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Adaptation and Evolution of Seaweeds under Environmental Change

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Chapter 3
The Dynamic Biogeography of the Anthropocene: The Speed of Recent Range Shifts in Seaweeds

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Abstract The biogeographic boundaries of seaweeds are largely determined by temperature tolerances, physical barriers and limitations to dispersal. Anthropogenic ocean warming and increasing connectivity through human activities are now causing rapid changes in the biogeography of seaweeds. Globally, at least 346 non-native seaweed taxa have been introduced to new regions, and at least 31 species of seaweed have shifted their distributions in response to recent temperature changes. Range-shift speeds were determined for 40 taxa, and compared between three drivers: (I) range expansions caused by introductions, (II) range expansions and (III) contractions caused by climate change (warming/cooling). The speed of change in seaweed biogeography differed between these drivers of change, with expansions significantly faster than contractions, and climate-driven shifts significantly slower than introductions. Some of the best documented introduced species expansions include *Sargassum muticum* (4.4 km/year in Denmark), *Undaria pinnatifida* (35–50 km/year in Argentina) and *Caulerpa cylindracea* (11.9 km/year in the Mediterranean Sea). Examples of seaweeds with recent climate-driven range shifts include *Scytothalia dorycarpa*, a native species in Western Australia, which retracted >100 km poleward as a consequence of a single event (a regional marine heat wave). However, climate-driven range shifts were generally assessed over long time periods (>10 years). *Fucus serratus* (1.7 km/year) and *Himanthalia elongata* (4.4 km/year) have slowly retracted westwards in northern Spain in response to

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warming in the Bay of Biscay. In England and South Africa, *Laminaria ochroleuca* (5.4 km/year) and *Ecklonia maxima* (36.5 km/year) have expanded their ranges in response to local warming and cooling, respectively. These changes in seaweed biogeography likely have had substantial implications for biodiversity and ecosystem processes, particularly where the shifting seaweeds have been canopy-forming foundation species. We discuss some of these consequences and different attributes of climate and invasion-driven range shifts in seaweeds.

3.1 Introduction

Species distributions are dynamic, continuously shifting in responses to changes in biological and environmental drivers. In the earlier history of the Earth, large-scale geological events and long-term climate fluctuations, such as continental drift or warming and cooling associated with planetary cycles, were the predominant drivers of changes to species' distributions (Wiens and Donoghue 2005). However, over the past millennium humans have increasingly modified the biological and physical properties of the planet (Worm et al. 2006), and we have now entered the Anthropocene, an era where the human influence on the global Earth system rivals or exceeds natural processes (Karl and Trenberth 2003), speeding up important drivers of species distributions influencing the biogeography of organisms across ecosystems. As a consequence, recent changes in the distribution of many marine taxa have been documented on all continents (Perry et al. 2005; Williams and Smith 2007; Sorte et al. 2010; Wernberg et al. 2011a; Poloczanska et al. 2013).

Seaweeds are dominant organisms on many intertidal and shallow subtidal reefs, where their species-specific distributions often shape local reef communities (Wernberg et al. 2003; Buschbaum et al. 2006; Ingólfsson 2008; Tuya et al. 2009). Although the local effects of biotic interactions can generate continental-scale patterns of species associations (Wootton 2001; Irving and Connell 2006), global biodiversity patterns are not explained by biotic interactions alone but are a consequence of both the biotic and abiotic environments (Lüning 1985; Harley et al. 2006; Tittensor et al. 2010). Two mechanisms have been particularly prevalent in driving recent changes in seaweed distributions: species introductions through the direct relocation of species (transported, deliberate or not, by various vectors) and responses to global climate change (Williams and Smith 2007; Wernberg et al. 2011a; Sorte et al. 2013).

Changes in seaweed distributions include both range extensions, where species colonize new, usually adjacent habitats, and range contractions, where species lose previously occupied areas, going locally extinct at the margins of their distribution range (Fig. 3.1) (Wernberg et al. 2011a; Bartsch et al. 2012; Bates et al. 2014).
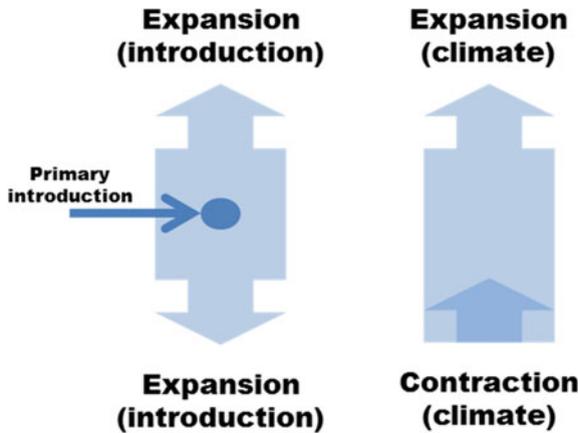
Fig. 3.1 Reconfiguration of seaweed range boundaries takes place as one of three general processes. Either species expand their boundaries in a new area following initial primary introduction to a site where climate conditions are not immediately limiting. Alternatively, native species can expand into previously unoccupied areas, tracking their climate envelope as changing conditions make these suitable. Similarly, species can retract from occupied areas as changing climate makes these unsuitable. The processes, and underlying physical and biological mechanisms, differ between these processes, with expansions driven by dispersal and recruitment dynamics and contractions by performance and mortality (Bates et al. 2014)

For species introductions and climate impacts, range shifts are underpinned by different mechanisms involving dispersal and recruitment (introductions, climate expansion) and attrition and mortality (climate contraction) (Bates et al. 2014). Moreover, whereas range expansion only requires the successful establishment of one or a few individuals in a new location, local extinction and range contraction requires the demise of all individuals and is often preceded by periods of declining abundance and failed recruitment while adult individuals persist in the unfavourable area (Hampe and Petit 2005; Bates et al. 2014). Conversely, environmental conditions are generally not limiting the expansion of introduced species following primary introduction, whereas climate-driven responses track shifts in the climate envelope (Fig. 3.1) (Pinsky et al. 2013; Sunday et al. 2015). Consequently, even if priority effects and other biological (competition, predation) processes can work against the expansion process (Waters et al. 2013), seaweed range shifts are expected to be faster for expansions than contractions and faster for introductions than climate responses (Sorte et al. 2010). The effects on the respective habitats and communities should, however, be of the same magnitude and direction (Sorte et al. 2010).

Here, we first provide a brief overview of natural and anthropogenic factors that shape the biogeography of seaweeds. We then provide a quantitative synthesis of how fast humans are affecting seaweed distributions through an analysis of the speed of reported human-mediated changes in seaweed range boundaries. We also review selected case studies of seaweed range shifts for both native species that have changed their ranges in response to changing environmental conditions, and

introduced species, spreading in their new environment. Finally, we discuss the challenges of identifying range shifts and the necessity for monitoring distributions to detect seaweed range shifts.

3.2 Drivers of Seaweed Biogeography

Seaweed biogeographers traditionally group the world's oceans into seven broad regions: the Arctic and Antarctic Polar regions, the cold- and warm-temperate regions of both hemispheres, and the tropical regions of the Atlantic and Indo-Pacific (Lüning 1985; Bartsch et al. 2012). The boundaries between these biogeographic regions are associated with large changes in species composition, maintained by species temperature tolerances (Van den Hoek 1982), natural barriers (Cowman and Bellwood 2013) and species dispersal limits (Wiens 2011). Humans are now assisting seaweeds and other organisms to overcome these geographic boundaries, which previously limited distributions.

3.2.1 Temperature

Seaweeds are confined to the photic zone, where temperature patterns are reasonably well understood, allowing species distributions to be compared to oceanographic patterns (Adey and Steneck 2001). Distribution limits of individual seaweed species typically follow major marine isotherms (Van den Hoek 1982; Lüning 1985), giving rise to strong relationships with the temperature signatures of major ocean currents (Wernberg et al. 2013b).

For seaweeds, these patterns are a product of two key types of temperature boundaries: lethal boundaries, determined by a species' capacity to survive during their unfavourable season; and growth and reproduction boundaries, determined by a species' ability to grow and reproduce during its favourable season (Van den Hoek 1982; Lüning 1985). Seaweeds can be abundant in areas within both boundaries that are within dispersal ranges of the species. However, as thermal windows have changed over geological time (e.g. following ice age cycles), they have biogeographic boundaries and seaweed distributions (Adey and Steneck 2001).

3.2.2 Barriers

If the oceans were a continuous open system, then most species should exhibit cosmopolitan distributions within their respective thermal windows (Myers 1997; Gaylord and Gaines 2000). However, barriers limit dispersal, which leads to discontinuities in species distribution (Myers 1997). These barriers can be 'hard' or

'soft', depending on their underlying mechanism (Luiz et al. 2012; Cowman and Bellwood 2013).

Hard barriers are physical obstacles such as land masses separating marine systems. For example, the final closure of the Tethys seaway around 12 Mya at the northern tip of the Red Sea created a physical barrier which cut off the low-latitude connection between the Indian and Atlantic Oceans (Cowman and Bellwood 2013).

In contrast, soft barriers refer to hydrographical features that disrupt connectivity. Large stretches without suitable substratum, such as deep oceanic basins (Lessios et al. 1998) or extensive beaches (Hidas et al. 2007), can limit the distribution of species with limited dispersal capacity. The greatest example could be the Eastern Pacific Barrier, a 5400-km stretch of deep open ocean between the central and eastern Pacific, likely in existence since the Cenozoic (Grigg and Hey 1992), where only a few marine species are represented on both sides (Lessios et al. 1998). Nearshore gradients in ocean properties, such as the direction and strength of ocean currents, differences in salinity and/or temperature as a result of currents or local upwelling (Luiz et al. 2012; Cowman and Bellwood 2013), can also function as barriers to dispersal. Therefore, many seaweeds show distribution limits concentrated at particular shorelines, often in locations where major currents collide (Gaylord and Gaines 2000; Schils and Wilson 2006; Waters 2008).

Barriers are, however, not permanent especially over geological time scales. Changes in ice cover and sea levels (glaciation, deglaciation, retreating ice caps, historical sea-level alterations) have led to significant alterations in seaweed biogeography. The Baltic Sea, for example, was entirely covered by glaciers during the last ice age, and all present-day seaweeds in the Baltic Sea have colonized following the opening of the Danish Straits about 8000 years ago (Björck 1995). Similarly, recent glacial retreat in the South Shetland Islands has enabled seaweed expansion into newly available habitat in Antarctica (Quartino et al. 2013). Over several glacial cycles, reduced sea levels exposed the Bassian land bridge, a historical barrier between Tasmania and mainland Australia, interrupting connectivity and colonization for several taxa for prolonged periods of time (Burridge et al. 2004; Waters 2008; York et al. 2008). Also, islands emerging due to volcanic activity (e.g. new island formation in Japans Ogasawara Island chain in 2013) create new space for seaweed colonization and can function as stepping stones for long-range dispersers to overcome deep oceanic stretches to reach distant areas (Nogales et al. 2012). Also, dispersal across large sandy stretches can be facilitated by small rocky platforms functioning as intermediate habitats to facilitate dispersal over the barrier (Dethier et al. 2003; Hidas et al. 2007; Mattio et al. 2015).

3.2.3 Dispersal

Dispersal is a critical process which allows seaweeds to extend their geographical distribution. Seaweeds employ a broad range of dispersal strategies with some species adapted to short-distance dispersal, typically settling close to their parental

populations, and others adapted to long-distance dispersal, typically favouring rapid colonization of new habitats (Santelices 1990).

Most seaweeds disperse by small, largely immotile propagules (zoospores or zygotes) that are transported by waves and currents (Norton 1992; Gaylord et al. 2002). The buoyancy of the propagules, storage components, metabolic rates, and the strength and direction of current flow determine how far these microscopic propagules can disperse (Gaylord et al. 2002), before they have to settle onto hard substrata in the photic zone. In addition to microscopic propagules, seaweeds can also disperse as floating fronds, where a parental thallus is dislodged (breakage of stipes, thallus fragmentation, storms, etc.) and transported by winds and currents (Rothäusler et al. 2012). Many positively buoyant seaweeds can survive, float and disperse for prolonged periods of time (Van den Hoek 1987; Norton 1992; Hobday 2000a; Rothäusler et al. 2012). This dispersal mechanism is particularly efficient for dioecious species that do not rely on concurrent dispersal of male and female thalli (e.g. *Sargassum muticum*) as these species can establish entire new populations from single floating reproductive fronds. Large drifting seaweeds can also function as a raft for smaller negatively buoyant animals and seaweeds (Van den Hoek 1987; Hobday 2000b; Hinojosa et al. 2010; Fraser et al. 2011; Gillespie et al. 2012; Rothäusler et al. 2012; Fraser and Waters 2013). Floating seaweeds can therefore facilitate the colonization of new habitats on remote shores, sometimes by crossing large ocean basins (Fraser et al. 2011; Rothäusler et al. 2012). Dispersal thus depends on both intrinsic seaweed traits such as buoyancy and propagule characteristics, as well as on external factors such as current speed and direction, and environmental conditions that enable survival, settlement and growth (Norton 1992; Hinojosa et al. 2010).

3.2.4 Species Introductions (Human-Assisted Dispersal)

A characteristic feature of the past millennium has been an explosion in travel for trade and colonization, over increasing distances and at decreasing travel times. Through the process of human-assisted dispersal, non-native seaweeds have spread (intentional or not) to habitats far away from their origins (also see Chapter by Neiva et al. (2016) in this volume).

Introduced seaweeds are species that have been relocated beyond their native range by human activities and have become successfully established at a new location. The introduction of seaweeds is a stepwise process, starting with transport and initial arrival through a vector (primary introduction, Fig. 3.1), which is followed by initial survival, establishment and finally successful reproduction and spread (expansion, introduction, Fig. 3.1) to nearby locales (Sakai et al. 2001; Bates et al. 2014). The main vectors responsible for seaweed introductions include hull fouling and aquaculture, but ballast water, breakdown of natural barriers (the Suez canal in particular) and the aquarium trade have also transported seaweed around the world (Williams and Smith 2007) (see Chap. by Neiva et al. (2016) in this

volume). Of all introductions, only a small subset establishes permanent populations in their new habitats. It has recently been estimated that at least 346 seaweed taxa have been introduced to, and successfully established populations in, new regions worldwide (many of these taxa having invaded multiple biogeographical regions), breaking down barriers evolved over millennia (see Chap. by Neiva et al. (2016) in this volume). Many of these taxa have also become invasive with significant effects on native species, biodiversity and ecosystem dynamics (Williams and Smith 2007; Thomsen et al. 2009, 2014) (see Chap. by Neiva et al. (2016) in this volume).

For successfully introduced seaweeds, it is implicitly assumed that climate is not the primary limiting constraint on their distribution (or they would not have successfully become established) and that secondary expansion can proceed largely as fast as dispersal allows. Expansion of introduced seaweeds should therefore be rapid relative to climate-induced range changes.

3.2.5 Environmental Change (Human-Induced Climate Change)

Climate and temperature, in particular, play pivotal roles in controlling the global biogeography of seaweeds (Sect. 3.2.1) (Lüning 1985). Consequently, changes in temperature, as for example those associated with anthropogenic greenhouse gas emissions, also alter the distribution of seaweeds (Zachos et al. 2008; Wernberg et al. 2011b; Harley et al. 2012).

On average, anthropogenic emissions of greenhouse gases have caused a decrease in ocean surface seawater pH of ~ 0.1 since the beginning of the industrial era (IPCC 2014) and ocean warming by ca. 1 °C over the past 4–5 decades, although with substantial local variation (Burrows et al. 2011). While a few regions have cooled due to increased upwelling (e.g., causing kelps to expand their ranges Bolton et al. 2012), most regions have warmed (Lima and Wethey 2012; Hobday and Pecl 2013). Importantly, climate change not only causes gradual and slow increases in temperatures and pH, but also in the frequency and intensity of extreme events (Coumou and Rahmstorf 2012; IPCC 2012). Seaweeds respond to these environmental changes through physiological and morphological acclimations (reversible, phenotypic changes on short timescales), adaptation (irreversible, genotypic changes on medium to long times scales), or migration (changes in distribution on medium timescales) (Bartsch et al. 2012).

Overall, climate change has altered local marine environments leading to changes in distribution and diversity of seaweed communities from local to global scales (Wernberg et al. 2011a; Tanaka et al. 2012; Duarte et al. 2013). As seaweed expansions and contractions follow the external driver of changes in the physical environment, changes in species distributions are expected to be slow relative to introductions (Sorte et al. 2010). Moreover, climate-induced contractions will, in

contrast to expansions, typically manifest as repeated recruitment failures and subsequent demise of long-lived populations (Hampe and Petit 2005; Bates et al. 2014). Contractions are therefore expected to be slower than expansions. One obvious exception is the rapid response to extreme events, which can alter local ecosystem structure and functioning abruptly (Wernberg et al. 2013b) and lead to rapid changes in seaweed distributions (Smale and Wernberg 2013).

3.3 Speed of Range Shifts in Seaweeds

In order to determine the rate at which humans have been modifying biogeographic boundaries of seaweeds, we undertook a meta-analysis of the rate of change in distribution limits for recently recorded range shifts for native and introduced seaweeds (range-shift speed). Data bases were searched using key words like 'climate change', 'warming', 'extreme events', 'temperature anomaly' 'heatwaves', 'introduced seaweeds', 'successful invaders', 'shift in distribution', 'shift rates', 'spread rates', 'range shift', 'range expansion' and 'range contraction'. We also backtracked references from relevant reviews and meta-analytical papers (Sorte et al. 2010; Poloczanska et al. 2013; Bates et al. 2014). We included studies that showed data for the directions, distances and time windows of seaweed range shifts, allowing us to calculate annual spread rates. Literature reporting changes in abundance without changes in location were excluded from the dataset, as were studies that did not report a range shift per se. Where rates were not reported directly, but identifiable locations given, rates were calculated (using the Google Earth distance calculator). For introduced species, we did not consider the initial primary introduction distance, only expansion from site of primary introduction into its new environment. Where time was reported as an interval, the midpoint was used. These strict data inclusion criteria limited the number of range-shifting seaweeds included in our analysis, which therefore represents a constrained view of seaweed range shifts.

Range-shift speeds were compared between three drivers of change (cf. Sect. 3.2.5, Fig. 3.1). (I) range expansions following introductions, (II) expansions caused by climate change (typically warm-water species) and (III) range contractions caused by climate change (typically cool-water species). More specifically, we tested (a) whether expansions generally are faster than contractions, and (b) whether introductions are faster than climate-driven changes. Tests were made with permutation-based analysis of variance (Logx + 1 transformed range-shift speeds, 9999 permutations of residuals), followed by two a priori defined planned contrasts (expansion vs. contraction and introduction vs. climate). These analyses did not include range shifts caused by primary introductions or in response to discrete extreme events. These range shifts were excluded due to their artificial and stochastic nature, respectively.

Table 3.1 Summary statistics for human-induced seaweed range shifts

	Expansion (introduction, $n = 13$ taxa)	Expansion (climate, $n = 22$ taxa)	Contraction (climate, $n = 9$ taxa)
Median shift (range)	280 km (40–1450)	192 km (26–593)	116 km (35–1250)
Median time (range)	7 years (1–47)	50 years (2–75)	31 years (1–66)
Taxa ($n = 41$)	*Caulerpa cylindracea* *Caulerpa ollivieri* *Caulerpa taxifolia var. distichophylla* *Codium fragile* ssp. *fragile* *Codium fragile* ssp. *Tomentosoides* *Fucus serratus* *Grateloupia doryphora* *Grateloupia turuturu* *Heterosiphonia japonica* *Mastocarpus* sp. *Sargassum filicinum* *Sargassum muticum* *Undaria pinnatifida*	*Ahnfeltia plicata* *Bifurcaria bifurcata* *Chondrus crispus* *Codium adhaerens* *Desmarestia aculeata* *Desmarestia ligulata* *Dumontia contorta* *Ecklonia maxima* *Fucus serratus* *Fucus vesiculosus* *Halidrys siliquosa* *Halopithys incurva* *Himanthalia elongata* *Hypnea musciformis* *Laminaria ochroleuca* *Padina pavonica* *Palmaria palmata* *Pelvetia canaliculata* *Sargassum flavifolium* *Sargassum illicifolium* *Turbinaria ornata* *Valonia utricularis*	Assemblage *Durvillea potatorum* *Ecklonia radiata* *Fucus serratus* *Fucus vesiculosus* *Himanthalia elongata* *Sargassum micracanthum* *Sargassum yamamotoi* *Scytothalia dorycarpa*

Details are reported in Appendix

Our literature search returned 71 individual estimates of seaweed range-shift speed (Appendix). In general, of the studies where range-shift speeds could be assessed, expansions following seaweed introductions were detected over larger distances and shorter time periods than expansions and contractions due to climate change (Table 3.1). Studies returning range-shift speeds were reported from all continents except Antarctica (Fig. 3.2), although we found strong geographical biases in what types of range shifts had been recorded. For example, no studies with sufficient information to calculate range-shift speed were reported for climate-driven range expansions or contractions in North and South America, nor expansions and introductions in Australia. Europe had the greatest concentration of range shifts reported with sufficient information for all three categories (Fig. 3.2).

The five areas where climate-induced range-shift speeds are available (SE and SW Australia, Japan, South Africa and SW Europe) are well-known 'temperature hotspots' where the rate of ocean warming since 1950 has been in the top 10 % of observations globally (Hobday and Pecl 2013). Interestingly, the range shift
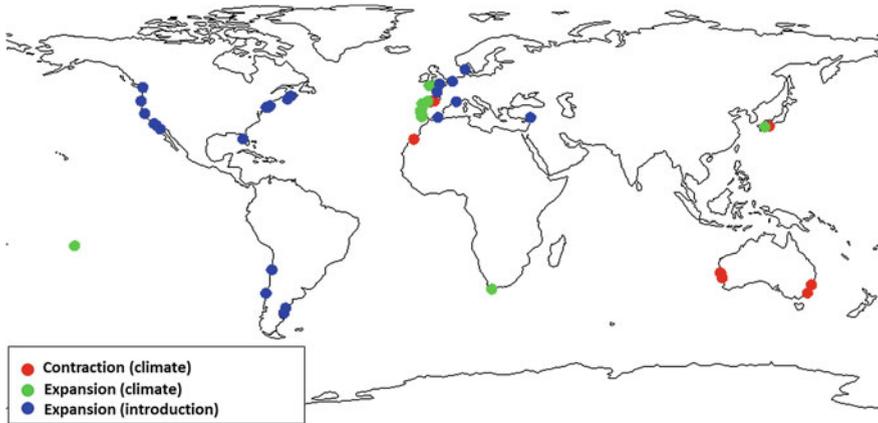
Fig. 3.2 Geographical location of studies reporting range shifts in seaweeds with sufficient information to calculate range-shift speed

reported in the South African warming hotspot was a range expansion of a cool-water kelp (*E. maxima*). However, this expansion was attributed to increased nearshore upwelling (Bolton et al. 2012), a consistent but small-scale phenomenon not captured by global satellite data (Smit et al. 2013). This example highlights that predictions about global range shifts from large-scale satellite images may not capture local distribution patterns, particular where upwelling occurs.

Range-shift speeds were determined for 40 taxa (n = 13, 22, 9 for each of the categories, respectively), with some genera represented by more than one species (Table 3.1). As might be expected, there was little overlap in taxa between categories but one species (*F. serratus*) was represented in all three range-shift categories (Appendix) and another two species (*F. vesiculosus* and *H. elongata*) in both climate change responses (Appendix). These responses highlight the context dependency of range shifts, with the direction of shift presumably determined by a combination of ecological interactions opening/closing opportunities for change as well as the relative position within the species' thermal envelope.

We found support for our range-shift hypotheses (Fig. 3.3). The speed of distributional changes in seaweed range limits differed significantly between the different types of shifts (Fig. 3.3, medians = 35.0, 4.5, and 4.0 km year^{-1}, respectively, P = 0.0001, $MS_{2,66}$ = 26.6, *pseudo-F* = 31.6). Expansions were significantly faster than contractions (P = 0.011, $MS_{1,2}$ = 10.1, *pseudo-F* = 6.9) and climate-induced shifts were significantly slower than those caused by species introductions (P = 0.0001, $MS_{1,2}$ = 53.1, *pseudo-F* = 64.1). However, this test did not include range contractions following a discrete extreme event—a large-scale marine heat wave—where two species of seaweeds were found to contract their ranges by $\sim$100 km in one year (Fig. 3.3, Appendix). These shifts remain some of the fastest observed range changes for any seaweed. When the two heatwave-driven
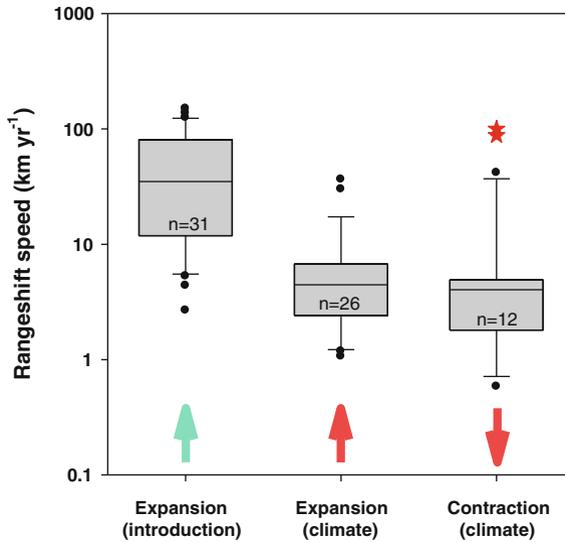
Fig. 3.3 Speed of range shifts in seaweeds. *Arrows* highlight direction (upwards = expansion; downwards = contraction) and underlying cause (*green* = after successful introduction; *red* = climate change) of range shifts. *Red* stars indicate shifts caused by an extreme marine heat wave. The very discrete nature of these shifts differs fundamentally from other reported shifts and consequently these have not been included in the analyses of rates (or the *box* in the plot)

contractions were included in the analysis, the difference between speed of climate-driven contractions and expansions disappeared ($P = 0.112$, $MS_{1,2} = 4.0$, *pseudo-F* = 2.5) but the difference in speed between introduction and climate-driven range shifts remained ($P = 0.0001$, $MS_{1,2} = 45.9$, *pseudo-F* = 44.8).

3.4 Case Studies of Seaweed Range Shifts and Ecological Implications

Many range-shifting seaweeds (cf. Table 3.1) are prominent members of their respective communities, where their addition or deletion is likely to have dramatic impacts on ecosystem structure and functioning (Williams and Smith 2007; Thomsen et al. 2010; Wernberg et al. 2013a; Bennett et al. 2015b) (see Chap. by Neiva et al. (2016) in this volume). The scale and nature of these ecological implications depends on the attributes of the shifting species and the impacted habitat (Thomsen et al. 2011). Here, we provide a range of examples of seaweed range shifts and their ecological implications. We also provide an example of a seaweed declining in abundance, a precursor to range contraction(Bates et al. 2014).

3.4.1 Range Contractions (Native Species)

In 2011 an unprecedented marine heat wave off the coast of Western Australia caused dramatic canopy loss of dominant seaweeds, including a 100 km southward range contraction of one of the main canopy-forming species, the fucoid *Scytothalia dorycarpa* (Fig. 3.4). During the heat wave, temperatures exceeded the physiological tolerance of *S. dorycarpa* for many weeks (Smale and Wernberg 2013). The contraction of *S. dorycarpa* co-occurred with a significant decrease in the densities
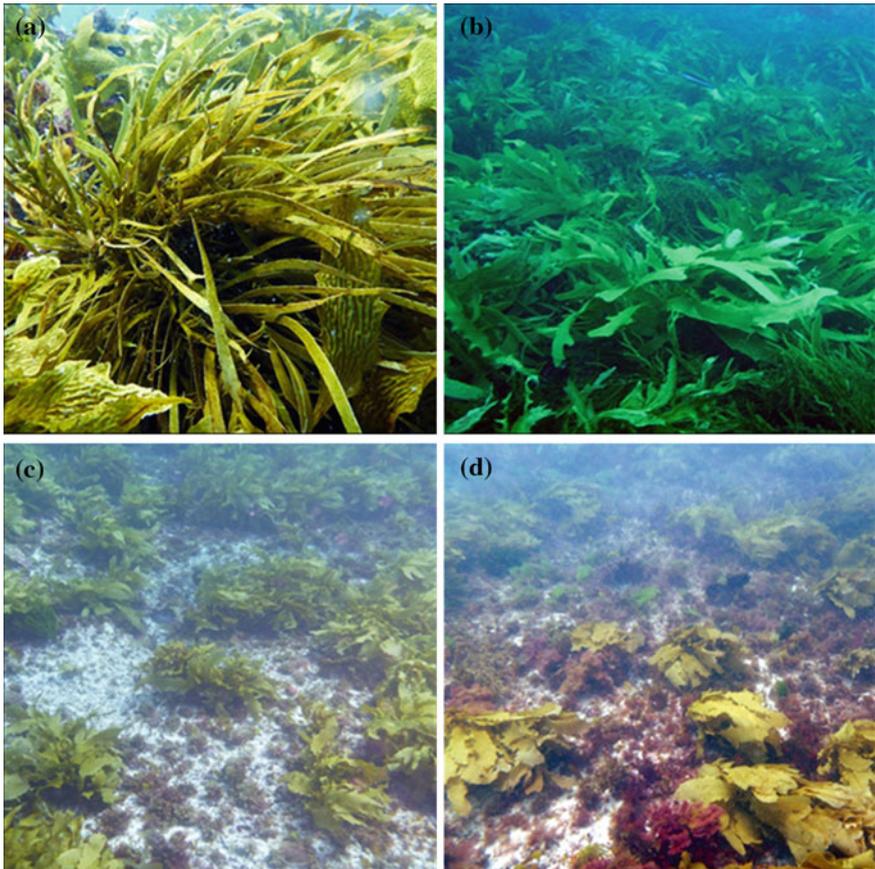

Fig. 3.4 *Scytothalia dorycarpa* (**a**) is a large ($\sim$1 m) fucoid endemic to southern Australia. During an extreme heat wave in 2011, *S. dorycarpa* contracted its range by $\sim$100 km in less than 1 year (Smale and Wernberg 2013). Prior to the heat wave (November 2010, **b**) reefs were covered by a dense mixed canopy of kelp (*Ecklonia radiata*) and *S. dorycarpa*. However, immediately after the heat wave (November 2011, **c**) the canopy had large gaps where *S. dorycarpa* had been extirpated. One year later (November 2012, **d**), the canopy had not recovered and gaps were filling in with foliose and turf algae (*All photos* © T. Wernberg)

of the kelp *Ecklonia radiata* (Wernberg et al. 2013a) and indirectly resulted in changes of the understorey community structure. The net effect was a shift from a dense three-dimensional canopy habitat to reefs with large open patches dominated by much smaller turf forming seaweeds among patches of *E. radiata* (Smale and Wernberg 2013) (Fig. 3.4). Concurrently, with the loss of seaweeds, the biomass and diversity of tropical herbivores increased, facilitating the new canopy-free state by suppressing seaweed reestablishment (Bennett et al. 2015b). The combined effects of the range contraction of *S. dorycarpa* and overall loss of seaweed canopies ultimately resulted in habitat and food loss (Wernberg et al. 2013a; Smale and Wernberg 2013) which are likely to have cascading impacts through altered benthic productivity and food web structure to a variety of higher trophic marine organisms including commercially important crustaceans, fishes and mammals (Lozano-Montes et al. 2011).

In northern Spain, range contractions have been reported for several canopy-forming seaweeds (Appendix), including *Fucus serratus* and *Himanthalia elongata* which have moved westwards in the Bay of Biscay since the late nineteenth century as a response to global warming (Duarte et al. 2013). *H. elongata* changed its range stepwise by 330 km over 120 years, whereas *F. serratus* retracted 197 km over 114 years but also reduced its abundance dramatically in its remaining range, i.e. in the westernmost part of northern Spain (Appendix). For both species the rate of contraction appears to have accelerated in recent years (Duarte et al. 2013). The ecological implications of these two range contractions are largely unknown (Duarte et al. 2013), although both species (and several other large, retreating canopy-forming seaweeds) are important habitat formers for smaller epiphytes and mobile animals (Hawkins and Hartnoll 1985; Lüning 1985; Wernberg et al. 2004; Ingólfsson 2008).

3.4.2 Range Expansions (Native Species)

The warm-water kelp *Laminaria ochroleuca* was first recorded in England in 1948, and subsequently expanded its range eastwards to the Isle of Wright at a rate of 5.4 km per year, as well as expanded northwards to Lundy Island at a rate of 2.5 km per year (Table 3.2). Recent resurveys of the inhabited area suggest that *L. ochroleuca* also expanded from the initially colonized sheltered coastline to moderately wave-exposed open coasts, accompanied by a significant increase in abundance, most likely in response to recent warming (Smale et al. 2014). In the area where *L. ochroleuca* most recently colonized, it competes with the native dominant congener *L. hyperborea*. As both species appear morphologically and functionally similar, it was initially assumed that they would have similar ecosystem function with little impact on the colonized ecosystem (Terazono et al. 2012). However, even small morphological differences may incur large cascading ecosystem effects. For example, Smale et al. (2014) showed that epiphyte cover on the smoother stipe of *L. ochroleuca* was dramatically lower than on the rough stipes

Table 3.2 Overview of the discussed five native and three non-native range shifts as well as the example of abundance change, with their according driver, direction and rate of shift and dispersal means

| Species	Division	Driver	Direction	Shift rate (km/year)	Size (cm)	Dispersal means
Fucus serratus	Ochrophyta	Warming	Contraction	1.7	70–100; <200	Negative buoyant, medium production of gametes, short-distance disperser
Himanthalia elongata	Ochrophyta	Warming	Contraction	4.4	300	Rafting of floating receptacles
Scytothalia dorycarpa	Ochrophyta	Heat wave	Contraction	100.0	50–200	Negative buoyant, medium production of gametes
Laminaria ochroleuca	Ochrophyta	Warming	Expansion	2.5–5.4	150	Release of large amounts of spores, short-distance disperser, negative buoyant
Ecklonia maxima	Ochrophyta	Cooling	Expansion	36.5	<1500	Release of very large amounts of spores
Caulerpa cylindracea	Chlorophyta	Introduction	Expansion	11.9	30	Negative buoyant, can regrow from fragments, fragments can re-attach into sediment, clonal spread, medium release of gametes (holocarpy, parental plant dies)
Sargassum muticum	Ochrophyta	Introduction	Expansion	4.4	<1600	Positively buoyant, monocious, selfy, high production of gametes
Undaria pinnatifida	Ochrophyta	Introduction	Expansion	35–50	200	Negative buoyant, local drift of reproductive individuals on dislodged mussels, massive production of gametes
Macrocystis pyrifera	Ochrophyta	Warming	Contraction	95 % cover reduction	<3000	Direct growth on female parental gametophyte; drifting thalli; spores
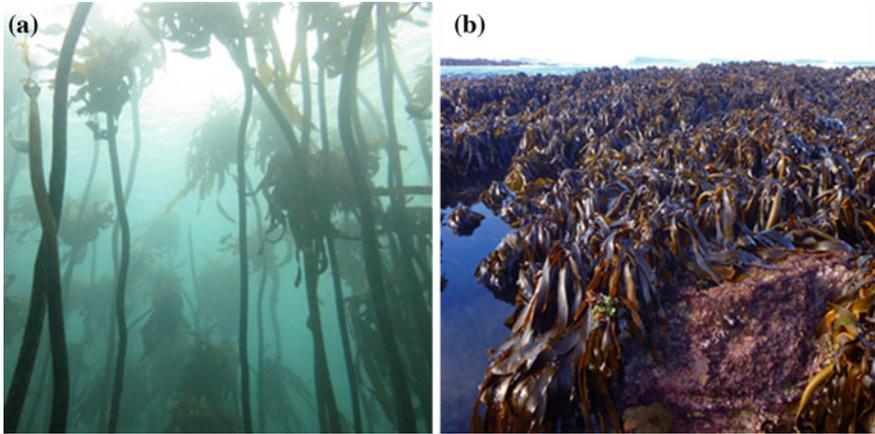
Fig. 3.5 The kelp *Ecklonia maxima* dominates nearshore reefs in the cold waters around southern Africa west of Cape Agulhas. It is a substantial seaweed which can grow to lengths in excess of 15 m (**a**: Buffels Bay, Cape of Good Hope). Between 2006 and 2008 this species expanded past Cape Agulhas, presumably due to cooling caused by upwelling (**b**: recently colonized intertidal populations at De Hoop Nature Reserve) (*Photos* © T. Wernberg)

of *L. hyperborea*. Thus, a reduction of the epiphytic habitat can be expected if *L. ochroleuca* replaces *L. hyperborea*, potentially with dramatic effects on associated fauna (Christie et al. 2009), trophic interactions (Smale et al. 2014) and biodiversity (Thomsen et al. 2010).

Another example of a recent and unusual range expansion of a native seaweed involves the dominant canopy-forming kelp *Ecklonia maxima* in South Africa (Fig. 3.5). The distribution of *E. maxima* along the southern coastline of South Africa appeared unchanged for ca. 70 years, but suddenly expanded eastwards (between 2006 and 2008) at a rate of 36.5 km per year (Bolton et al. 2012). It is suggested that gradual cooling caused the distribution expansion of *E. maxima*, crossing around Cape Agulhas which is considered a major barrier dividing the western and south coast regions (Anderson et al. 2009). As *E. maxima* is the major kelp along its distributional range, expansion of this species could have substantial ecological consequences (Bolton et al. 2012).

3.4.3 Range Expansion (Introduced Species)

Range expansions of non-native seaweeds can also alter ecosystem functioning after successful establishment. For example, *Caulerpa cylindracea* (Fig. 3.6a) is a highly invasive green seaweed which has spread along the Mediterranean Sea and Canary Islands since the early 1990s at an average rate of 11.9 km per year (Ruitton et al. 2005) (Table 3.2). *C. cylindracea* has invaded both soft and hard substrata and
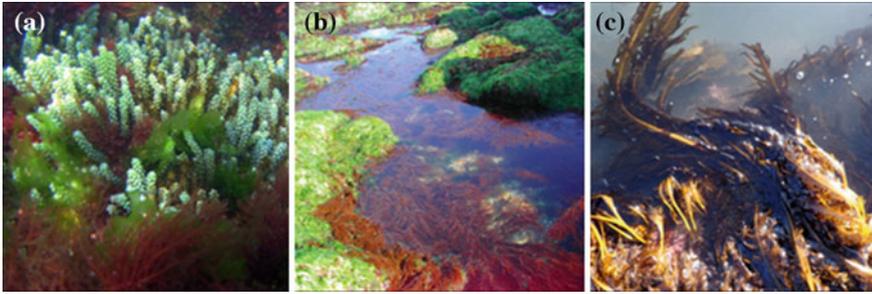
Fig. 3.6 Some of the most notorious invasive marine species are seaweeds, which have spread rapidly throughout many regions of the world where they have been introduced. *Caulerpa cylindracea* (**a**) growing among turf and foliose seaweeds in its native environment in Western Australia. *Sargassum muticum* (**b**) growing in tide pools in northern Spain, where it is now a dominant element of the seaweed flora. *Undaria pinnatifida* (**c**) growing on tidal platforms in southeastern New Zealand (*Photos* **a**, **c**: © M.S. Thomsen, **b**: © C. Olabarria)

can form dense monospecific stands. The introduction vector is unknown, but where the species has established dense monocultures it has been associated with a decrease in abundance, biodiversity and biotic homogenization of native species (Klein and Verlaque 2008; Verbruggen et al. 2013). By forming multilayered mats that trap sediment, *C. cylindracea* can lead to burial of communities by sediment (Piazzi et al. 2005). Specifically, Baldacconi and Corriero (2009) determined its impacts on sponge assemblages in the Ionian Sea suggesting decreases in sponge cover following the invasion.

The brown, canopy-forming seaweed *Sargassum muticum* (Fig. 3.6b) is also a well-studied invasive seaweed (Engelen et al. 2015). Originating from Asia, *S. muticum* has spread over the last few decades along coastlines in western Europe and western North America (Pedersen et al. 2005; Engelen et al. 2015). Within invaded locations, *S. muticum* can spread rapidly and become a dominant seaweed, sometimes leading to the suppression of local species and alteration of community structure (Stæhr et al. 2000). In 1941, *S. muticum* was first observed outside its native range in the Strait of Georgia (British Columbia, Canada) from where it subsequently spread along the adjacent coastline (Engelen et al. 2015). In 1984 *S. muticum* was sighted in Denmark for the first time in Limfjorden from where it subsequently spread at a rate of 4.4 km per year. *S. muticum* became the most abundant seaweed in Limfjorden, leading to a decrease in cover and abundance of several native canopy-forming seaweeds, including *Halidrys siliquosa*, *Saccharina latissima*, *Fucus vesiculosus* and *Fucus serratus* (Stæhr et al. 2000).

Undaria pinnatifida (Fig. 3.6c) is another high-profile invasive brown seaweed that is native to Japan, Russia and China. In the last 40–50 years, it has invaded Europe (Atlantic and Mediterranean Sea), North America (Pacific coast), south-western Australia, New Zealand and Argentina (Wallentinus 2007). In Argentina, *U. pinnatifida* was first recorded in 1992 and has since extended its range >1000 km southwards from its original site of introduction at a rate averaging

between 35 and 50 km per year. While *U. pinnatifida* can have negative impacts on some native seaweeds (Casas et al. 2004), positive effects have also been reported on benthic macrofauna and carbon flow (Dellatorre et al. 2014; Tait et al. 2015).

3.4.4 Abundance Change

Range shifts with a clear change of species distribution at the distribution limits represent extreme transitions from the presence to absence or vice versa. Prior to range contractions, seaweeds will first decrease in abundances within their ranges, where continued reductions in abundance near range limits represent the first steps towards a range shift (Bates et al. 2014). For example, Johnson et al. (2011) documented that previously widespread *Macrocystis pyrifera* (Fig. 3.7) kelp forests decreased drastically in cover at several sites in eastern Tasmania (Table 3.2), likely

Fig. 3.7 The giant kelp (*Macrocystis pyrifera*) is a majestic seaweed often attaining a size of more than 10 m, has declined dramatically in abundance in Tasmania (pictured) over the past couple of decades due to increased warming, nutrient poor water and urchin grazing (*Photo* © T. de Bettignies)

caused by a combination of ocean warming and a strengthening of the East Australian Current (characterized by nutrient poor water) over the past six decades (Johnson et al. 2011). Concurrently, the strengthening of the East Australian Current also led to the range expansion of the sea urchin *Centrostephanus rodgersii* into Tasmanian waters, facilitated by over-fishing of urchin predators (lobsters, Ling et al. 2009). The range-expanding urchins have likely contributed to the decline in *M. pyrifera* through destructive grazing, which has also negatively impacted other native seaweeds (Johnson et al. 2011). With the decrease in abundance of *M. pyrifera*, a fast-growing habitat and food provider, dozens of associated species are losing a unique three-dimensional habitat, resulting in loss of taxonomic diversity and food web complexity (Graham 2004; Ling 2008; Byrnes et al. 2011).

3.5 Perspective and Conclusion: Human Impacts on Seaweed Biogeography

Range shifts caused by species introductions and climate change need close monitoring as they are potentially irreversible and likely to have great ecosystem impacts (Madin et al. 2012). A critical problem, however, is that information on species' range boundaries is scarce and largely qualitative due to lack of baseline information and regular surveys (Wernberg et al. 2011b; Bates et al. 2015; Marcelino and Verbruggen 2015). Ecological niche models can assist to identify areas with suitable habitat, anticipate arrival points and predict the potential extent of range change after a successful introduction (Marcelino and Verbruggen 2015) or environmental change (Molinos et al. 2015; Takao et al. 2015). For example, Takao et al. (2015) found that the present distribution of *Ecklonia cava* around Japan is well represented by SST-based indices. Chronologically observed changes were well in agreement with the projections, and the results further indicated that temperature will be a key factor for distribution *of E. cava* in the future (Takao et al. 2015).

Monitoring laboratory experiments and models projecting future shifts combined will help to identify likely range-shift pathways of seaweeds. In response to range-shifting species, management is necessary and several management tools already in place can be applied through, for example education, raising awareness and protected areas. But existing management tools are not always sufficient, and especially the limited knowledge on range-shift limits adaptive management responses (Madin et al. 2012). Additionally, for successful monitoring, a more widespread use of molecular methods is necessary to determine origin of species to prevent misidentification based on plastic morphology (Bolton 2010) and to

identify loss of genetic variability at range edges (Provan and Maggs 2012; Assis et al. 2014; Neiva et al. 2015). Also, more regular surveys are required to be undertaken to determine range edges of populations and identify early range shifts and species introductions.

Future temperature increases are likely to result in more range shifts of seaweeds, especially along north–south orientated coastlines (Wernberg et al. 2011b; Molinos et al. 2015). These range shifts include poleward range extensions of warm-water tropical species, poleward range contractions of cold-water temperate species (Sorte et al. 2010; Wernberg et al. 2011a) and (potentially bidirectional) range expansion of introduced seaweeds (Sorte et al. 2013). Current models for marine species predict that expansions will be more prominent than contractions, leading to an overall increase in the biodiversity of many extratropical regions (Molinos et al. 2015). Globally, however, the narrative is likely to be different, because there will be a net loss of species (Cheung et al. 2009) as extinctions will be far more rapid than the evolution of new species. For seaweeds, this will be exacerbated by the juxtaposition of global patterns of species richness and endemicity (Bolton 1994; Kerswell 2006), hotspots of warming (Hobday and Pecl 2013) and barriers to range shifts (Wernberg et al. 2011a). In particular, southern Australia has the highest species richness and endemicity of seaweeds in the world, as well as some of the fastest warming regions in the world. However, the southern coastline is oriented east–west with very limited landmasses farther south. As seaweeds are pushed poleward towards the edge of the continent, there is great risk that they will 'drop off' to extinction—indeed, it has been estimated that range shifts could result in as much as a 25 % loss of the seaweed flora (Wernberg et al. 2011a).

To determine and model future biogeographic patterns of seaweed distribution, it is also necessary to take into account increasing threats to the coastal environments. Superimposed on temperature increases, increased ocean acidification will also change competitive hierarchies between fleshy, turf and calcifying marine algae, further altering local seaweed communities—and ultimately also range shifts (Hofmann et al. 2012). Also, interactive future effects, especially combined effects of warming and acidification with non-climate stressors, such as reduced water quality, will lower the resilience of communities and single species to perturbations like species invasions and storms (Wernberg et al. 2011a). Concurrently, more frequent and intense discrete events can drive stepwise changes in local environmental structure and cause larger more dramatic range- shifts (Smale and Wernberg 2013). Finally, ecological interactions are influencing the success of introductions and the speed of range shifts, possibly suppressing recovery, enhancing contraction or slowing down expansions (see *M. pyrifera* and *S. dorycarpa* case studies above). The extent to which the ecological context can suppress or enhance range shifts is a question in need of much research effort as we progress from simply detecting

change to understanding its underlying drivers and mediators. However, the magnitude of range shifts and biological responses from anthropogenic impacts differ widely among species (Poloczanska et al. 2013).

3.6   Conclusion

There is now substantial evidence that humans have influenced the global biogeography of seaweeds over the last few decades and will continue to do so in the near future. This evidence generally spans timescales of decades, and is unlikely to simply reflect short-term fluctuations such as ENSO events. Humans influence seaweed biogeography through three distinct processes (introductions, climate expansions and climate contractions), which manifest through different processes (dispersal, recruitment and mortality) (Bates et al. 2014) and therefore proceed at different speeds: introduction > expansion > contraction. These changes in seaweed distributions have also been associated with impacts on seaweed-based ecosystems. While we are still to see the long-term ecological and economic consequences, these are likely to be substantial given the ecosystem services derived from seaweed ecosystems (Bennett et al. 2015a).

Appendix

Review of published literature and citation searches to compile a global dataset of documented range shifts in native seaweeds or range expansions of successful seaweed invaders. Used key words include climate change, warming, extreme events, heat waves, invasive seaweeds, successful invaders, shift in distribution, range shifts, range expansion and range contraction. Literature was included when data was available for the direction, distance and time window of seaweed shift, so annual spread rates could be calculated. Literature stating a decrease in abundance or not pinpointing location and time window were excluded from the dataset. The two main drivers are Introduction (introduction) and Warming (contraction/expansion). When unusual driver it is added in brackets

Species	Division	Region	Driver	Annual spread (km/years)	First appearance/absence	Time window (years)	Distance (km)	Reference
Assemblage	Assemblage	SW Australia	Contraction	1.0	1940	50	51	Wernberg et al. (2011a, b)
Assemblage	Assemblage	SE Australia	Contraction	4.2	1940	50	211	Wernberg et al. (2011a, b)
Caulerpa cylindracea	Chlorophyta	Provence, France	Introduction	11.9	1997	7	83	Ruitton et al. (2005)
Caulerpa cylindracea	Chlorophyta	Ligurian Sea	Introduction	44.0	2009	5	220	Altamirano et al. (2014)
Caulerpa ollivieri	Chlorophyta	Mexico	Introduction	19.0	1968	42	800	Ortegón-Aznar et al. (2015)
Caulerpa taxifolia var. distichophylla	Chlorophyta	Mediterranean Sea	Introduction	33.3	2006	6	200	Aplikioti et al. (2016)
Caulerpa taxifolia var. distichophylla	Chlorophyta	Mediterranean Sea	Introduction	87.5	2006	8	700	Aplikioti et al. (2016)
Codium adhaerens	Chlorophyta	Portugal	Expansion	1.2	1955	50	59	Lima et al. (2007)
Codium fragile ssp. fragile	Chlorophyta	Nova Scotia	Introduction	11.1	1989	18	200	Watanabe et al. (2010)
Codium fragile ssp. tomentosoides	Chlorophyta	NW Atlantic	Introduction	16.0	1955	47	750	Scheibling and Gagnon (2006)
Codium fragile ssp. tomentosoides	Chlorophyta	NW Atlantic	Introduction	10.6	1955	47	500	Scheibling and Gagnon (2006)
Codium fragile ssp. tomentosoides	Chlorophyta	Northern Chile	Introduction	6.4	2005	7	45	Neill et al. (2006)
Valonia utricularis	Chlorophyta	Portugal	Expansion	3.9	1955	50	197	Lima et al. (2007)
Ahnfeltia plicata	Ochrophyta	Portugal	Expansion	6.6	1955	50	330	Lima et al. (2007)
Bifurcaria bifurcata	Ochrophyta	Britain, Ireland	Expansion	3.1	1964	45	140	Mieszkowska et al. (2006)
Bifurcaria bifurcata	Ochrophyta	Portugal	Expansion	5.1	1955	50	257	Lima et al. (2007)
Chondrus crispus	Ochrophyta	Portugal	Expansion	3.6	1955	50	180	Lima et al. (2007)

(continued)

(continued)

Species	Division	Region	Driver	Annual spread (km/years)	First appearance/absence	Time window (years)	Distance (km)	Reference
Desmarestia aculeata	Ochrophyta	Portugal	Expansion	4.5	1955	50	227	Lima et al. (2007)
Desmarestia ligulata	Ochrophyta	Portugal	Expansion	1.4	1955	50	70	Lima et al. (2007)
Dumontia contorta	Ochrophyta	Portugal	Expansion	1.2	1955	50	62	Lima et al. (2007)
Durvillea potatorum	Ochrophyta	SE Australia	Contraction	0.6	1945	60	35	Millar (2007)
Ecklonia maxima	Ochrophyta	South Africa	Expansion	36.5	2008	2	73	Bolton et al. (2012)
Ecklonia radiata	Ochrophyta	SW Australia	Contraction	88.0	2011	1	88	Wernberg and Bennett, unpublished data 2015
Fucus serratus	Ochrophyta	North Spain	Contraction	1.9	1894	60	116	Duarte et al. (2013)
Fucus serratus	Ochrophyta	North Spain	Contraction	5.1	1955	21	107	Duarte et al. (2013)
Fucus serratus	Ochrophyta	North Spain	Expansion	2.2	1977	12	26	Duarte et al. (2013)
Fucus serratus	Ochrophyta	Spain	Expansion	5.0	1982	20	100	Arrontes (2002)
Fucus serratus	Ochrophyta	North America	Introduction	11.8	1868	17	200	Johnson et al. (2012)
Fucus serratus	Ochrophyta	North America	Introduction	5.3	1868	17	90	Johnson et al. (2012)
Fucus vesiculosus	Ochrophyta	Morocco	Contraction	41.7	1985	30	1250	Nicastro et al. (2013)
Fucus vesiculosus	Ochrophyta	Portugal	Expansion	3.1	1955	50	157	Lima et al. (2007)
Halidrys siliquosa	Ochrophyta	Portugal	Expansion	1.8	1955	50	90	Lima et al. (2007)
Halydris siliquosa	Ochrophyta	Portugal	Expansion	1.1	2006	75	80	Lima et al. (2008)
Himanthalia elongata	Ochrophyta	North Spain	Contraction	1.8	1889	66	116	Duarte et al. (2013)
Himanthalia elongata	Ochrophyta	North Spain	Contraction	4.2	1955	20	84	Duarte et al. (2013)
Himanthalia elongata	Ochrophyta	North Spain	Contraction	26.0	2004	5	130	Duarte et al. (2013)

(continued)

Species	Division	Region	Driver	Annual spread (km/years)	First appearance/absence	Time window (years)	Distance (km)	Reference
Himanthalia elongata	Ochrophyta	Portugal	Expansion	4.4	1955	50	219	Lima et al. (2007)
Laminaria ochroleuca	Ochrophyta	SE Atlantic	Expansion	2.5	1948	60	150	Smale et a (2013)
Laminaria ochroleuca	Ochrophyta	SE Atlantic	Expansion	5.4	1948	60	325	Smale et al. (2013)
Padina pavonica	Ochrophyta	Portugal	Expansion	3.7	1955	50	187	Lima et al. (2007)
Pelvetia canaliculata	Ochrophyta	Portugal	Expansion	4.9	1955	50	245	Lima et al. (2007)
Sargassum filicinum	Ochrophyta	Mexico	Introduction	137.5	2003	4	550	Riosmena-Rodriguez (2012)
Sargassum flavifolium	Ochrophyta	Portugal	Expansion	11.9	1955	50	593	Lima et al. (2007)
Sargassum illicifolium	Ochrophyta	Japan	Expansion	10.5	1989	19	200	Tanaka et al. (2012)
Sargassum micracanthum	Ochrophyta	Japan	Contraction	3.9	1977	31	120	Tanaka et al. (2012)
Sargassum muticum	Ochrophyta	Denmark	Introduction	4.4	1984	16	70	Staehr et al. (2000)
Sargassum muticum	Ochrophyta	Canada	Introduction	111.2	1947	6	667	Engelen et al. (2015)
Sargassum muticum	Ochrophyta	northern California	Introduction	80.6	1965	18	1450	Engelen et al. (2015)
Sargassum muticum	Ochrophyta	Mexico	Introduction	35.0	1973	8	280	Engelen et al. (2015)
Sargassum muticum	Ochrophyta	Netherlands	Introduction	50.0	1979	6	300	Engelen et al. (2015)
Sargassum muticum	Ochrophyta	Denmark	Introduction	120.0	1984	5	600	Engelen et al. (2015)
Sargassum muticum	Ochrophyta	France	Introduction	81.8	1983	11	900	Engelen et al. (2015)
Sargassum muticum	Ochrophyta	Mexico	Introduction	2.7	1988	15	40	Espinoza (1990)

(continued)

(continued)

Species	Division	Region	Driver	Annual spread (km/years)	First appearance/absence	Time window (years)	Distance (km)	Reference
Sargassum yamamotoi	Ochrophyta	Japan	Contraction	4.4	1977	31	135	Tanaka et al. (2012)
Scytothalia dorycarpa	Ochrophyta	SW Australia	Contraction	100.0	2011	1	100	Smale and Wernberg (2013)
Scytothalia dorycarpa	Ochrophyta	SW Australia	Contraction	3.2	1961	50	160	Smale and Wernberg (2013)
Turbinaria ornata	Ochrophyta	French Polynesia	Expansion	30.0	1980	10	300	Stewart (2008)
Undaria pinnatifida	Ochrophyta	North America	Introduction	125.0	2000	2	250	Aguilar-Rosas et al. (2004)
Undaria pinnatifida	Ochrophyta	Mexico	Introduction	66.7	2003	3	200	Aguilar-Rosas et al. (2004)
Undaria pinnatifida	Ochrophyta	Argentina	Introduction	35.7	1999	7	250	Dellatorre et al. (2014)
Undaria pinnatifida	Ochrophyta	Argentina	Introduction	50.0	2005	6	300	Dellatorre et al. (2014)
Undaria pinnatifida	Ochrophyta	Argentina	Introduction	50.0	2012	20	1000	Dellatorre et al. (2014)
Grateloupia doryphora	Rhodophyta	Brittany, France	Introduction	150.0	1999	1	150	Simon et al. (2001)
Grateloupia turuturu	Rhodophyta	Gulf of Maine	Introduction	33.0	2007	4	132	Mathieson et al. (2008)
Halopithys incurva	Rhodophyta	Portugal	Expansion	9.5	1955	50	475	Lima et al. (2007)
Heterosiphonia japonica	Rhodophyta	Western North Atlantic	Introduction	66.7	2007	6	400	Newton et al. (2013)
Heterosiphonia japonica	Rhodophyta	Western North Atlantic	Introduction	16.7	2007	6	100	Newton et al. (2013)
Hypnea musciformis	Rhodophyta	Portugal	Expansion	5.4	1955	50	269	Lima et al. (2007)
Mastocarpus sp.	Rhodophyta	Chile	Introduction	18.2	1980	22	400	Macaya et al. (2013)
Mastocarpus sp.	Rhodophyta	Chile	Introduction	31.8	1980	22	700	Macaya et al. (2013)
Palmaria palmata	Rhodophyta	Portugal	Expansion	7.2	1955	50	358	Lima et al. (2007)

References

Adey WH, Steneck RS. Thermogeography over time creates biogeographic regions: a temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. J Phycol. 2001;37:677–98.

Aguilar-Rosas R, Aguilar-Rosas LE, Avila G, Marcos R. First record of *Undaria pinnatifida* (Harvey) Suringar (Laminariales,Phaeophyta) on the Pacific coast of Mexico. Bot Mar. 2004;47:255–58.

Altamirano M, Andreakis N, Souza-egipsy V, Zanolla M, De la Rosa J. First record of *Caulerpa cylindracea* (Caulerpaceae , Chlorophyta) in Andalusia (Southern Spain). An del Jardín Botánico Madrid. 2014;71:1–9.

Anderson RJ, Bolton JJ, Stegenga H. Using the biogeographical distribution and diversity of seaweed species to test the efficacy of marine protected areas in the warm-temperate Agulhas Marine Province, South Africa. Divers Distrib. 2009;15:1017–27.

Aplikioti M, Louizidou P, Mystikou A, Marcou M, Stavrou P, Kalogirou S, et al. Further expansion of the alien seaweed *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procacini (Ulvophyceae, Bryopsidales) in the Eastern Mediterranean Sea. Aquat Invasions. 2016;11:in press.

Arrontes J. Mechanisms of range expansion in the intertidal brown alga *Fucus serratus* in northern Spain. Mar Biol. 2002;141:1059–67.

Assis J, Serrão EA, Claro B, Pearson GA. Climate-driven range shifts explain the distribution of extant gene pools and predict future loss of unique lineages in a marine brown alga. Mol Ecol. 2014;23:2797–810.

Baldacconi R, Corriero G. Effects of the spread of the alga *Caulerpa racemosa* var. *cylindracea* on the sponge assemblage from coralligenous concretions of the Apulian coast (Ionian Sea, Italy). Mar Ecol. 2009;30:337–45.

Bartsch I, Wiencke C, Laepple T. Global seaweed biogeography under a changing climate: the prospected effects of temperature. In: Wiencke C, Bischof K, editors. Seaweed biology. Berlin Heidelberg: Springer; 2012. p. 383–406.

Bates AE, Pecl GT, Frusher S, Hobday AJ, Wernberg T, Smale DA, Sunday JM, Hill NA, Dulvy NK, Colwell RK, Holbrook NJ, Fulton EA, Slawinski D, Feng M, Edgar GJ, Radford BT, Thompson PA, Watson RA. Defining and observing stages of climate-mediated range shifts in marine systems. Glob Environ Change. 2014;26:27–38.

Bates AE, Bird TJ, Stuart-smith RD, Wernberg T, Sunday JM, Barrett NS, Edgar GJ, Frusher S, Hobday AJ, Pecl GT, Smale DA, McCarthy M. Distinguishing geographical range shifts from artefacts of detectability and sampling effort. Divers Distrib. 2015;21:13–22.

Bennett S, Wernberg T, Connell SD, Hobdav AJ, Johnson CR, Poloczanska ES. The "Great Southern Reef": social, ecological and economic value of Australia's neglected kelp forests. Mar Freshwater Res. 2015a. doi:10.1071/MF15232.

Bennett S, Wernberg T, Harvey ES, Santana-Garcon J, Saunders BJ. Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. Ecol Lett. 2015b;18:714–23.

Björck S. A review of the history of the Baltic Sea, 13.0-8.0 ka BP. Quat Int. 1995;27:19–40.

Bolton JJ. Global seaweed diversity: patterns and anomalies. Bot Mar. 1994;37:241–6.

Bolton JJ. The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. Helgol Mar Res. 2010;64:263–79.

Bolton J, Anderson R, Smit A, Rothman M. South African kelp moving eastwards: the discovery of *Ecklonia maxima* (Osbeck) Papenfuss at De Hoop Nature Reserve on the south coast of South Africa. African J Mar Sci. 2012;34:147–51.

Burridge CP, Hurt AC, Farrington LW, Coutin PC, Austin CM. Stepping stone gene flow in an estuarine dwelling sparid from south east Australia. J Fish Biol. 2004;64:805–19.

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel CV, Kiessling W, O'Connor MI,

Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ, Richardson AJ. The pace of shifting climate in marine and terrestrial ecosystems. Science. 2011;334:652–5.

Buschbaum C, Chapman AS, Saier B. How an introduced seaweed can affect epibiota diversity in different coastal systems. Mar Biol. 2006;148:743–54.

Byrnes JE, Reed DC, Cardinale BJ, Cavanaugh KC, Holbrook SJ, Schmitt RJ. Climate-driven increases in storm frequency simplify kelp forest food webs. Glob Change Biol. 2011;17:2513–24.

Casas G, Scrosati R, Luz Piriz M. The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). Biol Invasions. 2004;6:411–6.

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D. Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish. 2009;10:235–51.

Christie H, Norderhaug KM, Fredriksen S. Macrophytes as habitat for fauna. Mar Ecol Prog Ser. 2009;396:221–33.

Coumou D, Rahmstorf S. A decade of weather extremes. Nat Clim Change. 2012;2:491–6.

Cowman PF, Bellwood DR. Vicariance across major marine biogeographic barriers: temporal concordance and the relative intensity of hard versus soft barriers. Proc R Soc B. 2013;280:20131541.

Dellatorre FG, Amoroso R, Saravia J, Orensanz (Lobo) JM. Rapid expansion and potential range of the invasive kelp *Undaria pinnatifida* in the Southwest Atlantic. Aqua Invasions. 2014;9 (4):467–78.

Dethier MN, McDonald K, Strathmann RR. Colonization and connectivity of habitat patches for coastal marine species distant from source populations. Conserv Biol. 2003;17:1024–35.

Duarte L, Viejo RM, Martínez B, deCastro M, Gomez-Gesteira M, Gallardo T. Recent and historical range shifts of two canopy-forming seaweeds in North Spain and the link with trends in sea surface temperature. Acta Oecologica. 2013;51:1–10.

Engelen AH, Serebryakova A, Ang P, Britton-Simmons K, Mineur F, Pedersen MF, Toth G. Circumglobal invasion by the brown seaweed *Sargassum muticum*. Oceanogr Mar Biol Ann Rev. 2015; 53:81–126.

Espinoza J. The Southern Limit of *Sargassum muticum* (Yendo) Fensholt (Phaeophyta, Fucales) in the Mexican Pacific. Bot Mar. 1990;33:193–96.

Fraser CI, Waters JM. Algal parasite *Herpodiscus durvillaeae* (Phaeophyceae: Sphacelariales) inferred to have traversed the Pacific Ocean with its buoyant host. J Phycol. 2013;49:202–6.

Fraser CI, Nikula R, Waters JM. Oceanic rafting by a coastal community. Proc R Soc B. 2011;278:649–55.

Gaylord B, Gaines SD. Temperature or transport? Range limits in marine species mediated solely by flow. Am Nat. 2000;155:769–89.

Gaylord B, Reed DC, Raimondi PT, Washburn L, McLean SR. A physically based model of macroalgal spore dispersal in the wave and current-dominant nearshore. Ecology. 2002;83:1239–51.

Gillespie RG, Baldwin BG, Waters JM, Fraser CI, Nikula R, Roderick GK. Long-distance dispersal: a framework for hypothesis testing. Trends Ecol Evol. 2012;27:47–55.

Graham MH. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems. 2004;7:341–57.

Grigg R, Hey R. Paleoceanography of the tropical eastern Pacific Ocean. Science. 1992;255:172–8.

Hampe A, Petit R. Conserving biodiversity under climate change: the rear edge matters. Ecol Lett. 2005;8:461–7.

Harley CDG, Hughes AR, Hulgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Willams SL. The impacts of climate change in coastal marine systems. Ecol Lett. 2006;9:228–41.

Harley CDG, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA, Graham MH. Effects of climate change on global seaweed communities. J Phycol. 2012;48:1064–78.

Hawkins S, Hartnoll R. Factors determining the upper limits of intertidal canopy-forming algae. Mar Ecol Prog Ser. 1985;20:265–71.

Hidas EZ, Costa TL, Ayre DJ, Minchinton TE. Is the species composition of rocky intertidal invertebrates across a biogeographic barrier in south-eastern Australia related to their potential for dispersal? Mar Freshwater Res. 2007;58:835–42.

Hinojosa IA, Pizarro M, Ramos M, Thiel M. Spatial and temporal distribution of floating kelp in the channels and fjords of southern Chile. Estu Coast Shelf Sci. 2010;87:367–77.

Hobday AJ. Age of drifting *Macrocystis pyrifera* (L.) C. Agardh rafts in the Southern California Bight. J Exp Mar Bio Ecol. 2000a;253:97–114.

Hobday AJ. Persistence and transport of fauna on drifting kelp (*Macrocystis pyrifera* (L.) C. Agardh) rafts in the Southern California Bight. J Exp Mar Bio Ecol. 2000b;253:75–96.

Hobday AJ, Pecl GT. Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. Rev Fish Biol Fish. 2013;24:415–25.

Hofmann LC, Straub S, Bischof K. Competition between calcifying and noncalcifying temperate marine macroalgae under elevated CO_2 levels. Mar Ecol Prog Ser. 2012;464:89–105.

Ingólfsson A. The invasion of the intertidal canopy-forming alga *Fucus serratus* L. to southwestern Iceland: possible community effects. Estu Coast Shelf Sci. 2008;77:484–90.

IPCC (2012) Managing the risks of extreme events and disasters to advance climate change adaptation.

IPCC (2014) Climate change 2014 synthesis report summary chapter for policymakers.

Irving AD, Connell SD. Predicting understorey structure from the presence and composition of canopies: an assembly rule for marine algae. Oecologia. 2006;148:491–502.

Johnson L, Brawley S, Adey W. Secondary spread of invasive species: historic patterns and underlying mechanisms of the continuing invasion of the European rockweed *Fucus serratus* in eastern. Biol Invasions. 2012;14:79–97.

Johnson CR, Banks SC, Barrett NS, Cazassus F, Dunstan PK, Edgar GJ, Frusher SD, Gardner C, Haddon M, Helidoniotis F, Hill KL, Holbrook NJ, Hosie GW, Last PR, Ling SD, Melbourne-Thomas J, Miller K, Pecl GT, Richardson AJ, Ridgway KR, Rintoul SR, Ritz DA, Ross DJ, Sanderson JC, Shepherd SA, Slotwinski A, Swadling KM, Taw N. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. J Exp Mar Bio Ecol. 2011;400:17–32.

Karl T, Trenberth K. Modem global climate change. Science. 2003;302:1719–23.

Kerswell AP. Global biodiversity patterns of benthic marine algae. Ecology. 2006;87:2479–88.

Klein J, Verlaque M. The *Caulerpa racemosa* invasion: a critical review. Mar Pollut Bull. 2008;56:205–25.

Lessios HA, Kessing BD, Robertson DR. Massive gene flow across the world's most potent marine biogeographic barrier. Proc R Soc B. 1998;265:583–8.

Lima FP, Wethey DS. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nat Commun. 2012;3:1–13.

Lima FP, Ribeiro PA, Queiroz N, Hawkins SJ, Santos AM. Do distributional shifts of northern and southern species of algae match the warming pattern? Glob Chang Biol. 2007;13:2592–604.

Lima FP, Queiroz N, Ribeiro PA, Xavier R, Hawkins SJ, Santos AM. First record of *Halidrys siliquosa* on the Portuguese coast: counter-intuitive range expansion? Mar Biodivers Rec. 2008; doi: 10.1017/S1755267208000018.

Ling SD. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia. 2008;156:883–94.

Ling SD, Johnson CR, Frusher SD, Ridgway KR. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc Nat Acad Sci USA. 2009;106:2234–22345.

Lozano-Montes HM, Loneragan NR, Babcock RC, Jackson K. Using trophic flows and ecosystem structure to model the effects of fishing in the Jurien Bay Marine Park, temperate Western Australia. Mar Freshwater Res. 2011;62(5):421–31.

Luiz OJ, Madin JS, Robertson DR, Rocha LA, Wirtz P, Floeter SR. Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes. Proc R Soc B. 2012;279:1033–40.

Lüning K. Meeresbotanik: Verbreitung, Ökophysiologie und Nutzung der marinen Makroalgen. In: 1st ed. Stuttgart New York: Georg Thieme Verlag; 1985.

Macaya EC, Pacheco S, Cáceres A, Musleh S. Range extension of the non-indigenous alga *Mastocarpus* sp. along the Southeastern Pacific coast. Rev Biol Mar Oceanogr. 2013; 48: 661–65.

Madin EMP, Ban NC, Doubleday ZA, Holmes TH, Pecl GT, Smith F. Socio-economic and management implications of range-shifting species in marine systems. Glob Environ Change. 2012;22:137–46.

Marcelino VR, Verbruggen H. Ecological niche models of invasive seaweeds. J Phycol. 2015;51:606–20.

Mathieson AC, Dawes CJ, Pederson J, Gladych RA, Carlton JT. The Asian red seaweed *Grateloupia turuturu* (Rhodophyta) invades the Gulf of Maine. Biol Invasions. 2008;10:985–88.

Mattio L, Zubia M, Maneveldt GW, Anderson RJ, Bolton JJ, de Gaillande C, De Clerck O, Payri CE. Marine flora of the Iles Eparses (Scattered Islands): a longitudinal transect through the Mozambique Channel. Acta Oecologica. 2015. doi:10.1016/j.actao.2015.09.001.

Mieszkowska N, Kendall MA, Hawkins SJ, Leaper R, Willamson P, Hardman-Mountford NJ, et al. Changes in the range of some common rocky shore species in Britain - A response to climate change? Hydrobiologia. 2006;555:241–51.

Millar AJ. The Flindersian and Peronian Provinces. Algae Aust Introd. 2007:554–59.

Molinos JG, Halpern BS, Schoeman DS, Brown CJ, Kiessling W, Moore PJ, Pandolfi JM, Poloczanska ES, Richardson AJ, Burrows MT. Climate velocity and the future global redistribution of marine biodiversity. Nat Clim Change. 2015. doi:10.1038/nclimate2769.

Myers AA. Biogeographic barriers and the development of marine biodiversity. Estu Coast Shelf Sci. 1997;44:241–8.

Neill PE, Alcalde O, Faugeron S, Navarrete SA, Correa JA. Invasion of *Codium fragile* ssp. *tomentosoides* in northern Chile: A new threat for *Gracilaria* farming. Aquaculture. 2006;259:202–210.

Neiva J, Assis J, Coelho NC, Fernandes F, Pearson GA, Serräo EA. Genes left behind: climate change threatens cryptic genetic diversity in the canopy-forming seaweed *Bifurcaria bifurcata*. PLoS One. 2015;10:e0131530.

Neiva J, Serrão EA, Assis J, Pearson GA, Coyer JA, Olsen JL, Hoarau G, Valero M. Climate oscillations, range shifts and phylogeographic patterns of North Atlantic Fucaceae. In: Hu ZM, Fraser CI, editors. Seaweed phylogeography: adaptation and evolution of seaweeds under environmental change. Berlin Heidelberg: Springer; 2016.

Newton C, Bracken MES, McConville M, Rodrigue K, Thornber CS. Invasion of the red seaweed *Heterosiphonia japonica* spans biogeographic provinces in the Western North Atlantic Ocean. PLoS One. 2013;8(4):e62261.

Nicastro KR, Zardi GI, Teixeira S, Neiva J, Serrao EA, Pearson GA. Shift happens : trailing edge contraction associated with recent warming trends threatens a distinct genetic lineage in the marine macroalga *Fucus vesiculosus*. BMC Biol. 2013;11:6.

Nogales M, Heleno R, Traveset A, Vargas P. Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. New Phytol. 2012;194:313–7.

Norton TA. Dispersal by macroalgae. Br Phycol J. 1992;27:293–301.

Ortegón-aznar I, Rosado-espinosa LA, Aguilar-perera A. Occurrence of the introduced alga *Caulerpa ollivieri* Dostál, 1929 (Caulerpaceae, Chlorophyta) in the Southern Gulf of Mexico. BioInvasions Rec. 2015;4:17–21.

Pedersen MF, Staehr PA, Wernberg T, Thomsen MS. Biomass dynamics of exotic *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark—implications of species replacements on turnover rates. Aquat Bot. 2005;83:31–47.

Perry AL, Low PJ, Ellis JR, Reynolds JD. Climate change and distribution shifts in marine fishes. Science. 2005;308:1912–5.

Piazzi L, Balata D, Ceccherelli G, Cinelli F. Interactive effect of sedimentation and *Caulerpa racemosa* var. *cylindracea* invasion on macroalgal assemblages in the Mediterranean Sea. Estu Coast Shelf Sci. 2005;64:467–74.

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. Marine taxa track local climate velocities. Science. 2013;341:1239–42.

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel CV, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ. Global imprint of climate change on marine life. Nat Clim Change. 2013;3:919–25.

Provan J, Maggs CA. Unique genetic variation at a species' rear edge is under threat from global climate change. Proc R Soc B. 2012;279:39–47.

Quartino ML, Deregibus D, Campana GL, Juan Latorre GE, Momo FR. Evidence of macroalgal colonization on newly ice-free areas following glacial retreat in Potter Cove (South Shetland Islands), Antarctica. PLoS One. 2013;8(3):e58223.

Riosmena-Rodríguez R, Boo GH, López-Vivas JM, Hernandez-Velasco A, Saenz-Arroyo A, Boo SM. The invasive seaweed *Sargassum filicinum* (Fucales, Phaeophyceae) is on the move along the Mexican Pacific coastline. Bot Mar. 2012;55:547–51.

Rothäusler E, Gutow L, Thiel M. Floating seaweeds and their communities. In: Wiencke C, Bischof K, editors. Seaweed biology. Berlin: Springer; 2012. p. 359–80.

Ruitton S, Javel F, Culioli J-M, Meinesz A, Pergent G, Verlaque M. First assessment of the *Caulerpa racemosa* (Caulerpales, Chlorophyta) invasion along the French Mediterranean coast. Mar Pollut Bull. 2005;50:1061–8.

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Marker IM, Thompson JN, Weller SG. The population biology of invasive species. Ann Rev Ecol Syst. 2001;32:305–32.

Santelices B. Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanogr Mar Biol Ann Rev. 1990;28:177–276.

Scheibling RE, Gagnon P. Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). Mar Ecol Prog Ser. 2006;325:1–14.

Schils T, Wilson SC. Temperature threshold as a biogeographic barrier in northern Indian ocean macroalgae. J Phycol. 2006;42:749–56.

Simon C, Ar GE, Deslandes E. Expansion of the red alga *Grateloupia doryphora* along the coasts of Brittany (France). Hydrobiologia. 2001;443:23–29.

Smale DA, Wernberg T. Extreme climatic event drives range contraction of a habitat-forming species. Proc R Soc B. 2013;280:20122829.

Smale DA, Wernberg T, Yunnie ALE, Vance T. The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. Mar Ecol. 2014. doi:10.1111/maec.12199.

Smit AJ, Roberts M, Anderson RJ, Dufois F, Dudley SFJ, Bornan TG, Olbers J, Bolton JJ. A coastal seawater temperature dataset for biogeographical studies: large biases between in situ and remotely-sensed data sets around the coast of South Africa. PLoS One. 2013.

Sorte CJB, Williams SL, Carlton JT. Marine range shifts and species introductions: comparative spread rates and community impacts. Glob Ecol Biogeogr. 2010;19:303–16.

Sorte CJB, Ibáñez I, Blumenthal DM, Molinri NA, Miller LP, Grosholz ED, Diez JM, D'Antonio CM, Olden JD, Jones SJ, Dukes JS. Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecol Lett. 2013;16:261–70.

Stæhr PA, Pedersen MF, Thomsen MS, Wernberg T, Krause-Jensen D. Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. Mar Ecol Prog Ser. 2000;207:79–88.

Stewart HL. The role of spatial and ontogenetic morphological variation in the expansion of the geographic range of the tropical brown alga, *Turbinaria ornata*. Integr Comp Biol. 2008;48:713–19.

Sunday JM, Pecl GT, Frusher S, Hobday AJ, Hill N, Holbrook NJ, Edgar GJ, Stuart-Smith R, Barrett N, Wernberg T, Watson RA, Smale DA, Fulton EA, Slawinski D, Feng M, Radford BT, Thompson PA, Bates AE. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. Ecol Lett. 2015;18:944–53.

Tait LW, South PM, Lilley SA, Thompsen MS, Schiel DR. Assemblage and understory carbon production of native and invasive canopy-forming macroalgae. J Exp Mar Bio Ecol. 2015;469:10–7.

Takao S, Kumagai NH, Yamano H, Fujii M, Yamanaka Y. Projecting the impacts of rising seawater temperatures on the distribution of seaweeds around Japan under multiple climate change scenarios. Ecol Evol. 2015;5:213–23.

Tanaka K, Taino S, Haraguchi H, Prendergast G, Hiraoka M. Warming off southwestern japan linked to distributional shifts of subtidal canopy-forming seaweeds. Ecol Evol. 2012;2:2854–65.

Terazono Y, Nakamura Y, Imoto Z, Hiraoka M. Fish response to expanding tropical *Sargassum* beds on the temperate coasts of Japan. Mar Ecol Prog Ser. 2012;464:209–20.

Thomsen MS, Wernberg T, Tuya F, Silliman BR. Evidence for impacts of nonindigenous macroalgae: a meta-analysis of experimental field studies. J Phycol. 2009;45:812–9.

Thomsen MS, Wernberg T, Altieri A, Tuya F, Gulbransen D, McGlathery KJ, Holmer M, Silliman BR. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integr Comp Biol. 2010;50(2):158–75.

Thomsen MS, Wernberg T, Olden JD, Griffin GN, Silliman BR. A framework to study the context-dependent impacts of marine invasions. J Exp Mar Bio Ecol. 2011;400:322–7.

Thomsen MS, Wernberg T, Olden JD, Byers JE, Bruno JF, Silliman BR, Schiel DR. Forty years of experiments on aquatic invasive species: are study biases limiting our understanding of impacts? NeoBiota. 2014;22:1–22.

Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Vanden Berghe E, Worm B. Global patterns and predictors of marine biodiversity across taxa. Nature. 2010;466:1098–101.

Tuya F, Wernberg T, Thomsen MS. Habitat structure affect abundances of labrid fishes across temperate reefs in south-western Australia. Environ Biol Fishes. 2009;86:311–9.

Van den Hoek C. The distribution of benthic marine algae in relation to the temperature regulation of their life histories. Biol J Linn Soc. 1982;18:81–144.

Van den Hoek C. The possible significance of long-range dispersal for the biogeography of seaweeds. Helgol Meeresun. 1987;41:261–72.

Verbruggen H, Tyberghein L, Belton GS, Mineur F, Jueterbock A, Hoarau G, Gurgel CFD, De Clerk O. Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. PLoS One. 2013;8:e68337.

Wallentinus I. Alien species alert: *Undaria pinnatifida* (Wakame or japanese kelp). ICES Cooperation Research Report No. 283. Copenhagen: International Council for the Exploration of the Sea; 2007.

Watanabe S, Scheibling RE, Metaxas A. Contrasting patterns of spread in interacting invasive species: Membranipora membranacea and Codium fragile off Nova Scotia. Biol Invasions. 2010;12:2329–342.

Waters JM. Marine biogeographical disjunction in temperate Australia: historical landbridge, contemporary currents, or both? Divers Distrib. 2008;14:692–700.

Waters JM, Fraser CI, Hewitt GM. Founder takes all: density-dependent processes structure biodiversity. Trends Ecol Evol. 2013;28:78–85.

Wernberg T, Kendrick GA, Phillips JC. Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. Divers Distrib. 2003;9:427–41.

Wernberg T, Thomsen MS, Staehr PA, Pedersen MF. Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark). Helgol Mar Res. 2004;58:154–61.

Wernberg T, Russell BD, Thomsen MS, Gurgel CFD, Bradshaw CJA, Poloczanska ES, Connell SD. Seaweed communities in retreat from ocean warming. Curr Biol. 2011a;21:1828–32.

Wernberg T, Russell BDBD, Moore PJPJ, Ling SD, Smale DA, Campbell A, Coleman MA, Steinberg PD, Kendrick GA, Connell SD. Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. J Exp Mar Bio Ecol. 2011b;400:7–16.

Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettgnies T, Bennett S, Rousseaux CS. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Change. 2013a;3:78–82.

Wernberg T, Thomsen MS, Connell SD, Russell BD, Waters JM, Zuccarello GC, Kraft GT, Sanderson C, West JA, Gurgel CFD. The footprint of continental-scale ocean currents on the biogeography of seaweeds. PLoS One. 2013b;8(11):e80186.

Wiens JJ. The niche, biogeography and species interactions. Phil Trans R Soc B. 2011;366:2336–50.

Wiens JJ, Donoghue MJ. Historical biogeography, ecology and species richness. Trends Ecol Evol. 2005;19(12):639–44.

Williams SL, Smith JE. A global review of the distribution, taxonomy, and impacts of introduced seaweeds. Ann Rev Ecol Evol Syst. 2007;38:327–59.

Wootton JT. Local interactions predict large-scale pattern in empirically derived cellular automata. Nature. 2001;413:841–4.

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R. Impacts of biodiversity loss on ocean ecosystem services. Science. 2006;314:787–90.

York KL, Blacket MJ, Appleton BR. The Bassian Isthmus and the major ocean currents of southeast Australia influence the phylogeography and population structure of a southern Australian intertidal barnacle *Catomerus polymerus* (Darwin). Mol Ecol. 2008;17:1948–61.

Zachos JC, Dickens GR, Zeebe RE. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature. 2008;451:279–83.