ningaloo, six in Kalbarri before and after the 2011 marine heatwave and three in Perth (*38*). Samples from different times were averaged per reef before and after 2011.
	Kalbarri (27.7ºS, midwest)	2006 – 2007, 2013, 2015	
	Perth (31.8ºS, southwest)	2006– 2007	
	Fishes (Fig. S3), Ningaloo (23 – 21°S, northwest)	2013	Diver Operated stereo Videos (stereo DOVs, *40*), enabling accurate measurement of fish lengths (*44*) were recorded on each of six reefs (n = twelve 25 x 5m transects per reef) per region. All reefs were randomly selected, exposed to swells and between 6 – 10 m depth. Video footage obtained by stereo-DOVs was analysed using EventMeasure software and species abundances were converted to biomass using length – weight relationships from Western Australian Fisheries research reports, primary literature (*41, 42*) or FishBase (*43*).
	Port Gregory (28.2 ºS, midwest)	2006, 2013	
	Perth (31.8ºS, southwest)	2013	
	Mobile invertebrates (Fig 4A), Jurien Bay (30.3ºS)	2004, 2005, 2012, 2013	Common large gastropods and sea urchins were sampled at six reefs by counting all individuals along six $1 \times 5m$ belt transects (*47, 48*). Transects were pooled for each sampling year and averaged for each reef and time period.
	Corals (Fig 4B), Cervantes (30.6 ºS)	2005/06, 2013	Small (<6cm) hermatypic corals were sampled at 23 reefs distributed across four midwest locations by counting and measuring (maximum linear length) all individuals along three $1 \times 5m$ belt transects per reef (*49*). All transects were pooled for each sampling period and location.
	Jurien Bay (30.3ºS)	2005/06, 2013	
	Green Head (30.1ºS)	2005/06, 2013	
	Dongara (29.3ºS)	2005/06, 2013	

Table S2.

Seaweeds contributing most to changes in assemblage structure in the midwest (Kalbarri) before (2005) and after (2013) the warm summers of 2011 – 2013 (Fig. 3A), and their biogeographical affinities. Mean fresh weight [grams] per 1.5 m^2 (SE, n = 6 reefs). Top 20 species as identified by SIMPER. In order of declining biomass change (cf. Fig. 3C). Distribution records downloaded from The Atlas of Living Australia (http://www.ala.org.au/) on 14 October 2015. 30.3°S (Jurien Bay) represents the southern end of the midwest coast and observed impacts (17). Species names checked on Algaebase (http://www.algaebase.org/) and current as of 15 Dec 2015.

Species	Before	After	Affinity and distribution
Sargassum spp.[§]	324 (196)	989 (276)	Warm; wide-spread genus. Species difficult to separate. Characteristic and dominant element of tropical coral reefs and lagoons, including Ningaloo Reef in the northwest of Australia (*39*).
Lobophora variegata	3 (2)	422 (89)	Warm; widespread, mostly tropical to warm-temperate, characteristic and dominant of tropical coral reefs (*50*) incl. Ningaloo Reef in the northwest (*39*). 52.4% of 559 records north of 30.3°S.
Zonaria spiralis	0 (0)	52 (32)	Cool; 99.3% of 307 records south of 30.3°S.
Small geniculate coralline algae	10 (6)	39 (17)	Ambiguous; species of *Corallina*, *Haliptilon* and *Jania;* polyphyletic functional group. All genera widespread across Australia.
Padina spp.	0 (0)	20 (16)	Warm; widespread but generally a tropical genus. Characteristic of tropical reefs and lagoons including Ningaloo Reef in the northwest of Australia (*3*). 70.8% of 1040 records north of 30.3°S.
Stypopodium sp.	0 (0)	17 (14)	Warm; 80% of 115 records north of 30.3°S.
Asparagopsis taxiformis	0 (0)	14 (9)	Warm; Rottnest Island around northern Australia, cosmopolitan warm-water species (*50*). 74.3% of 393 records north of 30.3 °S.
Callophycus serratus	0 (0)	12 (9)	Warm; wide-spread in warmer waters (*50*). 82.8% of 29[#] records north of 30.3°S.
Tricleocarpa cylindrica	0 (0)	4 (2)	Warm; Cape Leeuwin around northern Australia (*50*). 73.5% of 117 records north of 30.3°S.
Myriodesma spp.	10 (8)	4 (3)	Cool; 83.3% of 474 records south of 30.3°S.
Hennedya crispa	35 (29)	29 (29)	Cool; midwest coast around southern Australia (*50*). 69.5% of 275 records south of 30.3°S.
Zonaria turneriana	11 (6)	2 (2)	Cool; midwest coast south to Tasmania and Victoria (*50*). 93.4% of 806 records south of 30.3°S.
Pterocladia lucida	17 (13)	2 (1)	Cool; midwest coast around southern Australia (*50*). 90.9% of 1107 records south of 30.3°S.
Halopeltis australis	16 (10)	1 (1)	Cool; midwest coast around southern Australia (*50*). 78.0% of 601 records south of 30.3°S.
Rhodopeltis australis	17 (6)	0 (0)	Cool; midwest coast south to Victoria (*50*). 93.2% of 133 records south of 30.3°S
Callophycus oppositifolius	73 (51)	32 (32)	Cool; midwest coast south to South Australia (*50*). 74.5% of 216 records south of 30.3°S.
Amphiroa anceps	197 (63)	114 (59)	Cool; Australia-wide(*50*) but not common in the northwest (e.g., *39*). 77.5% of 831 records south of 30.3°S.
Delisea pulchra	95 (41)	0 (0)	Cool; midwest coast, around the south coast to southern Queensland (*50*). 76.0% of 437 records south of 30.3°S.
Plocamium preissianum/mertensii	120 (58)	0 (0)	Cool; midwest/northwest around the south coast (*50*). Species not differentiated. 95.6% of 1617 records south of 30.3°S.
Ecklonia radiata	5569 (1419)	0 (0)	Cool; midwest coast, around the south coast and Tasmania to southern Queensland (*50*). Characteristic and dominant on the south coast (*51*). 95.7% of 843 records south of 30.3°S.

[#] Sparsely recorded. Affinity and distribution from these records should be interpreted with caution.

[§] Includes *Sargassopsis decurrens* (formerly *Sargassum decurrens*).

Table S3.

Reef fishes contributing most (top 20) to changes in fish assemblage structure in the midwest (Kalbarri) before (2006 – 2007) and after (2013, 2015) the warm summers of 2011 – 2013 (Fig. 3B), and their biogeographical affinities. Mean number of individuals per 125 m2 (SE, n = 3 reefs). Top 20 species as identified by SIMPER. In order of declining biomass change (cf. Fig. 3D). Species names checked on World Register of Marine Species (http://www.marinespecies.org/) and current as of 15 December 2015.

Species	Before	After	Affinity and feeding mode
Siganus canaliculatus & fuscescens	0 (0)	6.9 (3.2)	Warm; species difficult to separate, sub-tropical to tropical, browser (*10, 43, 52*).
Parma occidentalis	0.1 (0.1)	2.6 (0.4)	Warm; subtropical, grazer[§] (*10, 43*).
Parupeneus spilurus	0 (0)	2.4 (0.4)	Warm; tropical, carnivore (*10, 43, 52*).
Thalassoma septemfasciatum	0 (0)	0.8 (0.2)	Warm; subtropical to tropical, carnivore (*10, 43*).
Plectorhinchus flavomaculatus	0.2 (0.1)	0.9 (0.2)	Warm; subtropical to tropical, carnivore (*10, 43*).
Coris auricularis	1.6 (0.4)	2.3 (0.8)	Ambiguous; temperate to subtropical, carnivore (*10, 43, 52, 53*).
Scarus ghobban	0 (0)	0.6 (0.2)	Warm; tropical to subtropical, scraper[§] (*10, 43*).
Kyphosus sydneyanus	0.2 (0.2)	0.8 (0.6)	Cool; temperate, browser (*54, 55*)
Pomacentrus milleri	0 (0)	0.6 (0.3)	Warm; tropical, grazer (*10, 43*).
Scarus schlegeli	0.1 (0.1)	0.5 (0.3)	Warm; tropical, scraper[§] (*10, 43*).
Choerodon rubescens	0.01 (0.01)	0.4 (0.1)	Warm; subtropical, carnivore (*10, 43, 53*).
Chaetodon assarius	0 (0)	0.4 (0.1)	Warm; subtropical to tropical, carnivore (*43, 52*).
Kyphosus cornelii	0.1 (0.1)	0.4 (0.2)	Ambiguous; temperate to tropical grazer (*10, 54*).
Notolabrus parilus	0.2 (0.1)	0.4 (0.1)	Cool; temperate to subtropical, carnivore (*10, 43, 52, 53*).
Thalassoma lunare	0.2 (0.2)	0.2 (0.1)	Warm; tropical to warm temperate, carnivore (*10, 43, 52*).
Pseudolabrus biserialis	0.3 (0.1)	0 (0)	Cool; temperate, carnivore (*43*)
Parma mccullochi	0.8 (0.3)	0 (0)	Cool; temperate, grazer[§] (*45*)
Pempheris klunzingeri	2.0 (1.3)	0.9 (0.8)	Cool; temperate to subtropical, (*43, 52*).
Chromis klunzingeri	1.5 (1.5)	0 (0)	Cool; temperate, planktivore (*52*).
Schuettea woodwardi	12.6 (6.6)	0.1 (0.1)	Cool; temperate, planktivore (*43, 52*).

[§] Here we distinguish the more specific feeding modes, in the text, however, we refer to grazers, scrapers and excavators under one name ('grazers') as they all ultimately remove substratum, turfs and microscopic kelps, limiting the kelp recovery process.

Table S4.

Common (mean >1 per site in either time period) mobile invertebrates on reefs in the midwest (Jurien Bay) before (2005, 2011) and after (2013, 2014) the warm summers of 2011 – 2013. Mean number of individuals per 30 m2 (SE, n = 6 reefs). In order of declining density change (cf. Fig. 4A). Distribution records were downloaded from The Atlas of Living Australia (http://www.ala.org.au/) on 14 October 2015. 30.3˚S (Jurien Bay) represents the southern end of the midwest coast and observed impacts (17). Species names checked on World Register of Marine Species (http://www.marinespecies.org/) and current as of 15 December 2015.

Species	Before	After	Affinity and distribution
Centrostephanus tenuispinus	0.2 (0.2)	4.2 (1.3)	Warm; warm-temperate, range-limit at Shark Bay (25.3 ˚S), least abundant at most temperate latitudes (*47, T. Wernberg pers. obs.*)[‡]. Family characteristic of tropical reefs (*56*); 28.3% of 11[#] records north of 30.3˚S
Tripneustes gratilla	0 (0)	2.0 (1.7)	Warm; tropical, northern Australia (*56*), 68.8% of 288 records north of 30.3˚S.
Phyllacanthus irregularis	1.9 (1.0)	0.6 (0.3)	Cool; temperate (*56*), 70% of 20[#] records south of 30.3˚S.
Lunella torquatus	2.6 (1.2)	1.2 (0.6)	Cool; temperate (*56*), 87.4% of 372 records south of 30.3˚S.
Heliocidaris erythrogramma	8.3 (1.7)	5.9 (1.7)	Cool; temperate (*56*), 92.3% of 607 records south of 30.3˚S.

[§] Extensive searches in 2014 and 2015 did not discover a single individual at any of the reefs sampled for seaweed and fish in Kalbarri (27.7 °S), the species' range-limit prior to the heatwave and where it was previously common (*48*).

[‡] An unpublished survey of 90 identical transects across 18 similar reefs between South Australia (Adelaide) and Jurien Bay in 2005/06 did not find a single *C. tentuispinus* on these southern reefs (T. Wernberg unpublished data).

[#] Very sparsely recorded. Affinity and distribution from these records should be interpreted with caution.

Table S5.

Small (< 6 cm) hermatypic corals on reefs in the midwest (Cervantes to Dongara) before (2005/05) and after (2013) the 2011 marine heatwave. Mean number of colonies per 1000 m^2 (SE, n = 4 regions). In order of declining density increase (cf. Fig. 4B). Hermatypic (reef building) corals are the key foundation-species of tropical coral reefs, and while some species are frequently found at temperate latitudes, their core distributions are tropical (cf. data below) and as a group they are characteristic of warm and tropical environments. Distribution records were downloaded from The Atlas of Living Australia (http://www.ala.org.au/) on 2 October 2015. 30.3˚S (Jurien Bay) represents the southern end of the midwest coast and observed impacts (*17*). Species names checked on World Register of Marine Species (http://www.marinespecies.org/) and current as of 15 December 2015.

Species	Before	After	Affinity and distribution
Plesiastrea versipora	60 (4)	338 (83)	Warm; widespread; 81.3% of 283 records north of 30.3˚S
Alveopora fenestrata	0 (0)	10 (5)	Warm; 93.4% of 76 records north of 30.3˚S
Turbinaria mesenterina	0 (0)	6 (5)	Warm; widespread; 97.6% of 381 records north of 30.3˚S
Turbinaria reniformis	0 (0)	2 (3)	Warm;94.7% of 337 records north of 30.3˚S
Coelastea aspera	0 (0)	2 (3)	Warm; 97.7% of 299 records north of 30.3˚S
Pocillopora damicornis	6 (3)	5 (5)	Warm; widespread; 97.5% of 1088 records north of 30.3˚S
Montipora capricornis	2 (3)	0 (0)	Warm; subtropical; 90.0% of 10[#] records north of 30.3˚S
All species combined	68 (6)	365 (94)	
Species richness	3	6	

[#] Very sparsely recorded. Affinity and distribution from these records should be interpreted with caution.

Table S6.

Comparison of mean feeding rates by herbivorous fishes in the current study and rates reported in the coral reef literature. Seaweed browsing bite rates were standardized by herbivore biomass (kgH), seaweed assay biomass (kgA) available for consumption and by the period of exposure (hr). Coral reef feeding rates were only used where the seaweed assay was placed onto coral dominated areas (primarily reef crest or outer reef flat), where grazing rates are highest. All reported grazing rates were obtained by standardized video methods, following Hoey and Bellwood (57).

Feeding rates on the benthos by herbivorous fishes were standardized by the grazing area and time $(1 \text{ m}^2 \text{ hr}^{-1})$. For studies where bite rates per unit area were not reported, values were estimated based on the reported percentage of reef area grazed per unit time using mean bite sizes reported in the literature (16 mm^2, equivalent to a 10 – 15cm, TL, *Scarus rivulatus*) (58). Note that feeding rates by scrapers reported in the literature were not standardized by fish biomass. All values were extracted from the literature using 'Data Thief' software. Where the feeding rates of multiple species were individually reported, all reported species were summed to determine the total mean grazing pressure. Table modified from details in (10). Species names checked on World Register of Marine Species (http://www.marinespecies.org/) and current as of 15 December 2015.

Region	Mean bite rate	Dominant herbivores	References
Seaweed browsing (bites kg$_H$$^{-1}$ kg$_A$$^{-1}$ hr^{-1}) (*Ecklonia radiata*, *Sargassum* spp.)			
Port Gregory, midwest, WA	3836	*Kyphosus bigibbus*	(10)
Great Barrier Reef (5 locations)	459 (30 – 1251)	*Siganus canaliculatus* *S. doliatus* *Kyphosus vaigiensis* *Naso unicornis,*	(59-62)
Ningaloo Reef (5 locations)	163 (54 – 199)	*Kyphosus vaigiensis* *K. bigibbus* *Scarus* spp *Naso unicornis*	(63)
Fiji	189-787*	*Naso lituratus* *N. unicornis*	(64)
Seychelles	688*	*Siganus puelloides*	(65)
Seaweed turf grazing (bites m^2 hr^{-1}) (epilithic algal matrix/turf)			
Port Gregory, midwest, WA	172 ± 50	*Scarus ghobban* *Siganus fuscesens*	(10)
Great Barrier Reef (3 locations)	61* (45* – 1685)	*Scarus rivulatus* *Scarus* IP *Scarus psittacus* *Siganus* spp	(66-68)
Abrolhos Archipelago, NE Brazil	315	*Acanthurus bahianus*	(69)
Florida Keys, USA	59	n/a	(70)
Fiji	258	*Acanthurus nigricauda* *Ctenochaetus striatus* *Scarus* spp.	(64)

* Unstandardized bite rates as mass standardized bite rates not reported in the study.