

Microbiomes of Western Australian marine environments

CHARLIE M. PHELPS¹, RACHELE BERNASCONI¹, MELISSA DANKS², JOSEP M. GASOL^{1,3}, ANNA J. M. HOPKINS², JACQUELYN JONES⁴, CHRISTOPHER R. J. KAVAZOS^{2,5}, BELINDA C. MARTIN⁶, FLAVIA TARQUINIO¹, MEGAN J. HUGGETT^{1,2,7*}

¹ Centre for Marine Ecosystems Research, and ² Centre for Ecosystem Management, School of Science, Edith Cowan University, Perth, WA, Australia

³ Institut de Ciències del Mar, CSIC, Barcelona, Catalonia, Spain

⁴ Trace and Environmental Laboratory, Curtin University, Perth, WA, Australia

⁵ School of Biological, Earth and Environmental Sciences, The University of New South Wales, Sydney, NSW, Australia

⁶ School of Biological Sciences, The University of Western Australia, Perth, WA, Australia

⁷ School of Environmental and Life Sciences, The University of Newcastle, Ourimbah, NSW, Australia

*Corresponding author: ✉ megan.huggett@newcastle.edu.au

Abstract

Microbes are fundamentally important to the maintenance of all habitats, including those in the ocean: they govern biogeochemical cycles, contribute to resistance from disease and nutritional requirements of macroorganisms and provide enormous biological and genetic diversity. The oceanic environment of the west coast of Australia is dominated by the Leeuwin Current, a poleward flowing boundary current that brings warm water down the coastline from the north. Due to the influence of the current, tropical species exist further south than they would otherwise, and stretches of the coastline host unique assortments of tropical and temperate species. Seawater itself, as well as the benthic macroorganisms that inhabit ocean environments, form habitats such as extensive areas of seagrass beds, macroalgal forests, coral reefs, sponge gardens, benthic mats including stromatolites, continental slopes and canyons and abyssal plain environments. These environments, and the macroorganisms that inhabit them, are all intrinsically linked with highly abundant and diverse consortiums of microorganisms. To date, there has been little research aimed at understanding these critical organisms within Western Australia. Here we review the current literature from the dominant coastal types (seagrass, coral, temperate macroalgae, vertebrates and stromatolites) in Western Australia. The most well researched are pelagic habitats and those with stromatolites, whereas data on all the other environments are slowly beginning to emerge. We urge future research efforts to be directed toward understanding the diversity, function, resilience and connectivity of coastal microorganisms in Western Australia.

KEYWORDS: Marine microbiome, Western Australia, coral, seagrass, bacterioplankton, macroalgae

Manuscript received 24 July 2018; accepted 15 November 2018

INTRODUCTION

In terms of both abundance and diversity, all ecosystems on Earth are dominated by microbes which, although invisible to the naked eye, are essential for the functioning of the biosphere. We collectively refer to prokaryotes (bacteria and archaea), microscopic eukaryotes (such as protists and fungi) and viruses as “microbes”, all of which are abundant in every aquatic environment. The global ocean prokaryotic biomass alone is in the order of a petagram of carbon (10^{15} grams), with ocean sediment harbouring up to ten times more than this (Whitman *et al.*, 1998). Microbes also colonise biotic and abiotic surfaces in the marine environment to form complex biofilm communities, and proliferate in the tissues of many marine organisms, performing ecological functions essential to their hosts (see pull-out box, *microbiomes* Egan *et al.*, 2008).

The term ‘**microbiome**’ (from ‘microbe’ and ‘biome’) refers to the microbes living on a specific habitat, e.g., the ocean microbiome, which includes the water microbiome, the sediment microbiome, the microbiome of macroalgae, seagrasses, corals and sponges, as well as the microbiomes of marine fish and marine mammals. The microbiome also refers to the total genomic pool of the microbiota. In host-associated microbiomes, this extends the host’s functional genome well beyond its evolutionary capabilities.

In addition to their enormous abundance, microbial communities harbour a vast metabolic functional diversity to obtain energy from oxidation-reduction chemical reactions including photosynthesis. As a consequence, prokaryotes are essential to fulfilling many biogeochemical roles, and are likely to be responsible for most, if not all, key transformations in global cycling of carbon, nitrogen, phosphorus, sulphur and iron. About half of the Earth’s primary production (i.e. the conversion of atmospheric CO₂ into organic substances within living

organisms) is in the ocean, with most of this (ca. 90%) performed by microbes (Duarte & Cebrian, 1996; Field *et al.*, 1998). In addition, most of the global respiration (i.e. the degradation of organic carbon into CO₂) stems from microbial processes (del Giorgio & Duarte, 2002). This productivity sustains marine food webs and is fundamental to many of the services of the world's oceans.

Understanding the diversity and ecology of microbiomes has been facilitated by the recent development of 'omic' approaches. These methodologies are based on the cost-effective sequencing of either the whole DNA of the community (metagenomics), the whole mRNA (metatranscriptomics) or various taxonomic marker genes that are amplified before sequencing (typically the 16S rDNA for prokaryotes and the 18S rDNA for eukaryotes). Despite this explosion of sequence-based data and the dominance in both abundance and diversity of microbes in oceans, we understand relatively little of their population dynamics, metabolic complexity and synergistic interactions with macro-organisms. There is mounting evidence that the health of many marine organisms depends on their associated microbiome (e.g., Zozaya-Valdés *et al.*,

2015 and Sweet & Bulling, 2017). In addition, the large genomic diversity within oceanic microbes has a large biotechnological potential (Arrieta *et al.*, 2010; Arnaud-Haond *et al.*, 2011). Hence, there is a vital need to improve our understanding of the diversity, function, resilience and connectivity of microorganisms in the ocean.

MICROBIOMES OF WESTERN AUSTRALIA

With more than 20 000 km of coastline (of which 12 000 correspond to the mainland and the rest to islands), Western Australia has an estimated >300 000 km² of territorial waters, mostly over the continental shelf. Under the Integrated Marine and Coastal Regionalisation of Australia, this area can be divided either into several large Provincial Bioregions, or into eighteen mesoscale Bioregions (Fig. 1). Transitional zones, or biotones, are represented by the bioregions located between provincial water types and signify areas where species likely exist at the limit of their distributions. Three provincial zones and four associated biotones are represented along the Western Australian Coast. There are 18 defined bioregions located along the Western Australia coast,

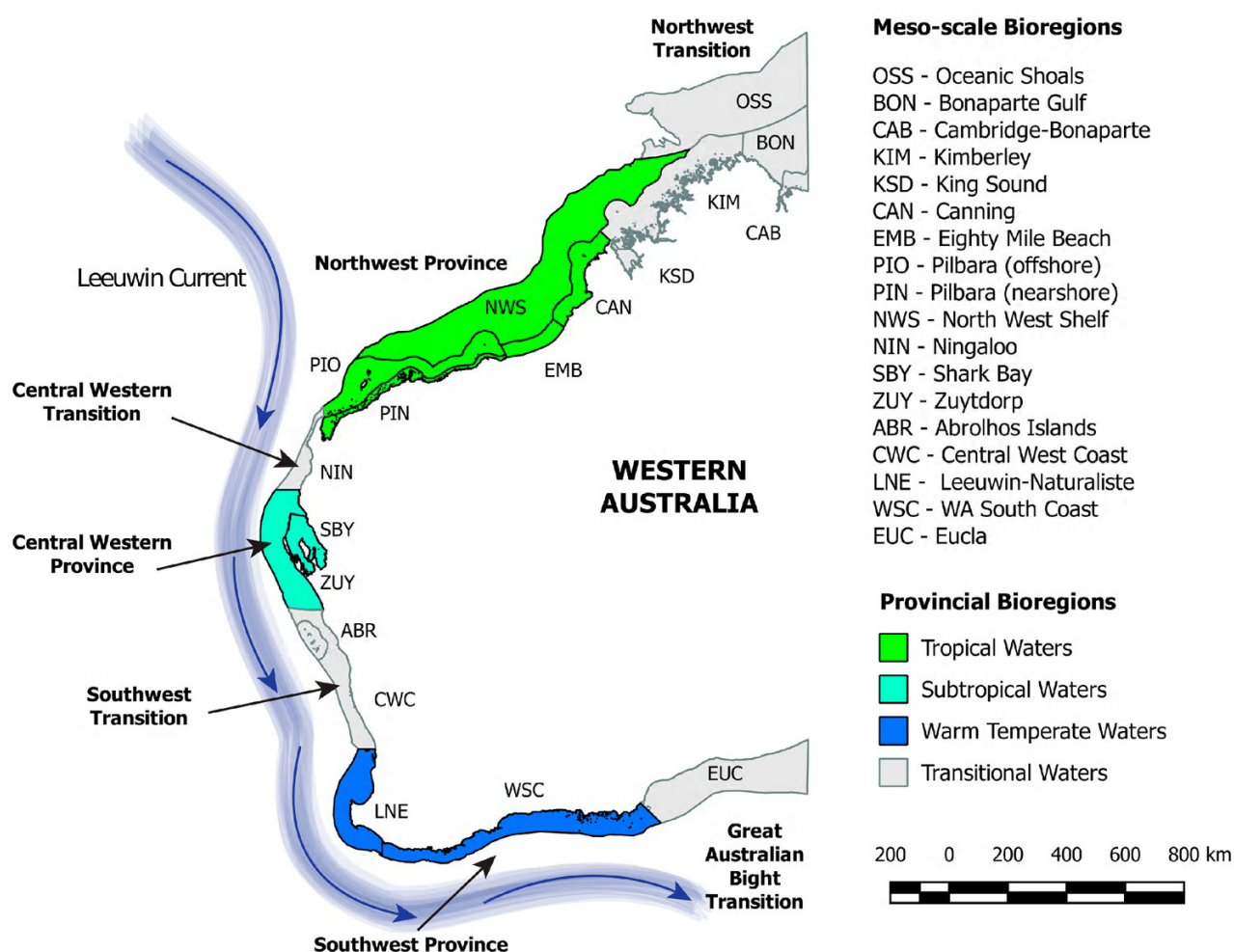


Figure 1. Location of Integrated Marine and Coastal Regionalisation for Australia (IMCRA) Provincial and Meso-scale Bioregions for the Western Australian Coast. Data Source: Commonwealth of Australia (2006). The warm southward flowing Leeuwin Current is represented by blue arrows.

10 of which are located within the tropical waters of the Northwest Province and Northwest Transition (Fig. 1). Across this large range of latitude ($> 20^\circ$ of latitude from ca. 14°S to 36°S) average sea surface temperatures (SST) vary from 28°C in the north to 17°C in the south. In addition, the Western Australian coast ranges from sandy microtidal sites in the southernmost parts, to structurally complex macrotidal environments in the north where there is a significant effect of shallow reefs and island archipelagos that create structure and small-scale variability.

Within Western Australian waters, a number of key ecological features have been identified that are expected to affect the distribution and activity of microbes. Both the pelagic and benthic environments of Western Australia are conditioned by the water current that transports warm tropical Indian Ocean waters along the coast, i.e. the Leeuwin Current that flows parallel to the coast from north to south and continues east after encountering Cape Leeuwin in the southwestern most extremity of the continent. In the South Australian Bight the Leeuwin Current is cooler as it is affected by the Antarctic Circumpolar Current from the west and is compressed towards the coast. In addition to these main currents, the Holloway Current in the north flows parallel to the northern Western Australian coastline and along the shelf, transporting warm, low salinity waters from the Arafura Sea and Gulf of Carpentaria into the Leeuwin Current. As the Holloway Current also flows parallel to the coast in the northern part of the coastline, it in part pushes the Leeuwin Current towards the coast. As a result, these warm waters found at southern latitudes in Australia's west coast set this coast apart from the oceanographic dynamics of the west coasts of other

continents such as America or Africa. This creates unique subtropical conditions that extend towards relatively high southern latitudes. Additionally, the Leeuwin Current generates warm-core and cold-core eddies, the former often entrapping productive shelf waters and creating a mosaic of waters with differences in temperature, phytoplankton and productivity (Waite *et al.*, 2007; Paterson *et al.*, 2013).

In addition to the oceanographic dynamics the shelf is very extensive in some regions (particularly in the north) with morphologically complex structure of shallow water habitats (Jones *et al.*, 2014). There are steep canyons that connect the shelf with deep ocean. In particular the Perth Canyon near the Rottnest Island in the Leeuwin-Naturaliste Bioregion (Fig. 1), allows episodic upwelling of nutrient-rich deep waters. Inshore lagoons are key sites of high benthic productivity (including macroalgae and seagrass). These lagoons support diverse and endemic invertebrate and vertebrate species that include commercial and recreational species of migratory fish. Finally, in the coastal regions of Western Australia are highly diverse, living stromatolites of various ages that hold extraordinary evolutionary significance (Gudhka *et al.*, 2015).

We chose to focus this review on a variety of microbiomes that reflect the importance of these Western Australian ecological features and the availability of published literature (Fig. 2). These microbiomes include: seagrass, coral, temperate macroalgal, vertebrate, benthic mats and stromatolites and planktonic (free-living) microbiomes (Fig. 3). In general, we have restricted our review to shallow waters, given the comparatively higher amount of research that has been focussed on shallow benthic systems versus deeper oceanic settings

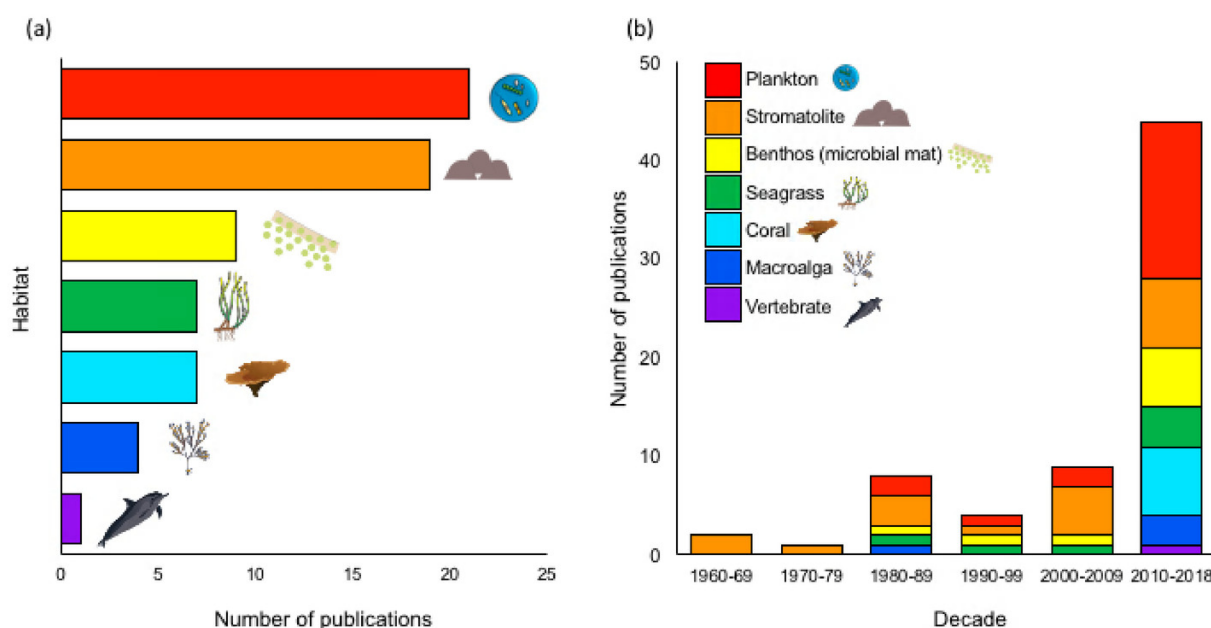


Figure 2. Number of journal articles published on marine microbes in Western Australia showing a) host/habitat they were from, and b) the decade they were published. A list of the references used in this figure are provided in Appendix 1. Symbols from the Integration and Application Network (ian.umces.edu/symbols/).

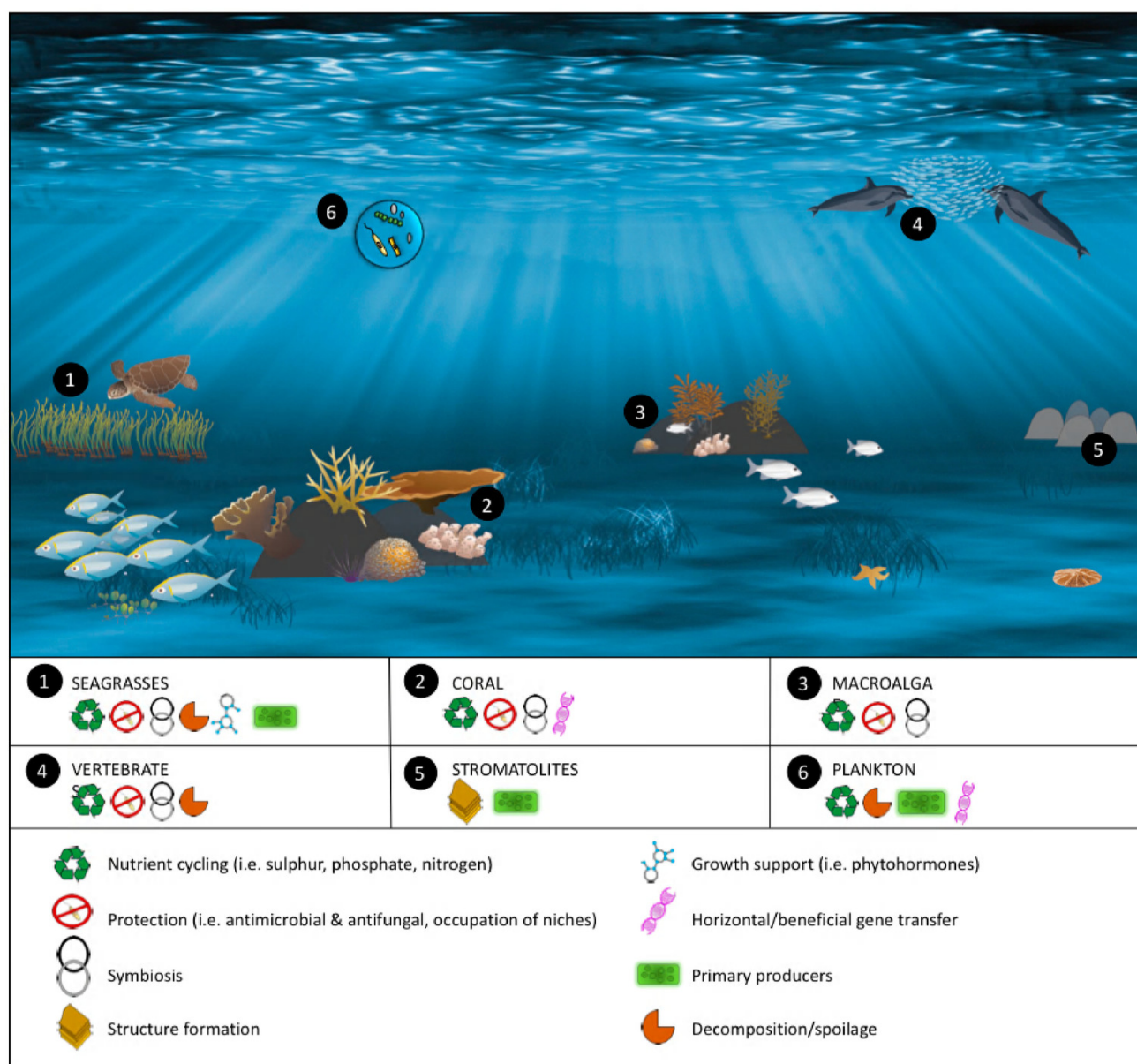


Figure 3. Conceptual diagram of Western Australian microbiomes and the functional roles that microbial communities play within each habitat. Symbols are from the Integration and Application Network (ian.umces.edu/symbols/).

in Western Australia. There are also a variety of other habitats and organisms (e.g., salt marshes, mangroves or invertebrates such as sponges, molluscs and arthropods) that are not included in our review due to scarcity of data, even though we recognise that these are also important components of the marine ecosystem. As it will become clear, the microbial ecology of the oceans surrounding Western Australia is poorly understood. We postulate that a full understanding of life in the ocean requires knowledge of the microbial taxa, their genomes, functioning, biogeographical patterns, and synergistic associations to themselves and larger eukaryotic hosts. A research agenda including these subjects will benefit our understanding of the oceanic environments and will facilitate development of techniques to be used as health diagnosis tools for both ocean organisms and environments.

Seagrass microbiomes

Seagrasses are marine flowering plants (angiosperms) that are distributed along the coastlines of every continent except Antarctica (Short *et al.*, 2007). Seagrasses can be referred to as ‘ecosystem engineers’ (see pull-out box, page 21; Jones *et al.*, 1994); they provide a multitude of ecosystem services such as coastal protection from erosion (Ackerman & Okubo, 1993), sediment stabilisation (Gacia & Duarte, 2001) and represent a habitat and source of food for a variety of organisms (Staples *et al.*, 1985; Heck *et al.*, 2008; Bertelli & Unsworth, 2014). Seagrasses also sequester and store an estimated 19.9 Pg of organic carbon, (roughly 10–18% of the total oceanic carbon sequestration; Fourqurean *et al.*, 2012; Lavery *et al.*, 2013; Serrano *et al.*, 2016).

The term '**ecosystem engineer**' refers to an organism that directly or indirectly modulates the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials, in so doing they modify, maintain and/or create an ecosystem.

The seagrass meadows of Western Australia are among the most diverse in the world, with 11 genera and 26 species of seagrass that represent 36% of global seagrass diversity (Short *et al.*, 2007). Seagrasses in Western Australia are distributed along a latitudinal range, which stretches from 13°S to 35°S (Short *et al.*, 2007). These meadows cover an estimated 20 000 km² (ca 43% of the total Australian seagrass area) and include both temperate and tropical species (Kilminster *et al.*, 2015). Northern Western Australia is dominated by the tropical species *Thalassia hemprichii* and *Thalassodendron ciliatum*, which both have ranges that reach to 22°S, a latitude that also corresponds to the northerly limit of the temperate seagrass *Amphibolis antarctica* (Walker, 1989; Kirkman, 1997). *Cymodocea angustata*, *Halodule uninervis*, *Halophila spinulosa* and *Syringodium isoetifolium* reach south to Shark Bay at 26°S (Walker, 1991; Kirkman, 1997). Southern Western Australia is dominated by Posidoniaceae with eight *Posidonia* species inhabiting either exposed or protected areas according to the habitat requirement of the species (Carruthers *et al.*, 2007). Over 1000 research papers and books have been published since the early 1980s on the ecology of Australian seagrasses, with much of this research conducted along Western Australia (York *et al.*, 2017). Within Western Australia, seagrasses play a central role in sustaining the aquaculture industry (Hanson *et al.*, 2005; Ince *et al.*, 2007; Blandon & Zu Ermgassen, 2014). For example, seagrass meadows provide foraging grounds for the western rock lobster *Panulirus cygnus*, whose fishery is valued at an estimated AUD \$200 million (De Lestang *et al.*, 2009). Seagrass wrack is also an important habitat when it is deposited in surf zones where it sustains various components of the coastal ecosystem by feeding amphipods, copepods, birds, crabs and a variety of juvenile fish (Lenanton, 1982; Robertson & Lenanton, 1984; Hyndes & Lavery, 2005; Ince *et al.*, 2007).

Despite the importance of seagrass meadows in Western Australia, there has been an extensive decline in their area across the State, largely as a result of coastal development and climate change (Hyndes *et al.*, 2016). For example, in Cockburn Sound (Leeuwin–Naturaliste Bioregion, Fig. 1), 97% of the seagrass meadow (34 km²) had been lost by 1978 due to development of heavy industries and the consequent flow of industrial waste and nutrients into the bay (Cambridge & McComb, 1984). Similarly, at Albany up to 66% of the seagrasses in Princess Royal Harbour and up to 46% of the seagrasses in Oyster Harbour (South Coast Bioregion; Fig. 1) have declined due to elevated nutrient flow from local factories and town sewage (Bastyan, 1986; Kirkman, 1987). In 2011, a particularly strong marine heat wave event caused damage to 36% of the seagrass meadow area in Shark Bay (Arias-Ortiz *et al.*, 2018). In most cases seagrasses have failed to recover despite improvements in water quality (Mohring & Rule, 2013; Fraser *et al.*, 2016). This has led to a greater research effort to identify possible reasons for continued seagrass decline, as well as more focused research effort into improving seagrass restoration.

A central, but overlooked, component to understanding drivers of seagrass decline is the role of microbes living in association with their host as a single biological unit also referred to as the 'holobiont' (see pull-out box, below; Ugarelli *et al.*, 2017). Seagrass tissues are colonised by a diverse microbiome that play a critical role in their growth and health due to their influence on nitrogen and phosphorus supply (Garcias-Bonet *et al.*, 2016; Tarquinio *et al.*, 2018), protection from pathogens (Marhaeni *et al.*, 2011; Supaphon *et al.*, 2013), sediment detoxification (e.g., removal of sulphides; Küsel *et al.*, 2006) and production of phytohormones that stimulate plant growth (Kurtz *et al.*, 2003). For example, cyanobacteria associated with seagrass leaves and sulphate-reducing bacteria present in the roots may supply up to a third of the nitrogen requirement by seagrass through nitrogen fixation and/or mineralisation of organic nitrogen (Welsh, 2000; Nielsen *et al.*, 2001; Cole & McGlathery, 2012). Seagrass epiphytic cyanobacteria and fungi also represent a source of antimicrobial, antifungal and antifouling molecules and can protect seagrasses from pathogens and biofouling (Gleason & Paulson, 1984; Supaphon *et al.*, 2013; Mazard *et al.*, 2016).

The term '**holobiont**' refers to an assemblage of different interacting organisms considered as a single unit. For example, a host organism (such as seagrasses, sponge, fish etc.) and the microbes that live in and on that host, and their entire genetic repertoire.

Microbial populations respond rapidly to environmental disturbance due to their fast generation times (Allison & Martiny, 2008). Consequently, monitoring their composition and activity can serve as a sensitive bio-indicator of environmental fluctuations and ultimately declines in seagrass health. Despite the globally recognised importance of microbiomes to seagrass health, research on their microbiomes is fundamentally lacking, particularly in regard to Australian taxa. A recently published overview of seagrass microbiome research revealed that only three of 58 studies worldwide were on Australian ecosystems (Ugarelli *et al.*, 2017). While this review was not exhaustive, it serves to highlight the discrepancy between the many studies on Australian seagrass and the small portion that focus on the microbiome.

Whereas few research articles have been published on Western Australian seagrass microbiomes compared to other host-associated microbiomes (Fig. 2), this research has led to several important discoveries. Research on temperate *Posidonia sinuosa* communities has revealed the importance of leaf-associated microbiota in translocating nitrogen into seagrass leaves (Tarquinio *et al.*, 2018). Ureolytic and ammonia-oxidising genes are significantly more abundant in the leaf microbiome than in the surrounding habitat, indicating that there is a specific ecological niche for ammonia-oxidising bacteria in a function traditionally considered to be dominated by archaea (Tarquinio, 2017). This work suggests a previously unrealised role of the leaf microbiome in nitrogen cycling, likely of global significance considering the abundance of seagrass habitats worldwide.

Other seagrass microbiome research in Western Australia focusses on identifying links between above ground disturbances to seagrasses and changes in the below ground microbial communities. For example, light

reduction at the leaves increased root exudation in three Western Australian tropical seagrass species (Martin *et al.*, 2018), and led to a reduction in the abundance of beneficial bacteria within the root microbiome (Martin *et al.*, 2017). Fraser *et al.* (2016) quantified threshold organic matter loads that cause shifts in microbial community structure of the seagrass sediment microbiome. This threshold coincided with a reduction in sediment pH, possibly favouring microbes such as sulphate reducers that require little or no oxygen.

The spatial structure and colonisation pattern of microbes have been examined in several Western Australian seagrass species. For example, scanning electron microscopy revealed that colonisation of microbes on *Posidonia australis* roots was lower (2.5×10^5 cells/cm²) than on Mediterranean *Posidonia* species (*P. sinuosa* 4.89×10^5 cells/cm² and *P. oceanica* 4.43×10^6 cells/cm²), possibly due to the older age of the Mediterranean species roots compared with their Western Australian counterparts (García-Martínez *et al.*, 2005). Scanning electron microscopy also revealed that microbial root colonisation of three tropical Shark Bay seagrasses was highest in the root hair zone compared to other parts of the root, possibly due to differences in root exudation and leakage of oxygen along the root length (Martin *et al.*, 2018). Transmission electron microscopy and light microscopy also revealed fungal hyphae penetrating the root cells of Western Australian *Posidonia* spp. (Kuo *et al.*, 1981) and the mesophyll shoot tissue of the seagrass *Zostera muelleri* (Kuo *et al.*, 1990), but little else is known about fungi on seagrasses in the State.

Seagrasses influence not only the microbes directly associated with their own root tissues, but they may also drive shifts in the bacterial communities within the immediate surrounding sediment (the rhizosphere), which, like terrestrial plants, represents a hot spot of microbial activity (Shieh & Yang, 1997). Rhizosphere microbes benefit from plant metabolism (e.g., delivery of photosynthetically produced oxygen and dissolved organic carbon by roots), but they may also profoundly influence seagrass fitness. For example, eutrophication of coastal waters has been linked to major seagrass die-off events due to the stimulation of nitrogen and phosphorus on decomposition and reduction processes of sulphate reducing bacteria; leading to an increase in the accumulation of phytotoxic sediment sulphides (Bagarinao, 1992; Borum *et al.*, 2005; Holmer *et al.*, 2006). However, nutrient additions and elevated temperatures were found to have negligible effects on the rate of decomposition of detritus from the seagrass *Zostera muelleri* under anoxic conditions, despite causing changes in microbial community composition (Trevathan-Tackett *et al.*, 2017). Further studies are needed to understand the delicate equilibrium that regulates seagrass and rhizosphere bacterial interactions.

Collectively, these studies represent the 'tip of the iceberg' with regards to understanding the importance of microbes in Western Australian seagrass ecosystems. It is clear that there are large gaps in our knowledge of the microbial ecology of seagrass ecosystems from both a national and local context. As the global extent of seagrasses has been declining at an increasing rate (Waycott *et al.*, 2009), focused efforts on effective science-based management, such as an improved understanding

of the role and diversity of eukaryotic microorganisms associated with seagrasses, together with their resilience to change, is essential (York *et al.*, 2017). Priorities for future research should include focusing on sediment detoxification and nutrient acquisition processes, as well as those involved in pathogen defence (York *et al.*, 2017). Given recent marine heat waves along the Western Australian coast (Arias-Ortiz *et al.*, 2018), understanding how increasing temperature affects seagrasses and their associated microbiomes should also be a priority (Hyndes *et al.*, 2016) to improve our current knowledge of seagrass die-off events and to help restorative efforts across Western Australia.

Coral Microbiome

Globally, shallow-water coral reef systems represent one of the most diverse, complex, productive and valuable ecosystems (Crossland *et al.*, 1991; Moberg & Folke, 1999). Such reefs are mostly located in oligotrophic, intra-tropical regions, where environmental characteristics (i.e. salinity and temperature) lie within the range necessary to support the growth of reef organisms (Kleypas *et al.*, 1999). However, Western Australian shallow coral reefs also include fringing and atoll reefs found in the transition zones between temperate and tropical waters where mean water temperature ranges between 20 to 24°C, several degrees cooler than the optimal coral reef temperatures of 23 to 29°C. These environmental features have generated diverse habitats with unique coral communities along the coast. The Ningaloo Reef, approximately 260 km long, is the only extensive coral reef fringing the west coast of the continent (Ningaloo Bioregion, Fig. 1). Most other reefs in northern Western Australia either surround offshore islands or are on emergent points along the continental shelf where waters are clearer than inshore regions (e.g., Rowley Shoals, Scott and Seringapatam Reefs, Pilbara Bioregion; Fig. 1). The most southerly reef-forming coral species in Western Australia are found in the Abrolhos Islands Bioregion (Fig. 1). Those reefs lie within a region of convergence between temperate and tropical waters, and are considered unique as corals coexist with temperate macroalgae communities. Coral species are also present as far south as the Leeuwin–Naturaliste Bioregion, i.e., Rottnest Island, Geographe Bay and Recherche Archipelago, but have a patchy distribution in these regions and do not form extensive reef substrate (Veron & Marsh, 1988).

Shallow water corals are able to grow in otherwise oligotrophic waters due to their ability to establish mutualistic symbiotic relationships with unicellular dinoflagellate algae of the Family Symbiodinaceae, as well as with bacteria and archaea. Corals also host fungi and viruses, whose functional roles are not well understood (Rosenberg *et al.*, 2007). Functionally, coral-associated symbionts are involved in nutritional pathways, i.e. photosynthesis, nitrogen fixation, phosphate production and solubilisation, degradation of dimethylsulfonylpropionate (DMSP); bacterial cell–cell chemical signalling (also known as quorum sensing); genetic exchange; and protection of the host (Muller-Parker & Delia, 1997; Rosenberg *et al.*, 2007; Siboni *et al.*, 2008; Sharp & Ritchie, 2012; Fournier, 2013). For instance, through their ability to produce secondary metabolites and nutrients (Lesser *et al.*, 2007; Olson *et al.*

al., 2009; Howard *et al.*, 2011; Raina *et al.*, 2013), bacteria belonging to specific lineages (i.e. *Vibrio*, *Pseudomonas* and Cyanobacteria) are likely to contribute to the control of Symbiodinaceae's growth, density and nutrition (Ritchie & Smith, 1997; Lesser *et al.*, 2007). Conversely, the ability of the Symbiodinaceae to produce DMSP potentially controls nutrient availability and consequently the growth of bacterial populations, some of which may be pathogenic (Curson *et al.*, 2011; Raina *et al.*, 2016; Raina *et al.*, 2017). Preliminary studies suggest a role for archaea in the recycling of nitrogen within the coral host (Siboni *et al.*, 2008), whereas viruses may help in controlling bacterial abundance in the coral mucus (Wood-Charlson *et al.*, 2015).

Most coral microbiome research across Australia has been conducted on the iconic Great Barrier Reef, in north eastern Australia, with far fewer investigations on the west coast (Crabbe & Carlin, 2009; Ceh *et al.*, 2011; Ainsworth *et al.*, 2015; Thompson *et al.*, 2015a). However, there are several important examples of coral microbiome research from Western Australia. For instance, the role of nitrogen transfer to coral larvae by two strains of Gammaproteobacteria was investigated within the cosmopolitan coral species *Pocillopora damicornis* via nanoscale secondary ion mass spectrometry (Ceh *et al.*, 2013a). When larvae were exposed to either strain, there was increased nitrogen uptake, providing evidence for the role of microbes in nutrient transfer during this critical early life history phase (Ceh *et al.*, 2013a). Two other examples have focused on microbial community structure during and after spawning. The first examined *Acropora tenuis*, *P. damicornis* and *Tubastrea faulkneri* and detected an increase in Alphaproteobacteria after spawning, with the *Roseobacter* clade found to be conspicuous in all three species after spawning, suggesting they may play a role in coral reproduction (Ceh *et al.*, 2012). The second of these studies found that *A. tenuis* (a broadcast spawning species), and *P. damicornis* (a brooding species) each released specific microbial assemblages into the surrounding seawater during spawning (Ceh *et al.*, 2013b). In particular, *A. tenuis* released, in decreasing order, *Roseobacter*, *Flavobacteriaceae*, *Alteromonas* and *Shewanella*, again implying a role for some *Roseobacter* in the reproductive processes of corals. In contrast, *P. damicornis* released *Alteromonas*, *Vibrio*, *Shewanella* and *Marinomonas* with only minimal amounts of *Roseobacter* detected in the water column post-spawning. These studies add to several others from different geographical locations (e.g., Apprill *et al.*, 2009 and Sharp & Ritchie, 2012) and indicate the presence of Alphaproteobacteria, and in particular the *Roseobacter* clade, as key coral associates in either spawning corals or early life-history stages.

Several studies have examined geographic variation of distinct components of the coral holobiont in contrasting regions within Western Australia. Given the extensive coastline, Western Australia presents opportunities to examine microbiomes of coral species in vastly different environmental conditions. Thomas *et al.* (2014) examined Symbiodinaceae community variation within *Acropora* from the Kimberley region (mean SST from 26 to 31°C) and the Abrolhos Islands (mean SST from 20 to 25°C), whereas Ceh *et al.* (2011) examined coral-associated bacteria in the coral species *Pocillopora damicornis* at Ningaloo Reef (mean SST from 22 to 28°C) and Rottnest

Island (mean SST from 19 to 23°C). Interestingly, both studies found minimal variation in microbial community structure despite the large distance between sampling sites and substantial differences in annual mean SST. One possible mechanism for the similarity between sampling regions may be the connectivity of Western Australian reefs via oceanographic features (e.g., the Leeuwin Current) that are likely to be the main pathways connecting Symbiodinaceae and bacterial communities of the tropical north with the temperate south regions of Western Australia. With regards to Symbiodinaceae communities in Western Australian *Acropora* corals, Thomas *et al.* (2014) show that most colonies had a high level of specificity to clade C, as well as a novel association with clade G, in contrast to studies in other regions where clade G has not been detected in *Acropora*. A biogeographical study of bacteria and archaea associated with the coral *Stylophora pistillata* from seven major regions across the globe also showed unique features of the holobiont in corals from Western Australia (Neave *et al.*, 2017): among these regions, only Western Australian corals were found to host distinct lineages of the coral-associated Gammaproteobacterial genus *Endozoicomonas*. *S. pistillata* from Western Australia also contained high numbers of *Pseudomonas*, not seen in other regions. Although this comparison is based on just two studies, taken together they suggest Western Australian corals exhibit unique microbial assemblages, arguably promoting the importance of Western Australian corals as an endemic reservoir of microbial diversity.

Despite their isolation, Western Australian coral reefs are not immune to climatic events and other human related impacts. Large-scale disturbances (such the marine heatwave in 1998) have had relatively little impact on Western Australian corals (Speed *et al.*, 2013). However, record temperatures of up to 5°C above long-term averages during 2010/11 caused major bleaching (loss of Symbiodinaceae) and significant loss in coral cover along parts of the Western Australian coast (Pearce *et al.*, 2011, Moore *et al.*, 2012, Depczynski *et al.*, 2013). Local impacts of sedimentation due to dredging is also an important environmental impact in Western Australia, particularly in the Northwest Province Bioregion (Jones *et al.*, 2015). Increased sedimentation rates and turbidity caused by dredging and deposition of dredge spoil can reduce light available to Symbiodinaceae for photosynthesis (Bessell-Browne *et al.*, 2017), with potential consequences for other components of the coral microbiome, and as a result coral health. For example, altered coral holobionts have the potential to make corals more susceptible to disease and bleaching events (Hughes *et al.*, 2017), as well as reducing rates of fertilisation, larval survival and settlement (Erftemeijer *et al.*, 2012). However, the consequences of altered environmental conditions on Western Australian coral microbiomes are still poorly understood with regards to diversity, abundance and functionality, including their connection with coral health (Pollock *et al.*, 2014).

Temperate macroalgal microbiomes

Temperate reefs, dominated by macroalgae, are ecologically, culturally and economically important (Harley *et al.*, 2012). Macroalgae provide many essential roles in marine ecosystems (Steneck *et al.*, 2002), such as

primary production, the provision of habitat (see pull-out box, *ecosystem engineers*, page 21), nutrient retention/cycling, as well as CO₂ storage (Egan *et al.*, 2013; Koch *et al.*, 2013). Macroalgal growth, health, resilience and ecological function are all influenced by the interactions with the associated microbiome (Case *et al.*, 2011; Egan *et al.*, 2013). The relationship between microbes and macroalgae can be mutually beneficial, parasitic, or commensalistic (Armstrong *et al.*, 2001; Case *et al.*, 2011; Abby *et al.*, 2014). For example, a study from the United Kingdom using the green alga *Ulva linza*, found that particular strains of bacteria positively influenced the growth and morphology of seaweed, whereas algae without these bacterial isolates displayed abnormal growth and morphology (Marshall *et al.*, 2006). Fungi also form beneficial associations with macroalgae and obligate symbioses, termed mycophycobioses, and have been described in brown, red and green macroalgae (Raghukumar, 2017). Overall, microbial communities are an integral component of sustaining normal algal function and are therefore important for the entire macroalgal ecosystem (Burke *et al.*, 2011).

Western Australian benthic reef ecosystems, from the Northwest to the Southwest Province (Fig. 1), host diverse assemblages of macroalgae (e.g., Huisman, 2018). An early study of macroalgal microbiomes examined aerobic heterotrophic bacteria containing bacteriochlorophyll on various substrates, including red and green species of macroalgae, and found high abundances on Western Australian algae (Shiba *et al.*, 1991). More recently, the microbiome of the brown kelp, *Ecklonia radiata*, was found to be stable in composition among healthy individuals across the entire southern coast of Australia (Marzinelli *et al.*, 2015). The two other studies of macroalgal microbiomes from Western Australia indicate important ecological roles, including being the main decomposers of beach wrack on Western Australian sandy beaches (McLachlan, 1985) and cues for settlement of marine invertebrates (Huggett *et al.*, 2018).

There has been a substantial body of work on the microbial ecology of several macroalgal species from eastern Australian temperate waters, including several species also present in Western Australia. These include studies of the red alga, *Delisea pulchra*, and its role in preventing microbial biofilms forming on algal surfaces (Maximilien *et al.*, 1998; Rasmussen *et al.*, 2000; Manefield *et al.*, 2002), as well as the ability of bacteria from the green alga *Ulva lactuca* to prevent biofouling (Holmström *et al.*, 1996; Egan *et al.*, 2000; Egan *et al.*, 2001; Holmström *et al.*, 2002). Given the different oceanographic characteristics that influence the macroalgal communities of Australia's east and west coasts and the high levels of macroalgal endemic species on the west coast, similar studies on the western microbiomes are required.

In temperate Australian waters, including those in the west, the brown kelp *Ecklonia radiata* is the dominant habitat-forming alga (Kirkman, 1981). In recent years, kelp distribution and biomass has declined on both the east and west coastlines mainly due to rising water temperature (Wernberg *et al.*, 2011a) and associated bleaching (loss of algal photosynthetic pigment) in this species (Phelps *et al.*, 2017). Some evidence suggests that microbes could play a substantial role in the decline

of macroalgal biomass and habitat (Egan *et al.*, 2014; Beattie *et al.*, 2017). For example, Marzinelli *et al.* (2015) observed dysbiosis (see pull-out box below) of *Ecklonia radiata* microbiomes along the temperate Australian coastline (Marzinelli *et al.*, 2015) and *Ecklonia radiata* infected with a putatively pathogenic bacteria displayed bleaching (Beattie *et al.*, 2017). These observations show that the kelp microbiome is linked to both bleaching and temperature and may play a direct role in decline of kelp health.

The term 'dysbiosis' refers to a microbial community shift that has a negative impact on the host.

Changes in environmental conditions such as sunlight, chlorophyll-*a*, water temperature and salinity impact the community structure of macroalgae microbiomes (Gilbert *et al.*, 2010). Future microbial studies should seek to understand the influence and interactions of environmental, biological and anthropological factors on the Western Australian macroalgae holobiont. In particular, rising seawater temperatures have been flagged as a major contributor to diminishing macroalgal cover and range contraction of many macroalga species along this coastline (Wernberg *et al.*, 2011b, 2016b) suggesting that improved understanding of the influence of rising water temperatures on macroalgal microbiomes is timely. Increasing urbanisation also has an impact on macroalgal microbiomes, with the kelp growing on harbours and other marine structures displaying microbiomes similar to those found on diseased algae (Marzinelli *et al.*, 2018). Further research is needed to understand the flexibility, resilience and ecological significance of macroalgal microbiomes and their role in reef health along the Western Australian coast.

Marine vertebrates

A number of endangered marine mammals live, or migrate, along the west coast of Australia, including blue and humpback whales, dugongs and sea lions. In addition, Western Australian coastal waters support six of the world's seven species of sea turtles as well as recreational and commercially valuable finfish and aquaculture fisheries. The role of the microbiome in vertebrates has been extensively studied in terrestrial systems, facilitated by the explosion of human microbiome research in the last decade. Mutualistic relationships between microbes and vertebrate hosts have evolved through co-evolutionary processes over long periods (Bäckhed *et al.*, 2005) and have been linked to changes in host phylogeny (Colston & Jackson, 2016). Virtually all external surfaces including the skin, gastrointestinal tract and respiratory tract of vertebrates are colonised by microbes (Montalban-Arques *et al.*, 2015). Within these microbial communities, selective pressures exhibited by the host and microbial members produce highly structured populations of microbiota (Moeller & Ochman, 2014). Our understanding of the metabolic capabilities of the microbiome and its role in host health has been mostly advanced through molecular studies involving humans and captive mammals (Colston & Jackson, 2016). However, there are over 17 000 marine vertebrate species (Appeltans *et al.*, 2012) and most of these have received little or no attention with regards to microbiome research.

Despite the continual exposure of marine vertebrates to seawater, species-specific communities of microbiota have been found on the external surfaces of marine fish (Larsen *et al.*, 2013, Lowrey *et al.*, 2015), whales (Apprill *et al.*, 2014, 2017), dolphins and sea lions (Bik *et al.*, 2016). Microbial communities are further structured according to unique environments in different niches in and on vertebrate hosts, with the gastrointestinal (GI) tract the most well studied region. Marine fish GI tracts have been the most studied, especially for commercially important species (Colston & Jackson, 2016). The first meal (first feeding) taken by a fish has a strong influence on the overall composition of the GI microbiome (Ingerslev *et al.*, 2014), but the homeostatic composition is continually modified by interconnecting factors including host genetics, environment (water, diet, toxins, antibiotics, pH, temperature), and microbial inhabitants (competitive inhibition, metabolic activity). If the community composition is altered, and key microbial members are lost (see pull-out box, *dysbiosis*, page 24), host benefits such as metabolic functioning (Ríos-Covián *et al.*, 2016), pathogenic exclusion, and immune function (Maynard *et al.*, 2012) are impaired, and inflammation and disease may progress (Montalban-Arques *et al.*, 2015). Infections are common among marine mammals (Nelson *et al.*, 2015), and the role of the resident microbiota in the etiology of these conditions is poorly understood. Dysbiosis is a relatively new way of considering disease progression, and, as disease is one of the main causes of death in marine mammals (Waltzek *et al.*, 2012), it may be an important focus for marine vertebrate microbiome research.

With the exception of sea lions, the microbiome associated with marine mammals has not been studied within Western Australian populations. Healthy humpback whales from the North Atlantic, North Pacific and South Pacific have a similar skin microbiome dominated by specific bacteria (*Tenacibaculum* and *Psychrobacter*) that is greatly reduced on entangled or deceased whales (Apprill *et al.*, 2014). On the east coast of Australia, faecal microbiomes from captive dugongs are less diverse than those of wild dugongs and are missing many bacterial members that dominate the wild dugong microbiome (Eigeland *et al.*, 2012). Delpont *et al.*, (2016) found a similar result in wild and captive Australian sea lions and presumed for both cases that contrasting diets between wild and captive animals played a key role in the development of the different GI microbiomes. Furthermore, the captive dugongs were orphaned at one and three weeks, so it is possible they may not have had sufficient suckling time to develop a 'normal' gut microbiome (Eigeland *et al.*, 2012). It would be valuable to do comparable studies, examining differences between west coast wild and captive vertebrates as well as their east coast counterparts to further understand the structure of Western Australian vertebrate microbiomes. In particular, respiratory microbiomes are likely to be a useful target as the respiratory tract is one of the most commonly affected sites in cetaceans (Apprill *et al.*, 2017), and oil exposure is known to cause respiratory problems (Thomas *et al.*, 2016). Conducting similar research on humpback whales and bottlenose dolphins along the North West Shelf—an extensive oil and gas region—may be of particular importance.

Despite the requirement for long-term protection of sea turtles, the microbiome of Western Australian populations, including the endemic flatback turtle, and the Indian Oceans largest population of hawksbill turtle, have not been described (Pendoley *et al.*, 2016). Sea turtles receive little to no maternal care, consuming seagrass from an early age and rely heavily on the hindgut microbial fermentation for digestion. The gut microbiota is therefore strongly influenced by environmental and dietary factors which change as the turtles mature from juvenile to adult (Price *et al.*, 2017). Building on this work, how the gut microbiome influences the development of marine hindgut fermenters, particularly in terms of dietary requirements, would be relevant for rehabilitation and protection programs in Western Australia.

Finally, aquaculture is an important economic development in Western Australia, with production expected to continue increasing especially within the Midwest Aquaculture development zone, declared in 2017 (Western Australian fisheries) and the Central West Coast Bioregion (Fig. 1). A number of tropical native species are raised in aquaculture, and one of the greatest challenges they face is bacterial disease, with most bacterial species isolated from Australian aquaculture environments (including those from Western Australia) presenting antibiotic resistance (Akinbowale *et al.*, 2006). Due to the broad target range of antibiotics, both pathogenic and beneficial bacteria are affected, which can lead to dysbiosis, immune suppression and possibly an increase in pathogen susceptibility (Becattini *et al.*, 2016). As an alternative, probiotics and prebiotics are being investigated as an effective method for combating disease in aquatic animals (Banerjee & Ray, 2017). Probiotics have been shown to deliver the same health benefits to the host as a healthy microbiome (immune system, nutrition, pathogen exclusion), although there have also been reports that probiotics are not fully retained (Akhter *et al.*, 2015). The increasing demand for sustainable seafood and the growing Australian population means the health management within aquaculture must be a top priority if disease-free fish production is to be maintained.

The high biodiversity and endemism of Western Australian marine organisms makes the coast an exciting place to study marine vertebrate microbiomes and with the past warming anomalies in sea surface temperature, the resulting range shifting species (Wernberg, 2012) present a unique system in which biogeographic patterns of the microbiome can be studied within a single species in the wild. Both captive animals, and single systems (such as the Zebrafish) have been used to reveal the functional role of the microbiome, improving our understanding of co-evolutionary mechanisms that influence community structure. However, to understand how the host-symbiont relationship responds to changes in the natural environment, the resilience and metabolic flexibility of bacterial members should be studied within a single host species, eliminating variation caused by capture, or interspecies differences. When a host moves into a new environment, key questions arise such as: will the microbiome be restructured by the new metabolites and populated by new seeding bacteria, or can the same species persist by changing their metabolic output? Such questions can be addressed by targeting range shifting species along the Western Australian coast such as *Choerodon rubescens* (Cure, 2018), and *Chaetodon assarius*

(Wernberg, 2012), and comparing the microbiome from distinct populations over large distances. Furthermore, researchers could track the movement of potential pathogens from historic to new populations, which could improve conservation efforts as well as improve our understanding of the relationship between dysbiosis and disease in marine vertebrates.

Plankton microbiome

Seawater is amongst the most abundant compounds on the Earth's surface, covering more than 70% of the planet. One millilitre contains approximately 10 million viruses, 1 million prokaryotic cells and 1000 unicellular eukaryotes (e.g., Kirchman, 2008). In addition to their enormous biomass, planktonic microorganisms also harbour extensive genetic diversity, and thus drive global biogeochemical transformations including the nitrogen and carbon cycles (Falkowski *et al.*, 1998). While recent 'omics technologies and global ocean surveys (e.g., Sunagawa *et al.*, 2015 and Yooseph *et al.*, 2007) have greatly facilitated our knowledge of global oceanographic patterns and processes, understanding key drivers of oceanic microbial community diversity and function remain a global challenge. In spite of that, we know very little of which microbes dominate in Western Australian marine waters, in what abundances, what are the drivers of planktonic microorganism abundance, activity or diversity, and how global change is affecting them.

Within Western Australian waters, phytoplankton, the microbes at the base of the food chain, were first to be investigated among the planktonic marine microbes, possibly because measures of chlorophyll-*a* concentration, an indicator of phytoplankton biomass, were an easy way of characterising the trophic conditions of an aquatic environment. Conspicuous eukaryotic phytoplankton were the first studied microbes (e.g., Hallegraeff & Jeffrey, 1984), and monographs exist about diatoms (Jameson & Hallegraeff, 2010; McCarthy, 2013a), dinoflagellates (McCarthy, 2013b) and coccolithorids (Hallegraeff, 1984), as well as the phytoplankton of Western Australian estuaries (John, 1983). Recent syntheses of phytoplankton abundance and biomass (Davies *et al.*, 2016) and chlorophyll-*a* measurements (Davies *et al.*, 2018) around Australia have been published, and the data made public through the Australian Ocean Data Network system (<http://portal.aodn.org.au/>). Comparison of phytoplankton communities in the east (affected by the Eastern Australian Current) and the west (affected by the Leeuwin Current) showed an overall difference in total chlorophyll (0.14 to 0.25 µg Chl *a* l⁻¹ in the west, about half the annually integrated value in the east (Thompson *et al.*, 2011). The Southwest coast has also been shown to have relatively few smaller eukaryotes (pelagophytes, prasinophytes, cryptophytes, chlorophytes) and fewer larger eukaryotes (bacillariophytes and dinophytes) reflecting the differences in seasonality of the two major boundary currents, the vertical stability of the water column, and the average availability of nutrients in the euphotic zone (Blondeau-Patissier *et al.*, 2011).

In particular, there are few records of picophytoplankton (cyanobacteria of the genera *Prochlorococcus* and *Synechococcus*, as well as small eukaryotes) in Western Australia. Thompson & Bonham (2011) observed a significant contribution of the two

cyanobacteria in the Kimberly region and a recent study from Rottnest Island in southwestern Australia found similar amounts of the two cyanobacterial groups, and about one order of magnitude fewer picoeukaryotes (Thomson & Pattiaratchi, 2018). The study reports little seasonality in picophytoplankton abundance, and suggests that their abundance increases following marine heat waves. These microbes are good markers of long-term tropicalization as *Prochlorococcus* prefers warmer temperatures and less nutrients (Li, 2009). They also indicate oceanographic features, such as the warm-core eddy linking Leeuwin Current, shelf and oceanic waters, observed off southwestern Australia by Paterson *et al.* (2013). A study of their relative abundances between El Niño and La Niña periods (July 2009 – June 2010 vs La Niña of July 2010 – June 2011) showed increased abundances of cyanobacteria, and particularly of *Prochlorococcus* in the Rottnest Island and Esperance regions, indicating a general tropicalization of the waters (Thompson *et al.*, 2015b).

Despite the abundance, activity, diversity and trophic role of the heterotrophic prokaryotes as essential components of the microbial food web affecting the ocean carbon cycle (Whitman *et al.*, 1998), we know little of their role in the marine waters of Western Australia. Patten *et al.* (2011) enumerated bacterioplankton, virioplankton and picoautotrophs across the Ningaloo Reef and into the sandy lagoon and also measured active depletion through the coral reef of all groups. They found that *Synechococcus* removal was biogeochemically more relevant, in terms of C and N, and that viruses were less affected by the coral than the other microbial groups. Jones *et al.* (2014) compared the abundances of bacteria, picophytoplankton and viruses across a macrotidal complex archipelago in Collier Bay, north of Broome. They observed a mosaic of concentrations with abundances typical of a tropical site (1 × 10⁴ *Synechococcus*, 3 × 10⁵ bacteria, 1 × 10⁶ viruses, with a larger variability in viruses), with lower abundances near the coast where waters were more turbid.

In terms of diversity, Raes *et al.* (2014) used a fingerprinting approach to study bacterioplankton community composition across a large latitude gradient (10°S to 32°S) following the continental shelf break from Fremantle to Darwin in a study of nitrogen fixation. The authors found that bacterial communities were unique among the different water masses that are well defined by oceanographic parameters. In a subsequent study Raes *et al.* (2018), used tag sequencing to show a powerful diversity gradient between the northernmost area, characterised by high temperatures and low diversity, and the lowermost area, characterised by lower temperatures and higher diversity. Bacterial richness almost doubled between the two areas, and was positively correlated to total dissolved inorganic nitrogen, chlorophyll-*a*, phytoplankton community structure, and primary productivity. Further analysis of these data (Raes *et al.*, 2018) showed that the differences in bacterial diversity existed even though most communities were dominated by the same groups (SAR11, *Synechococcus*, *Flavobacteriaceae*, *Rhodobacteraceae*, etc.) in similar proportions. The communities could be differentiated into three groups, according to whether they originated in the Timor Sea, the subtropical waters, or the Leeuwin

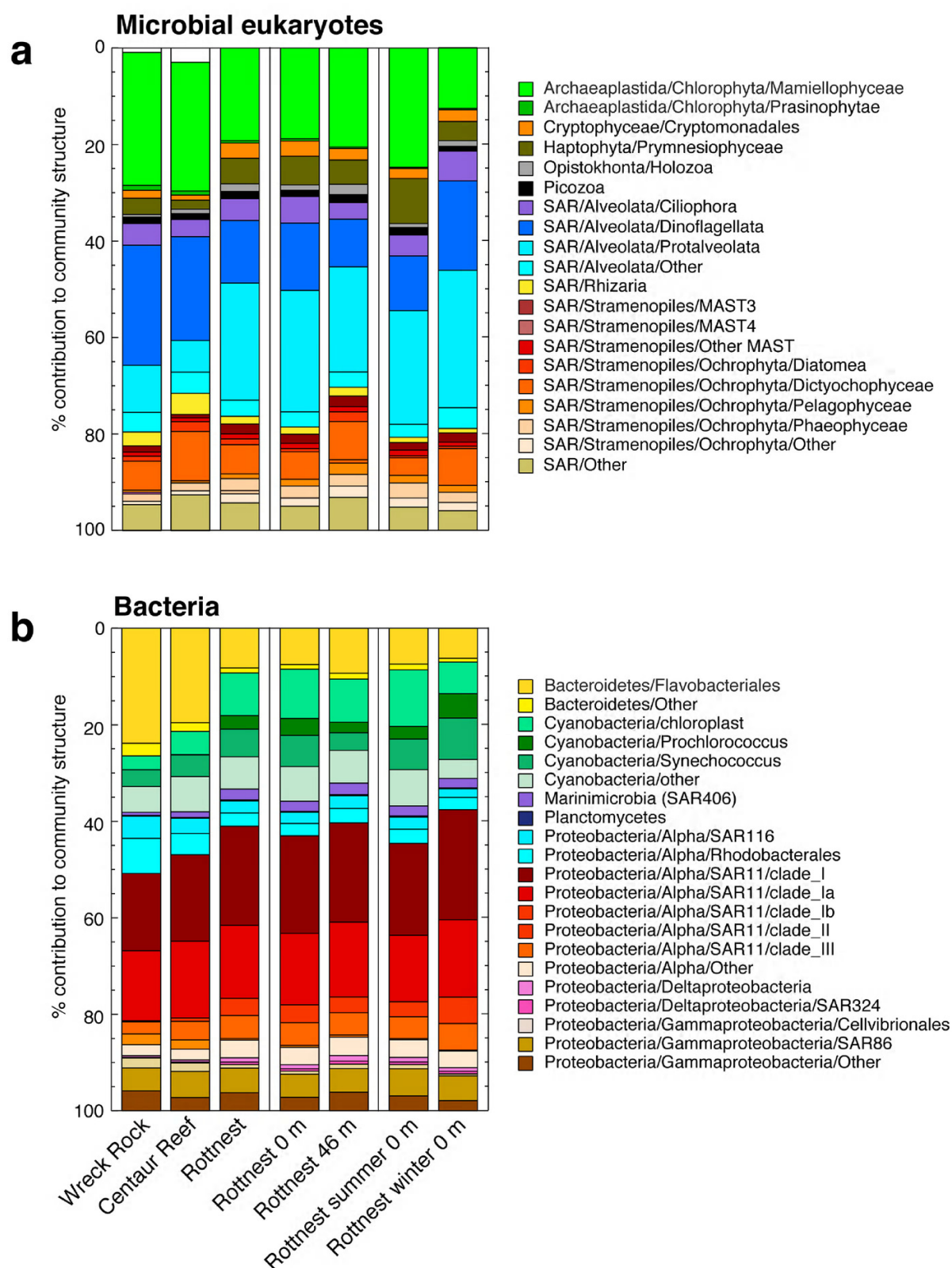


Figure 4. Overview of the microbiome community composition of water samples collected in Western Australia and sequenced as part of the BioPlatform Australia Marine Microbes project. The station at Rottnest Island corresponds to the IMOS National Reference site. Wreck Rock is a shallow (~5 m deep) rocky coastal site and Centaur Reef (~10 m deep) is the site of an 1874 shipwreck, approximately one mile offshore. Data are averaged from monthly samples and over two years. Data from Rottnest Island are averaged by all depths and seasons or separated into averages for surface and for deep (46 m) samples or split into summer (January–April) and winter (July–September) months (surface data only). Sequences of metazoa and macroalgae were removed from panel A.

Current-affected southernmost waters. These microbial communities also differentiated according to warm- or cold-core eddies and shelf waters. In their studies of the oceanic nitrogen cycle, these authors also measured the diversity of the *nifH* gene (nitrogen fixation, Raes *et al.*, 2018), and the *nosZ* gene (N₂O reduction, the final step of denitrification; Raes *et al.*, 2016) in the same transect cited above. Most *nifH* genes were from Gammaproteobacteria and not correlated to the latitude and temperature gradient, while most of the *nosZ* genes belonged to the Roseobacteraceae and were more abundant in the warm areas. Total bacterial abundance was also positively related to temperature.

More recently, the BioPlatforms Australia initiative on Marine Microbes (BPA-MM) sequenced 138 samples from various depths at the IMOS Rottneest Island station, and 134 at two more coastal sites (Wreck Rock and Centaur Reef) each month for one year. (Brown *et al.*, 2018). About 70 000 different organisms were identified out of a total of 2×10^7 sequences. On average, these communities were dominated by the SAR11 Alphaproteobacteria and Bacteroidetes with relatively low numbers of Gammaproteobacteria. Bacteroidetes and Roseobacteriales were more relevant at the coastal stations while more “oceanic” bacteria, such as *Prochlorococcus*, SAR234 and SAR406 were more important at Rottneest (Fig. 4). There were few differences between the surface and the bottom of the station at 46 m, which given the lack of strong stratification in temperature and few differences between summer and winter, could be expected given the influence of temperature on microbial community structure. These data from represent critical baselines that can be utilised to measure and predict changes in microbial community structure under future local and global environmental change (Brown *et al.*, 2018).

Despite our limited knowledge of prokaryotes in Western Australian waters, even less is known of small protists, fungi and viruses. A few reports exist of microzooplankton biomass and grazing activity (e.g., Paterson *et al.*, 2007), but there are no reports we are aware of about small protist diversity or even abundances in Western Australia. The BPA-MM project used 18S rDNA sequencing of eukaryotes collected on 0.2 µm filters at the IMOS reference stations (Brown *et al.*, 2018). Figure 4 shows the main groups at the Rottneest station and at the two coastal sites of Centaur Reef and Wreck Rock after removal of the sequences of metazoa and metaphyta. Chlorophyta (in particular Mamiellophyceae), Dinoflagellates and Protalveolata (mostly heterotrophic species) and Stramenopiles (in particular Diatoms) dominate the communities, with, again, differences between the two coastal sites and the Rottneest Island station and less differences between seasons and along the (well mixed) water column. A few reports of viral abundance also exist, but we are not aware of any viral diversity data or any mycoplankton data for Western Australian waters.

In estuaries and coastal lagoons, bacterioplankton communities are shaped by their proximity to the ocean and their connectivity to terrestrial inputs (e.g., Yeo *et al.*, 2013). By definition estuaries are connected to the ocean, but many coastal lagoons are also connected either by storm-related seawater inputs, or by seawater flowing through underground limestone. A large variety

of these systems exist in Western Australia (Brearley, 2005; Kavazos *et al.*, 2017). However, little is known of the bacteria, protists, fungi and viruses in Western Australian estuaries, although the (large and conspicuous) phytoplankton has been studied for decades (e.g., Jeffrey & Hallegraeff, 1980 and John, 1983). A recent study of bacterial diversity in water bodies of the Lake MacLeod basin indicated a large degree of between-lake microbial community variability with each pond despite similarities in size, environment and position in the landscape (Huggett *et al.*, 2017), which was also reflected in the sediment bacterial and ciliate communities (Kavazos *et al.*, 2018). A variety of previously unknown microbial taxa were identified within Lake Macleod, as well as rare marine taxa (Huggett *et al.*, 2017) consistent with the seawater nurturing these environments (Kavazos *et al.*, 2017). These data add to ideas that identify microorganisms as important players in coastal (carbon, but also species) connectivity and spatial subsidies. Additionally, the microorganisms’ activities affect coastal habitats and probably also influence coastal water bodies (e.g., Sävström *et al.*, 2016) and thus support the incorporation of microbial oceanography into future studies of the Western Australian oceanic environment.

Benthic microbial mats

Sedimentary biofilms, or microbial mats, have been present throughout most of the geological history of Earth (Edgcomb *et al.*, 2014; Ruvidy *et al.*, 2016). Microbial mats have had important impacts on past biogeochemical cycles and continue to persist particularly in hypersaline regions around the world. Microbial mats are composed of layers, where each layer is dominated by different microbial metabolic processes that are determined by different abiotic conditions (Dupraz *et al.*, 2004). Together, the layers represent a complex network of redox reactions characterised by steep chemical gradients, which results in efficient cycling of nutrients (Kunin *et al.*, 2008; Baumgartner *et al.*, 2009; Dupraz *et al.*, 2009; Schneider *et al.*, 2013; Pages *et al.*, 2014). Western Australian coastal environment supports a diverse range of microbial mats, both lithifying and non-lithifying, and represents one of the most well-studied microbiomes in the State (Fig. 2).

Stromatolites, a form of microbial mat, are often referred to as living rocks as they form conspicuous aragonite domes, and are often exposed during low tides or in lakes when there has been sufficient evaporation. The greatest diversity of stromatolites on the planet is found along the Western Australian coast, which makes it an important region for modern stromatolite research. Stromatolites represent modern analogues of the ancient microbial communities, which formed the earliest known biosphere during the Archean, some 3.5 billion years ago (Grotzinger & Knoll, 1999). Stromatolites are typically domal organo-sedimentary deposits with planar to sub-planar laminae formed by a complex benthic bacterial community (Burne & Moore, 1987). Thrombolitic stromatolites, on the other hand, are of similar benthic bacterial origin but lack the internal laminae (Aitken, 1967). Stromatolites are mostly found in Western Australian coastal lake systems and embayments where dissolved calcium levels are sufficient to facilitate aragonite precipitation. It has also been hypothesised

that the extreme abiotic stressors of stromatolite habitats inhibit predation through the exclusion of grazers (Playford & Cockbain, 1976; Macintyre *et al.*, 1996; Steneck *et al.*, 1998), although predation by protozoan flagellates is unlikely to be reduced by high salinities (Al-Qassab *et al.*, 2002).

The intertidal and subtidal areas of the Shark Bay Bioregion (Fig. 1) provide suitable habitats for stromatolites, which occupy over 600 km² (Jahnert & Collins, 2012; Collins & Jahnert, 2014). Because of the extent of these stromatolites, they are perhaps the most well studied in Western Australia. Early work concentrated on the intertidal stromatolites (Logan & Cebulski, 1970; Logan *et al.*, 1974; Playford & Cockbain, 1976), but recent work has also documented the distribution and morphology of subtidal structures (Reid *et al.*, 2003; Jahnert & Collins, 2011, 2012, 2013; Collins & Jahnert, 2014). Within Shark Bay, and particularly Hamelin Pool, there are a diverse range of morphological forms which have largely been described by Jahnert & Collins (2012). They consist of blister, tufted and pustular mats in the supra- and inter-tidal regions and smooth, colloform and pavement structures in the subtidal region. The different structures consist of several microbial communities in which filamentous cyanobacteria dominate blister, tufted and smooth structures, and coccoid cyanobacteria bacteria dominate pustular, colloform and pavement structures (Jahnert & Collins, 2013).

Broadly, stromatolite development consists of three phases in which different filamentous and coccoid cyanobacterial communities alternate as a consequence of different sedimentation conditions (Reid *et al.*, 2000). These three phases have distinct microbial communities that have been referred to as pioneer communities, bacterial biofilm communities, and climax communities (Reid *et al.*, 2000), where changes in sedimentation cause the stromatolite community to shift between phases. Pioneer communities are distinguished by a population of filamentous cyanobacteria that entwine entrapped carbonate sediment grains, embedding the grains to the surface of the stromatolite. Pioneer communities probably account for 70% of the growth stage cycle and persist during sediment accretion. The bacterial biofilm community, which will mature into the climax community, establishes when sedimentation ceases and are the phases responsible for lithification. The bacterial biofilm phase is characterised by the formation of a 20–60 µm thick calcified biofilm on the upper surface and cementation of silty carbonate material that have been embedded in the pioneer community. The climax community represents a mature bacterial biofilm community consisting mainly of coccoid cyanobacteria. Many of these taxa are endolithic and will bore into the embedded carbonate sand grains and fuse adjacent grains. This phase represents a period of high metabolic activity which enhances aragonite precipitation and formation of the distinctive stromatolite structures. The fusing of sediment grains and aragonite formation further develops the carbonate crust which persists into the subsurface and facilitates further development of the stromatolite. This process, however, is unlikely to be universal. In Hamelin Pool, for example, subtidal and intertidal stromatolites have slightly different

morphogenesis characteristics (Reid *et al.*, 2003). Nonetheless, the process of sediment entrapment by filamentous cyanobacteria and coccoid cyanobacterial biofilm lithification appears common to stromatolite development (Grey *et al.*, 1990; Moore & Burne, 1994; Jahnert & Collins, 2012).

Many coastal lakes in Western Australia provide other habitats for stromatolites, although they have received much less attention than those of Hamelin Pool. The northernmost of these habitats are the Northern Ponds of Lake MacLeod (Shark Bay Bioregion; Fig. 1) where some of the ponds contain colloform stromatolites (Logan, 1987; Shepherd, 1990). The MacLeod basin also contains vast areas of blister, tufted and pustular mats like those found in the supratidal and intertidal regions of Shark Bay (Logan, 1987; Shepherd, 1990; Kavazos & Horwitz, 2016). Lake Thetis, near Cervantes (Central West Coast Bioregion; Fig. 1), contains stromatolites that closely resemble the dome structures found in the Precambrian fossil record (Grey *et al.*, 1990; Grey & Planavsky, 2009). In Lake Clifton, 120 km south of Perth (Leeuwin–Naturaliste Bioregion; Fig. 1), large thrombolitic stromatolites inhabit the shallow waters (Moore, 1993; Moore & Burne, 1994). Similar to stromatolites, the thrombolites are composed of coccoid and filamentous cyanobacteria taxa (Warden *et al.*, 2016) which build large lithified domal structures (John *et al.*, 2009) by facilitating development of calcium carbonate minerals; aragonite and stevensite (Burne *et al.*, 2014). The Clifton thrombolites also share a complex microbial–metazoan relationship, which includes amphipods and isopods grazing on the microbialite structure (Konishi *et al.*, 2001).

Stromatolites are found in other lakes along the Western Australian coast, including Government House Lake, Rottnest Island (Playford, 1983; John *et al.*, 2009), Pink Lake near Esperance (Burne & Moore 1987), and near Rockingham in Lake Richmond (Kenneally *et al.*, 1987; Chilton *et al.*, 2012) and Lake Walyungup (Coshell *et al.*, 1998). These lakes are susceptible to anthropogenic impacts largely because of the degradation within their catchment regions from urban development and agricultural use. Salinity and phosphate concentrations in Lake Clifton, for example, have increased above previously recorded levels (Knott *et al.*, 2003). These chemical shifts in water quality are thought to be responsible for reduction in the filamentous cyanobacteria essential to the growth of the thrombolite structure (Smith *et al.*, 2010).

Recent phylogenetic analyses of Shark Bay stromatolites have identified a diverse community of cyanobacteria, archaea and sulphate-reducing bacteria (Goh *et al.*, 2009). Specifically, Alpha- and Gammaproteobacteria are highly abundant in Shark Bay stromatolites and cyanobacterial communities where they are represented by species of *Euhalothea*, *Gloeocapsa*, *Gloeotheca*, *Chroococcidiopsis*, *Dermacarpella*, *Acaryochloris*, *Geitlerinema* and *Schizothrix* (Goh *et al.*, 2009). Typically, the surface mats are dominated by cyanobacteria (Garby *et al.*, 2013), although members of Alphaproteobacteria and Bacteroidetes have also been detected on the surface of smooth and pustular mats (Wong *et al.*, 2015). Recently, a new photosynthetic pigment, chlorophyll-f, was discovered in the cyanobacteria *Halomicronema hongdechloris* (Li *et al.*, 2014). Archaea,

represented by members of Methanomicrobiales, Methanosarcinales, Methanococcales, Methanobacteriales, Methanomassiliicoccaceae, Halobacteria (Goh *et al.*, 2006; Allen *et al.*, 2008) and Parvarchaeota (Wong *et al.*, 2017), are abundant in Shark Bay stromatolites (Burns *et al.*, 2004) and likely have critical roles in the metabolic pathways within the microbialite communities (Ruvindy *et al.*, 2016). Despite the importance of microbial environments along Western Australia's coastline, their ecologies are poorly researched. This is a serious omission considering the important roles these communities play in the biogeochemical cycling of many essential elements. There is a critical need to understand the functioning and taxonomic diversity driving the complex redox reactions within microbial communities as such studies will continue to reveal novel ecological processes, metabolic pathways and biologically important molecules.

MICROBIOMES AND ENVIRONMENTAL CHANGE

Oceans are critical for many ecological and economic activities: they are valuable in climate regulation, tourism, carbon sequestration, buffering of atmospheric gases, recreation and culture, aquaculture, biodiversity, conservation, biogeochemical cycling and provision of pharmaceuticals. In Australia, the combined value of the benefits that oceans will provide by 2025 is estimated to be in excess of \$100 billion per annum (Ocean Policy Science Advisory Group, 2013). Despite their tremendous importance, marine ecosystems are currently facing unprecedented environmental change due to warming and acidification within coastal zones as well as eutrophication, sedimentation, overfishing, and increasing frequency and intensity of cyclones, storm events and heat waves. The critical nature of these issues has led many marine scientists to focus research on understanding, predicting, modelling and mitigating the outcomes of global and local stressors to oceans. Studies from Western Australia have led the world in some of these areas with seminal work on oceanographic modelling (Feng *et al.*, 2003, 2013; Lowe & Falter, 2015), impacts of ocean acidification (Cornwall *et al.*, 2017), tropicalization of temperate systems (Wernberg *et al.*, 2011a, 2016a) and thermal tolerance and recovery of coral reefs (Gilmour *et al.*, 2013; Schoepf *et al.*, 2015).

On a regional scale, Western Australian coastal zones are subject to many of the concerns that face the global ocean, with notable environmental changes in the State such as increasingly frequent heat waves (Feng *et al.*, 2013), warming and acidification (IPCC) and sediment resuspension from dredge activities (Jones *et al.*, 2015). In situ temperature measurements at a coastal monitoring station on the State's continental shelf have shown a mean temperature rise of $0.013^{\circ}\text{C year}^{-1}$ since 1951, corresponding to $\sim 0.6^{\circ}\text{C}$ over the past five decades. Measurements from three other shallow stations between 1985 and 2004 indicated even higher warming trends of $0.026 - 0.034^{\circ}\text{C year}^{-1}$ (Pearce & Feng, 2007). Recorded impacts of environmental changes to coastal services in Western Australia include widespread mortality of fish and invertebrates (Pearce *et al.*, 2011) resulting in declining fisheries production (Caputi *et al.*, 2014), range shifts of ecosystem engineer species such as corals and

macroalgae (Wernberg *et al.*, 2011b, 2013), tropicalization of temperate regions (Vergés *et al.*, 2014) and substantial loss of seagrass and coral habitat (Fraser *et al.*, 2014; Fig. 5). Examining marine microbes can reveal key impacts of environmental change. For an example, recent evidence suggests that tropicalization of the ocean reduces bacterial diversity (Raes *et al.*, 2018) and many of the key functional roles of microbial communities are altered under stressors such as temperature and acidification (Webster *et al.*, 2016; Huggett *et al.*, 2018; Westwood *et al.*, 2018).

An important component for understanding the response of marine systems to environmental change are field-based studies, a powerful tool that enables scientists to observe likely impacts of environmental change under natural conditions. Such studies measure specific responses by marine communities where variation in multiple factors (warming, heat waves, trophic interactions, range-shifts and so on) are at play in situ. In particular, the western coastline of Australia offers a unique opportunity to directly examine in situ impacts of temperature on marine ecosystems, due to the steady temperature gradients and the lack of other stressors such as high anthropogenic influence and nutrient inputs via upwelling (Smale *et al.*, 2010). The extreme temperatures in the Kimberley region may also provide an important natural system in which to study genetic adaptation to heat stress (Camp *et al.*, 2018). Aquaria-based experiments are a complementary and valuable approach to field studies (Wernberg *et al.*, 2012; Cornwall & Hurd, 2015) as the measurement of how specific organisms respond to discrete changes under controlled conditions can provide essential data on the impacts of environmental change. Given that microbes have rapid generation times they are often the first responders to environmental alterations and are thus critical for incorporation into management, early warning and modelling of the response of marine ecosystems to environmental change.

Whereas microbiomes have mostly been overlooked, field and aquaria-based studies of marine microbial responses to environmental change in Western Australia are beginning to emerge. For instance, Luter *et al.*, (2015) examined the biogeography of the abundant Indo-Pacific sponge *Carteriospongia foliascens* and concluded that light plays a significant role in shaping the microbiome of this species. Also, the rabbitfish *Siganus fuscescens* has been identified as an important range-shifting herbivore that is now common on southern reefs in both the east and west of the continent. A biogeographic analysis of the gut microbiome of wild populations of *S. fuscescens* across over 2000 km of Western Australia's coastline indicates that, despite substantial difference in diet and habitat between populations, there is a persistent and abundant microbial community in all populations. In addition, short chain fatty acid production by their microbial community is comparable in some tropical and temperate populations, suggesting that this fish is well suited to its new environment (Jones *et al.*, 2018). Aquaria-based studies testing the direct response of microbial communities are also emerging; some of these are based directly on key Western Australian benthic microbiomes (Huggett *et al.*, 2018) whereas others are focused on organisms that reside in Western Australia but examine responses by populations from the east coast (Pineda

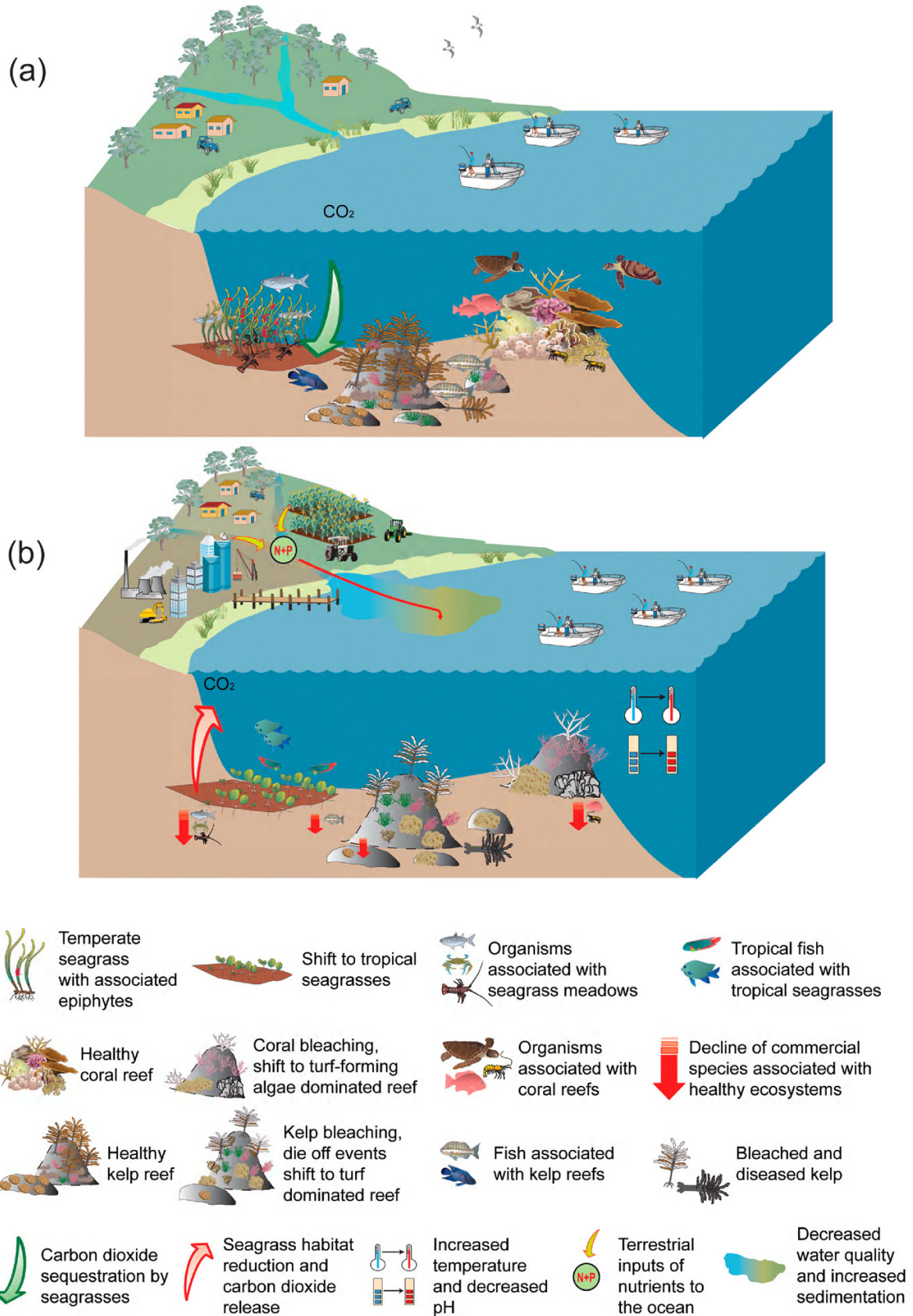


Figure 5. Summary of predicted environmental changes to key habitats from Western Australia. a) illustrates the state of various reef environments under stable/healthy environmental conditions whereas b) indicates possible effects in response to significant environmental change. Symbols are from the Integration and Application Network (ian.umces.edu/symbols/)

et al., 2017). These studies indicate that temperature, acidification and sediment resuspension will all have substantial impacts to microbiomes in the State's benthic marine ecosystems and enable us to understand the processes that underpin the persistence of some species and the decline of others under environmental change.

Encouragingly, the largest marine science research organisation in the State, the Western Australian Marine Science Institution (WAMSI) recently identified "enhanced understanding of the marine microbial systems that underpin all marine biological activity in the Western Australian marine environments" as a high priority for future research to be addressed by year 2020. In addition, the BPA-MM project (<https://data.bioplatforms.com/organization/bpa-marine-microbes>) is the focus of a long-term monitoring program examining microbial communities in situ at both benthic and pelagic sites across Australia, (Fig. 4). The BPA-MM program is of a world-class standard and will provide critical data facilitating our ability to predict potential climate impacts (Webster & Bourne, 2012). Microbes respond quickly to alterations of the environment and we can now determine the structure of microbial communities relatively simply and easily. Therefore, the development of microbial indicator species and indicative microbial community shifts as early warnings of environmental stress and ecosystem health, both in water (Ferrera *et al.*, 2016) and microbiomes of other organisms (Glasl *et al.*, 2017), is a viable and achievable goal. Incorporation of microbial ecology within marine research and management is now urgent for the State.

CONCLUSIONS

We anticipate that the coming years will uncover additional fundamental knowledge of microbes from the west coast of Australia. This review highlights that this coastline is vast, encompassing a wide range of marine habitats, with unique features due to the attendant currents in the region. There are many reasons why marine microbial studies are lacking: the isolation of the coastline, the large distances that it encompasses, the difficulties in reaching remote coastal areas, the persistent swell that batters a considerable portion of the southern region and the substantial tides in the north. Whereas there remain challenges to studying these coastal environments, we conclude by highlighting that the region has been home to some influential studies not mentioned above. For example, Usher *et al.* (2001) were the first to demonstrate that the microbial symbionts of sponges could be passed directly from parent to offspring via vertical transmission. These authors have since discovered the first photosynthetic cyanobacterial symbionts from mesophotic temperate sponges (Keesing *et al.*, 2012) and have provided one of the few reports of the microbial assemblages of any calcarean sponge (Fromont *et al.*, 2016). Furthermore, a recent environmental DNA (eDNA) study in Coral Bay, intended to identify all organisms across the Tree of Life, including bacteria and eukaryotes, uses metagenomics and metabarcoding (Stat *et al.*, 2017). The metagenomics approach recovered mostly bacteria, while the metabarcoding approach uncovered 2000 sequences and 195 different bacterial OTUs. For eukaryotes, the metabarcoding approach was much more informative,

revealing comparatively more biodiversity than metagenomics. This study is *avant-la-lettre* and shows the promise of these techniques and their usefulness as applied to different portions of the Tree of Life.

It is an exciting time for microbiologists across the globe, no matter what their subject area is. All fields of environmental research have experienced exponential growth in the understanding of the abundance, diversity and importance of microbes via the new generations of 'omics technologies. Now we are poised on the edge of new era that moves from the discovery of organisms and their genes to the incorporation of 'omics' within fieldwork, experimental manipulations, modelling and bench work. This era will forge new, multidisciplinary datasets that will undoubtedly uncover even more of the remarkable capabilities of the microbes of our planet. Western Australia is one of the most isolated and pristine coastlines on the earth, provides a steady gradient of temperature and, uniquely, co-hosts both tropical and temperate organisms for much of the coastline. Whereas much of the basic work remains to be done, we argue that this region also presents an unparalleled opportunity for the next era of marine microbial research, and as such should be the focus of further research efforts.

ACKNOWLEDGEMENTS

We thank J. Raes for access to his unpublished manuscript, and A. Bissett for bioinformatics analysis of data for Figure 4. These data were accessed from <https://data.bioplatforms.com/organization/pages/australian-microbiome/tools>, which is a contribution of the Marine Microbes (MM) and Biomes of Australian Soil Environments (BASE) projects, through the Australian Microbiome Initiative. The Australian Microbiome Initiative is supported by funding from Bioplatforms Australia through the Australian Government National Collaborative Research Infrastructure Strategy (NCRIS). We thank L. Bodrossy, T. Thomas, A. Fitzgerald and A. Bissett for access to the seawater microbiome data. David Haig is thanked for the supporting F. Evans to attend the Royal Society of Western Australia Symposia "Landscapes, Seascapes and Biota: Unique Western Australia – Past, Present and Future" associated with this publication.

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APPENDIX 1

Meta-analysis references for Figure 2.

Articles were searched using the University of Western Australia's OneSearch (accessed January 2018), which searches across multiple databases including ISI Web of Science, Scopus, ScienceDirect, and PubMed. Articles were searched using the terms: microbiome/microorganisms/microbes + ("host") + Western Australia and manually checked for relevance. Additional articles were also added when uncovered during the preparation of this review.

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