Chapter 22

Centrostephanus rodgersii and *Centrostephanus tenuispinus*

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1 Biogeography

In subtropical and temperate regions, sea urchins in the family Diadematidae, are represented by the genus *Centrostephanus* with two species in Australasia, *Centrostephanus rodgersii* (A. AGASSIZ, 1863) and *Centrostephanus tenuispinus* (H.L. CLARK, 1914) (Fig. 22.1). *C. rodgersii* occurs on the east coast of Australia and across to New Zealand. It has been the focus of research as an ecologically important species that forms barrens habitat. Less is known about *C. tenuispinus*, which occurs along the coast of Western Australia. It is also capable of forming barrens. As typical of diadematids, these *Centrostephanus* species are large and are reported to have a similar maximum test diameter of 133 and 120 mm, respectively (Ling, 2013; Thilakarantha, 2017) and are characterized by long spines. *C. rodgersii* is black, while *C. tenuispinus* ranges in color from reddish brown to green, slate gray, and black. *C. tenuispinus* is distinguished from *C. rodgersii* in having a prominent tubercle on each genital plate and in having thinner primary spines.

C. rodgersii and *C. tenuispinus* have distinct ranges in eastern and western Australia, respectively (Fig. 22.2). Like other echinoderm sister taxa in southern Australia, these species may have been separated by formation of the Bass Strait land bridge and changes in oceanographic flow through interglacial periods (Byrne and O'Hara, 2017). Recent climate-related changes to ocean circulation may facilitate contact between them.

1.1 *C. rodgersii*: A range extending species

C. rodgersii has increased its range southwards in southeast Australia and across the Tasman Sea to northeast New Zealand (Figs. 22.2 and 22.3). Until the 1960s, the southern limit of *C. rodgersii* in Australia was on islands in eastern Bass Strait and northeastern Tasmania (Dartnall, 1980), but this species is now prominent in eastern Tasmania and extends around to the southwest (Fig. 22.2). The extension of *C. rodgersii*, modeled to approximate 160 km per decade over the past 40 years (Ling et al., 2009a), is attributed to the transport of larvae in the East Australian current (EAC). This major boundary current has increased its southerly flow over the last 60 years, driven by climate change (Ridgway, 2007). This potential source of *C. rodgersii* was suggested by Dartnall (1980) on discovery of *C. rodgersii* in Tasmania. The strengthened flow of the EAC, particularly in winter (Hobday and Lough, 2011), when the larvae of *C. rodgersii* are in the plankton (Byrne et al., 1998), facilitated expansion of this species from New South Wales to Tasmania, a distance of ∼1500 km.

The hypothesis of larval driven range extension is supported by the strong genetic connectivity between *C. rodgersii* populations in New South Wales and Tasmania (Banks et al., 2007, 2010). The age structure of *C. rodgersii* indicates that the Tasmanian populations are the result of multiple recruitment events with younger populations in more southern areas (Ling, 2013).

In Australia, *C. rodgersii* has a broad distribution from Queensland to Tasmania over 17° latitude (Figs. 22.2 and 22.3). Isolated individuals have been identified from southern Queensland and southwestern Tasmania. *C. rodgersii* also occurs on the islands of the Tasman Sea including Norfolk Island, Lord Howe Island, the Kermadec Islands and on the northeast
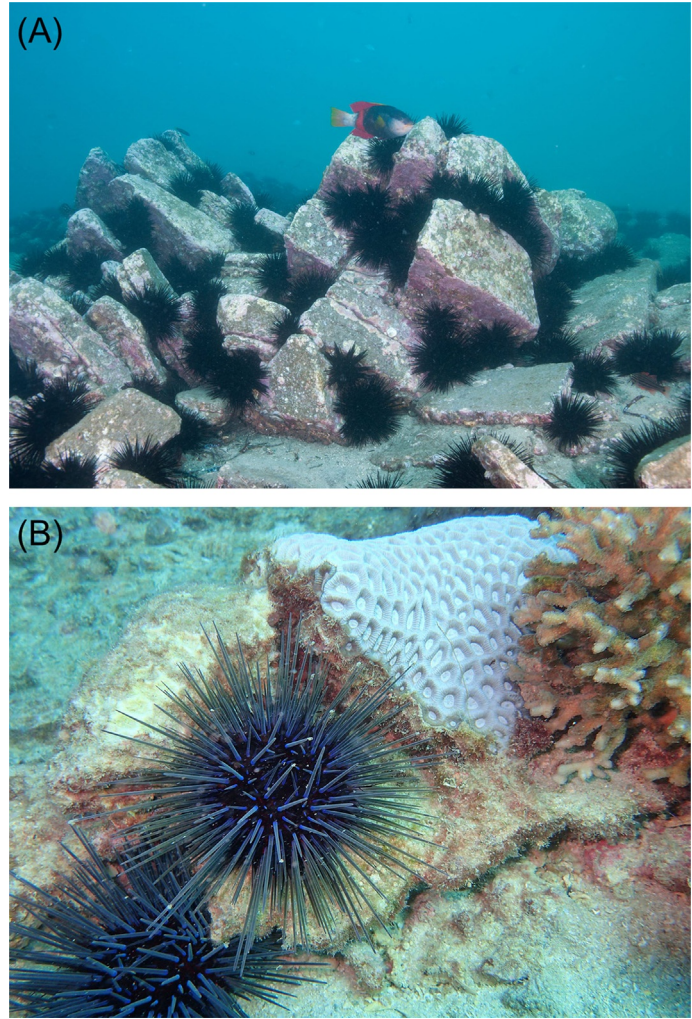
coast of New Zealand. Along the coast of Australia, its main distribution is from the mid-coast of New South Wales to southeast Tasmania. In the north, *C. rodgersii* occurs with scleractinian corals and other tropical species in the Solitary Islands (Fig. 22.3), a tropical-temperate transition zone (sea surface temperatures—SST range 18–27°C). Southwards, *C. rodgersii* occurs with temperate rocky reef species (Figs. 22.1A and 22.2) and cooler temperatures (e.g., Tasmania, SST range 11.8–17.4°C). At its southern limit, *C. rodgersii* is found with cold-water algae such as *Macrocystis pyrifera* and *Durvillaea potatorum*.

In New South Wales, *C. rodgersii* is most abundant between 2 and 20 m depth (Andrew and Underwood, 1989; Underwood et al., 1991; Andrew and O'Neill, 2000; Curley et al., 2002). At depths of ca. 20 m (depending on wave exposure), *C. rodgersii* becomes less dense and individuals are found in crevices among sponges and other sessile animals. In southern New South Wales, occasional barrens are found at 30 m (Marzinelli et al., 2015).

In Tasmania, *C. rodgersii* is found in deeper water (10–25 m) along the coast (Ling and Johnson, 2009, 2012; Ling et al., 2009a, 2015). Offshore, *C. rodgersii* is found at high densities on low-relief granite outcrops (50 m) in the Star Bank, Bass Strait in association with sea whips and sponges (Beaman et al., 2005). Recent surveys revealed extensive *C. rodgersii* barrens at 16–58 m depth off Tasmania (Perkins et al., 2015; Ling et al., 2016). These are the deepest recorded *C. rodgersii* barrens. It seems that *C. rodgersii* form barrens in deeper water in Tasmania than in New South Wales.

In New Zealand, *C. rodgersii* was noted in the Poor Knights Islands in the late 1960s (M. Barker personal communication) and subsequently noted further south in offshore islands including the Mokohinau Islands (Choat and Schiel, 1982; Cole et al., 1992; Pecorino et al., 2012). This species also occurs the northeast coast of New Zealand (Fig. 22.3). Changes in the flow of the eastern branch of the EAC, the Tasman Front, may have influenced the expansion of this species in New Zealand through transport of larvae from New South Wales. Strong genetic connectivity between Australian and New Zealand populations of *C. rodgersii* supports this hypothesis (Banks et al., 2007). Thus, for both areas where *C. rodgersii* has extended its range, colonization appears to map to the pattern of the flow of the EAC and associated eddies (Banks et al., 2007).
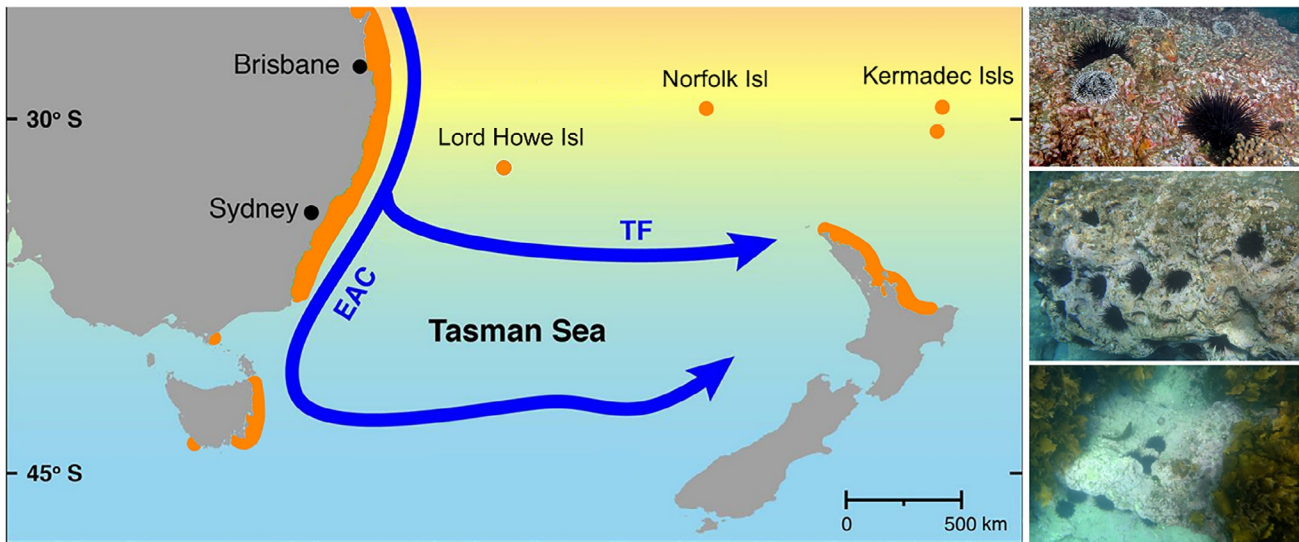
FIG. 22.3 Distribution of *Centrostephanus rodgersii* in Australia and New Zealand and oceanic currents in the region, the East Australia Current (EAC) and its branch the Tasman Front (TF), that have facilitated range extension poleward to Tasmania and across the Tasman Sea to New Zealand. *Top photo* shows *C. rodgersii* with corals and *Tripneustes kermadecensis* in the Solitary Islands, a tropical-temperate transition zone. *Middle and bottom* photos show *C. rodgersii* in home scars during the day and in fringe habitat. *Top: Photo S. Smith; Middle and bottom: Photos N. Soars.*

The range extension of *C. rodgersii*, along with other co-occurring range shifting species is one of the most prominent examples of alteration of marine ecosystems due to climate change (Johnson et al., 2011; Przeslawski et al., 2012). The ecological studies of *C. rodgersii* in its invasive range have resulted in major advances in understanding the biology and ecology of this species.

1.2   *C. tenuispinus*

C. tenuispinus occurs mainly in western and southwestern Australia where it has a broad subtropical to temperate range and is found to 104 m depth. Its main distribution along the west coast is from the Houtman Abrolhos Islands to Albany, over 6° latitude (Fig. 22.2). *C. tenuispinus* occurs with tropical corals in the north and a cold temperate community in the south. The region is strongly influenced by the Leeuwin Current, which like the EAC, is a boundary current that carries warm tropical water poleward. *C. tenuispinus* also has a broad longitudinal extent along the south coast to South Australia and western Victoria (Fig. 22.2). Following the 2011 marine heat wave off Western Australia, and associated increased poleward flow of the Leeuwin Current, the abundance of *C. tenuispinus* increased in southern areas, potentially due to poleward larval dispersal (Smale et al., 2017). Many parallels are seen between this species and *C. rodgersii*. Despite its ecological similarity to *C. rodgersii*, it is interesting to note that *C. tenuispinus* does not form extensive barres. It is not known if this is due to different characteristics of the two species or of their environment.

2   Ecological impacts

The creation, persistence, and demise of sea urchin barrens habitat is arguably the most significant ecological dynamic on temperate rocky reefs, with barrens considered to be an alternative stable states of collapsed kelp ecosystems (Filbee-Dexter and Scheibling, 2014). As it is the case elsewhere (Lawrence, 1975; Filbee-Dexter and Scheibling, 2014; Scheibling, Chapter 31; Rogers-Bennett, Chapter 32), barrens created by C. *rodgersii* are dominated by a cover of crustose coralline algae (CCA) and a surface devoid of large brown algae.

C. rodgersii barrens have high though variable densities of sea urchins and a different assemblage of algae, invertebrates, and fish from those in neighboring areas of reef with a large biomass of algae (Andrew and Jones, 1990; Jones and Andrew, 1990; Underwood et al., 1991; Gillanders and Kingsford, 1998; Curley et al., 2002; Ling, 2008; Ling et al., 2009b). Densities of *C. rodgersii* can be very high in barrens ($>$60 inds m^{-2}), but the average density is much lower ($<$6 inds m^{-2}) (Andrew and Underwood, 1989; Connell and Irving, 2008; Ling and Johnson, 2009). Interestingly, the biomass density of *C. rodgersii* (g m^{-2}) does not differ between macroalgal and barrens habitat (Ling and Johnson, 2009).

Due to their crevice dwelling and nocturnal behavior (see below), the mechanism of barrens formation by *Centrostephanus* species differs from that by *Strongylocentrotus* species. *Centrostephanus* barrens are created "from within" in association with daytime occupation of shelters (Andrew, 1994) rather than by invasion of feeding fronts as seen in *Strongylocentrotus*, which also form day–night active aggregations (see Steneck, Chapter 15; Scheibling, Chapter 31; Rogers-Bennett, Chapter 32). In addition, *C. rodgersii* does not climb up large macroalgal plants and does not respond to olfactory cues from feeding conspecifics as *Strongylocentrotus* species do (Flukes et al., 2012).

For *C. rodgersii* each small or incipient barrens patch is an isolated system centered around shelter and is relatively independent of other patches (Andrew, 1994; Flukes et al., 2012). In Tasmania, these patches can coalesce to increase the extent of barrens (Flukes et al., 2012). Thus, within a reef, the areal extent and arrangement of barrens habitat is influenced by the biology and feeding dynamics of *C. rodgersii*. Areas of barrens habitat vary from small "halos" within the foraging range of one or several sea urchins to many hectares with high densities of sea urchins (Andrew, 1993, 1994; Ling and Johnson, 2012). The affinity for shelter and nocturnal foraging underlies the mechanism of barrens formation by *C. rodgersii*.

Where population densities are high and crevices are limiting, *C. rodgersii* occurs in aggregations of individuals during the day with closely interwoven spines. Pearse and Arch (1969) suggested that similar aggregations of *Diadema savignyi* function as protective social units. In pavement habitat with minimal shelter, these aggregations in shallow grooves and gutters are conspicuous during the day (Andrew and O'Neill, 2000; Flukes et al., 2012).

C. tenuispinus also forms barrens, but to a much smaller extent than *C. rodgersii*. In a high latitude coral reef off Western Australia, *C. tenuispinus* maintains sea urchin-coral barrens, facilitating the extension of tropical corals by preventing overgrowth of algae (Fig. 22.1) (Thomson and Frisch, 2010; Thilakarantha, 2017). For *C. tenuispinus,* the average density in barrens habitat is 3–5 inds m^{-2} (Thomson and Frisch, 2010; Thilakarantha, 2017).

2.1   Habitat structure and associated species

Investigation of the ecological dynamics of *C. rodgersii* in New South Wales has largely focused on comparison of kelp fringe and barrens habitats. The kelp fringe or fringe habitat is generally found in the shallow subtidal adjacent to the shoreline and is dominated by *Phyllospora comosa* and *Sargassum* spp. (Underwood et al., 1991). An analogous habitat in Tasmania is dominated by large brown algae (Stuart-Smith et al., 2010). In the fringe habitat, *C. rodgersii* may be

abundant in crevices and depressions and maintain patches of adjacent substrate free of algae. Wave turbulence and the physical disturbance of macroalgal movement can reduce foraging activity by *C. rodgersii* (Ling and Johnson, 2009), as also noted for *C. coronatus* in California (Lissner, 1983). In slightly deeper water the algal fringe can abut CCA-dominated barrens. The location and depth of the transition between fringing algae and barrens habitats appear to be related to wave exposure and the degree of topographic complexity of the reef and therefore exposure of sea urchins to the sweeping action of large brown algae. Below this transition reefs are typically a mosaic of brown macroalgal and barrens habitats (Andrew and Underwood, 1993). On reefs where there are few sea urchins (e.g., harbors, estuaries) beds of the kelp *Ecklonia radiata* and other macroalgae dominate (Underwood et al., 1991). In areas where *C. rodgersii* are numerous and the physical environment allows them to graze away from shelter, the barrens habitat is dominant.

In New South Wales spatial patterns in the mosaic of algal and barrens habitats appear relatively stable over years and even decades (Underwood et al., 1991; Andrew, 1994; Kingsford and Carlson, 2010). Along 7° latitude in central and southern New South Wales, ca. 50% of near-shore reef (>150 m from shore) is *C. rodgersii* barrens habitat (Andrew and O'Neill, 2000). Reefs in eastern Tasmania are now showing signs of developing barrens that are becoming extensive with a 3%–15% increase in the barrens cover equating to a ∼10.5% increase per annum over the last 15 years (Ling and Keane, 2018). Toward the northern range of *C. rodgersii*, the incidence of barrens declines (Andrew and O'Neill, 2000; Connell and Irving, 2008). In southern New South Wales kelp habitat, *C. rodgersii* occurs in greater abundance in association with *Phyllospora* than *Ecklonia* kelp beds (Marzinelli et al., 2014). In New Zealand, *C. rodgersii* occurs as scattered individuals and barrens have not been observed (Choat and Schiel, 1982; Schiel et al., 1986; Cole et al., 1992).

The barrens habitat is structurally less complex. With respect to benthic invertebrates, this habitat is taxonomically much less diverse than alternate habitats dominated by large brown algae (Underwood et al., 1991; Ling, 2008; Ling et al., 2009b). In Tasmania, the transition from macroalgal-dominated reefs to patches of barrens has a strong negative effect on biodiversity resulting in the disappearance of ca. 370 species of algae and ca.150 species of invertebrates (Ling, 2008). The biggest change for the invertebrates was for small crustaceans (amphipods and isopods) and polychaetes. A suite of small cryptic fishes are also absent from barrens habitat in Tasmania compared with macroalgal habitat (Ling, 2008).

Long-term studies (20–30 year) of fish diversity and abundance in barrens and macroalgal habitats in New South Wales provide insights into the ecology of these habitats that have been stable for decades (Kingsford and Carlson, 2010). There are distinct differences in the fishes associated with the two habitats (Holbrook et al., 1994; Curley et al., 2002; Kingsford and Carlson, 2010). Species such as the large wrasse *Ophthalmolepis lineolatus* are present in both habitats whereas habitat specialists such as the herbivorous fish *Odax cyanomelas* and the serranid *Hypoplectrodes maccullochi* are only present in macroalgal or barrens habitats, respectively (Andrew and Jones, 1990; Kingsford and Carlson, 2010). Overall there is a greater species diversity of fishes in barrens habitat compared with kelp habitat and many species are also most abundant in barrens (Curley et al., 2002). Barrens habitat provide the key spawning sites for the pomacentrid *Parma microlepis*. This species uses the same nesting sites in barrens habitat over years (Holbrook et al., 1994; Tzioumis and Kingsford, 1995, 1999; M. Kingsford, personal communication).

C. tenuispinus facilitates tropical coral reef habitat and associated biota by preventing overgrowth of algae (Thomson and Frisch, 2010; Thilakarathna, 2017). A similar facilitation of coral growth is reported for the interaction between *C. rodgersii* and a poleward range extending subtropical hermatypic coral (Ling et al., 2018).

Centrostephanus species create habitat for a suite of small benthic and mobile invertebrates including amphipods and chitons, and fish (Hartney and Grorud, 2002; Griffiths, 2003; Worthington and Blount, 2003) and its grazing is necessary for the presence of limpets (*Patelloida* and *Cellana* spp.) (Fletcher, 1987). The ophiuroid *Clarkoma pulchra,* which is similar in color to *C. rodgersii*, lives among the spines and under the spine canopy during the day but at night the two species separate (M. Byrne, personal observation).

2.2   *Centrostephanus* behavior in determining habitat structure

As characteristic of diadematids (Ogden, 1973; Kennedy and Pearse, 1975; Nelson and Vance, 1979; Lisser, 1980, 1983; Muthiga, Chapter 23), *C. rodgersii* is light sensitive, becoming active after dusk and foraging through the night returning to crevices by dawn (Jones and Andrew, 1990; Flukes et al., 2012). This innate behavior is also evident in deeper water *C.rodgersii* barrens (Ling et al., 2016). Individual *C. rodgersii* can forage up to 5 m (mean 1–3 m) from their daytime crevices (Jones and Andrew, 1990). Peaks in the velocity of movement occur at the end of the night when dawn appears to trigger a burst of rapid and directional movement (Flukes et al., 2012). *Centrostephanus* species exhibit strong site fidelity and may return to the same crevice (Nelson and Vance, 1979; Flukes et al., 2012). As a result of their feeding forays and the limited distance traveled, *C. rodgersii* creates halos of barrens devoid of macroalgae and sharp boundaries between barrens and macroalgal habitat (Andrew, 1994; Ling and Johnson, 2012).

The substratum beneath *C. rodgersii* is often grazed to the underlying rock. Depending on the rock type, the home scar can be a distinct pit created by the eroding activity of sea urchin teeth (Fig. 22.3). Bioerosion is an important ecological function of *C. rodgersii* and diadematids in general (Muthiga, Chapter 23). Grazing by *C. rodgersii* in barrens results in an abundance of small CCA covered rock pellets in the gut (M. Byrne, personal observation). This erosive activity has not been quantified. *C. tenuispinus* is estimated to have bioerosion rates of over 1000 g of $CaCO_3$ m^{-2} year m^{-1} in barrens habitat (Thilakarantha, 2017).

The strong crepuscular activity of *C. rodgersii* contributes to the dawn and dusk biological chorus in ambient noise recordings of the habitat (Soars et al., 2016), similar to other sea urchins (Radford et al., 2008). Comparisons of the sounds produced by *C. rodgersii* in captivity and ambient reef sound in barrens with dense populations of this species revealed that the chorus peaks with an intensity (2–8 kHz) corresponding with the sounds produced by *C. rodgersii* (Soars, 2015; Soars et al., 2016). There is an emerging appreciation of the ecological importance of the marine soundscape and it is likely that dense sea urchin barrens will have an important, yet not understood impact in this regard.

2.3   Barrens in New South Wales and Tasmania

Many lines of evidence support the conclusion that *C. rodgersii* causes and maintains barrens habitat. In response to *C. rodgersii* removal/caging experiments and after mass mortality of this species, filamentous and foliose algae increase often followed by the establishment of large brown algae (Fletcher, 1987; Andrew and Underwood, 1989, 1993; Andrew, 1991; Andrew et al., 1998; Hill et al., 2003; Ling, 2008). On the other hand, experimental augmentation of shelter in kelp habitat results in colonization by *C. rodgersii* followed by creation of barrens (Andrew, 1993). The remarkable transformation of Tasmanian reefs following the appearance of *C. rodgersii* is testament to the barrens forming powers of this species.

In Tasmania, the term "incipient barrens" is used to describe newly created patches of barrens, differentiating them from the much larger "barrens habitat" (Johnson et al., 2005). Such small areas are centered on a few sea urchins and are viewed as precursors to the development of more extensive areas of barrens. Similar small patches of barrens also occur in New South Wales, mostly in habitats defined by the abundance of large brown algae (Underwood et al., 1991), but do not appear to be transient patches that will eventually coalesce into extensive barrens habitat. In New South Wales, these are not considered to be transient states in the evolution of large barrens areas.

The differences between *C. rodgersii* in New South Wales and Tasmania offer insights into the dynamics of barrens creation. It may be argued that the threshold for the switch to a barrens dominated reef has long since occurred in New South Wales and that current patterns are more stable and constrained by the availability of shelter and that their sizes are highly correlated with the number of sea urchins (Andrew and Underwood, 1992; Andrew, 1993). Andrew (1993) moved large boulders into a kelp forest to create shelters. This was followed by colonization by *C. rodgersii* and creation of new barrens patches, providing evidence that the availability of shelter limits the extent of barrens habitat.

The importance of shelter in barrens formation is likely also to be true for a given patch in Tasmania. However, on reefs newly colonized by *C. rodgersii*, suitable shelters do not appear to be saturated and larval supply and/or recruitment processes will play a larger role. Over time, shelters will fill with sea urchin recruits, patches will coalesce, and new barrens habitat will be created (Flukes et al., 2012; Ling and Johnson, 2012).

2.4   *Centrostephanus* barrens as an alternative stable state

Once created, areas of *C. rodgersii* barrens can persist for decades requiring relatively few sea urchins to maintain them. Densities within patches of barrens can be reduced by more than a half and still remain as barrens (Andrew and Underwood, 1989; Hill et al., 2003). Although there are subtle changes in the abundance of limpets, and filamentous and algal turf on partial removal of *C. rodgersii* (Fletcher, 1987; Andrew and Underwood, 1989, 1993), brown algae remain vulnerable to herbivory and are unable to recolonize in the presence of *C. rodgersii*. This important finding suggests that more sea urchins are needed to create large barrens than maintain them, making barrens resistant to change.

As Ling et al. (2009b, 2015) elegantly describe, this is a classic example of alternative stable states and hysteresis in an ecological system (Filbee-Dexter and Scheibling, 2014; Hughes et al., 2017). The barrens habitat is resilient in the face of perturbations—in this case declining sea urchin densities. This feedback loop will likely be maintained as declining sea urchin densities make more shelter available facilitating recruitment to replenish *C. rodgersii* populations. The "reverse-shift" from barrens to kelp habitat is clearly nonlinearly related to sea urchin density. As a result, there appears to be thresholds in the system involved in the shift back to the kelp habitat state. The dynamics of the transition between the alternative seaweed dominated and sea urchin barrens state is unclear and influenced by many processes operating across spatial and temporal scales (Ling, 2013). These are likely to depend on disturbance regime, processes affecting dispersal, the vagaries of larval supply and recruitment, habitat preferences, storm events, predation, and other interacting factors.

2.5   Food and feeding ecology

C. rodgersii and *C. tenuispinus* are omnivorous, consuming a wide range of algal species from CCA to macroalgae as well as consuming invertebrates including gastropods, bryozoans, polychaetes, and sponges (Jones and Andrew, 1990; Andrew, 1993, 1994; Hill et al., 2003; Vanderklift et al., 2006; Strain and Johnson, 2009; Thilakarantha, 2017). The high trophic levels consumed by *C. tenuispinus* is evident in their stable isotope signatures (Vanderklift et al., 2006; Thilakarantha, 2017).

Field observations show the generalist grazing by *C. rodgersii*, where all species large brown algae are removed (Andrew and Underwood, 1992; Andrew, 1994). In contrast to *Strongylocentrotus* species, *C. rodgersii* is tolerant of high concentrations of phlorotannins in brown algae (Steinberg and van Altena, 1992).

3   Population regulation

3.1   Recruitment

Recruitment in *C. rodgersii* appears sporadic and correlated with larval supply. Poor recruitment over four consecutive years in two *C. rodgersii* populations was associated with lack of small individuals, whereas two other populations exhibited recruitment (Andrew and Underwood, 1989). At sites off Sydney, *C. rodgersii* with a test diameter <40mm were consistently observed during the mid-1980s (Andrew and Underwood, 1989) but were absent in 1997 (N.L. Andrew, personal observation). In New South Wales, most populations are dominated by larger and older sea urchins. Across 40 sites, the modal test diameter ranges between 70 and 100mm (Andrew and Underwood, 1989; Andrew and O'Neill, 2000; Blount, 2004).

C. tenuispinus also has a unimodal population structure with a mean test diameter of 66 and 100mm at barrens and macroalgal sites, respectively (Thilakarantha, 2017). The requirement that small individuals find larger crevices as they grow may lead to a demographic bottleneck and competition with adults. Care is required in interpreting population structure, however, as small individuals are cryptic, and may be underrepresented in observed size-frequency distributions.

Small *C. rodgersii* are found almost exclusively under small boulders and in crevices (Andrew and Underwood, 1989; Ling and Johnson, 2012). This can be in the presence or absence of adults (Andrew, 1991; Johnson et al., 2005). They are often found behind adults in recesses of crevices. In manipulative experiments, when adults are removed, recruitment as seen in the presence of new small individuals increases with decreasing adult density (Blount, 2004). Complete experimental removal of large individuals results in recruitment that is 900% higher than in controls (Blount, 2004), although this did not occur after complete removal of the population due to a storm (see below). Under experimental conditions, *C. rodgersii* recruits to boulders irrespective of habitat, whether these boulders are covered by kelp or whether conspecific adults are present (Andrew, 1993). There is no evidence that there is an association between the juveniles and the spine canopy of adults as seen for *Strongylocentrotus* species (Rodgers-Bennett, Chapter 32). Although small individuals appear scarce in *C. rodgersii* populations, once they grow beyond the size constraints of their recruitment habitat they grow quickly (Ebert, 1982; Andrew, 1991; Blount, 2004; Pecorino et al., 2012).

3.2   Predation

The nocturnal foraging habits of *Centrostephanus* species are suggested to be a strategy to avoid day active predatory fishes such as the wrasses *Achoerodus viridis* and *Notolabrus tetricus* (Nelson and Vance, 1979; Andrew and Underwood, 1989; Andrew, 1993; Gillanders, 1995; Ling et al., 2009b; Ling and Johnson, 2012). Indeed, availability of daytime shelter for *C. rodgersii* is important for survival from predators in protected areas compared with fished reefs (Ling and Johnson, 2012). Higher predation of *C. tenuispinus* also occurs in protected areas where the wrasse *Achoerodus gouldii* preys on this species (Cook and Vanderklift, 2011).

C. rodgersii also succumbs to nocturnally active predators, including the Port Jackson shark, *Heterodontus portusjacksoni* and the rock lobster, *Jasus edwardsii* (McLaughlin and Ó Gower, 1971; Ling et al., 2009b; Ling and Johnson, 2012). The eastern rock lobster, *Sagmariasus verreauxi*, is likely to feed on sea urchins but the feeding ecology of this species is poorly described. Numerous species of smaller predators including wrasses, octopus, and a suite of microcarnivores co-occur with *C. rodgersii* and are potential predators on small adult and juvenile *C. rodgersii*, but nothing is known of their impact. The western rock lobster, *Panulirus cygnus*, is not known to prey on *C. tenuispinus*. Its preferred prey species are crustaceans (Dumas et al., 2013).

Both rock lobsters and wrasses, including *A. viridis*, the largest of the near shore fishes in New South Wales (maximum length >1 m), feed by flipping *C. rodgersii*, exposing the peristome to attack. Rock lobsters are nocturnal foragers and

therefore have access to a wider size range of sea urchins than do the day-active fishes. Large rock lobsters (≥ 140 mm carapace length, ca. 1.4 kg weight) are the most important predator of *C. rodgersii* in Tasmania and the only predators capable of preying on the largest sea urchins (Ling et al., 2009b; Ling and Johnson, 2012). Thus, predation success in this species pairing is size-specific. The day-active predator *N. tetricus* is only able to exploit small (test diameter ≤ 60 mm) sea urchins not protected by shelter (Ling et al., 2009b).

Clearly, rock lobsters and wrasses are capable of consuming *C. rodgersii* and only the largest predators can consume large sea urchins. However, this natural history alone is not definitive evidence that predators regulate the abundance of this species. Predatory control of sea urchin populations is a recurrent theme sea urchin ecology (Elner and Vadas, 1990; Scheibling, Chapter 31) and has been offered as a hypothesis to explain high densities of *C. rodgersii* (e.g., Andrew, 1993; Wright et al., 2005; Ling et al., 2009b; Ling and Johnson, 2012).

It could be argued that present-day populations of predators in New South Wales, particularly the eastern rock lobster, *S. verreauxi*, wrasse *A. viridis*, and shark *H. portusjacksoni*, are at low levels and that, historically, they played a greater role in limiting sea urchin numbers. If this is correct, the stability and high occurrence of barrens habitat is a new baseline that does not represent historical patterns in the ecology of New South Wales reefs.

A. viridis has been partially protected from fishing in New South Wales since 1969. Since the late 1970s, it has been-protected from all fishing except recreational line fishing. *H. portusjacksoni* is not protected but, although taken as a by-catch in prawn trawl fisheries, it is not targeted by commercial or recreational fishers on rocky reefs.

S. verreauxi occurs on rocky reefs in southern New South Wales and has been heavily fished since at least the 1960s. The status of the stock in New South Wales is fully fished with a recent annual catch (2009–2016) being 122–160 tons (NewSouth Wales Department of Primary Industries, 2017). However, this lobster fishery occurs in water deeper than the depth range of *C. rodgersii*.

In marine reserves in New South Wales, *S. verreauxi* reach very large sizes (M. Byrne, personal observation), but the interaction between rock lobsters and *C. rodgersii* in these reserves has not been investigated. In New South Wales, *C. rodgersii* are often found in the open during the day (see Byrne and Andrew, 2013). This could suggest that *C. rodgersii* has been released from predation but there is no evidence that the densities of predators differ along the coast (Gillanders and Kingsford, 1998). Credible experimental tests of the regulation of *C. rodgersii* by *S. verreauxi* would require monitoring populations of both species in and outside marine reserves. A politicized policy-making environment in New South Wales means that the hypothesis of population regulation of *C. rodgersii* by predators will remain untested, at least in the near future.

In Tasmania, evidence in support of the predator control hypothesis comes from experimental work in marine reserves (Ling et al., 2009b; Ling and Johnson, 2012). Marine reserves have more and larger rock lobsters and other large predators such as the wrasse *N. tetricus* (Edgar and Barrett, 1999; Ling et al., 2009b; Ling and Johnson, 2012). They would be predicted to have fewer sea urchins and a reduced frequency and spatial extent of barrens habitat. Surveillance of tethered *C. rodgersii* revealed that predation pressure is much higher inside than outside marine reserves due to abundance of large lobsters (Ling et al., 2009b; Ling and Johnson, 2012). This is similar to that observed in marine reserves for *C. tenuispinus* in Western Australia where the predators are fishes (Cook and Vanderklift, 2011).

The evolving ecosystem shift from macroalgal to barrens habitat in eastern Tasmania is occurring on reefs where rock lobster populations are at very low levels (<10% of unfished biomass) (Ling and Johnson, 2012). Based on low predation rates observed where predators are heavily fished (i.e., outside marine reserves), Ling and Johnson (2012) infer that, subject to larval supply from a changed EAC, barrens habitat will likely develop on reefs wherever there is suitable shelter. Based on the distribution of reef types, *C. rodgersii* barrens could ultimately account for 50% of rocky reef in eastern Tasmania (see Ling, 2013), as in New South Wales (Andrew and O'Neill, 2000).

At the broad geographic scale of eastern Tasmania, the resilience of system will increase if a proportion of reefs are within marine reserves where large predatory lobsters and fishes are abundant. Grazing will be restricted to more spatially complex reef habitats, thus minimizing the risk, extent, persistence, and types of habitats on which widespread barrens may manifest (Ling and Johnson, 2012).

3.3   Disease

C. rodgersii occasionally succumbs to an epithelial infection where the surface turns white. This quickly spreads around the sea urchin test, which dies within 5 days (B. Mos, personal communication). The disease is contagious and can infect and kill other sea urchins in captivity. Parasitic nematodes are common in the gonads of *C. coronatus* where they interfere with gametogenesis or partially castrate the host (Pearse and Timm, 1971). They are not reported for *C. rodgersii*.

3.4 Competition

Intraspecific competition can bring about changes in the growth, reproduction, and morphometry of *C. rodgersii* (Blount, 2004; Ling and Johnson, 2009; Strain and Johnson, 2009). Experiments and in situ observations indicate great plasticity in growth and form in different habitat types (Ling and Johnson, 2009). Doubling conspecific densities in enclosures reduces gonad weight (Strain and Johnson, 2009) while decreasing density increases gonad weight (Blount, 2004).

The ecological overlap and potential competitive relationship between *C. rodgersii* and the black lip abalone, *Haliotis rubra* has prompted studies into their ecological interactions (Shepherd, 1973; Andrew and Underwood, 1989; Andrew, 1993; Andrew et al., 1998; Strain and Johnson, 2009, 2013; Strain et al., 2009). With its ability to influence the availability of food and shelter, *C. rodgersii* has a negative impact on abalone populations. *Haliotis rubra* are rare in *C. rodgersii* barrens (Shepherd, 1973; Andrew and Underwood, 1992; Andrew et al., 1998).

In New South Wales, *C. rodgersii* and *H. rubra* co-occur in fringe habitats, but densities of the two species are negatively correlated at a spatial scale of $10\,m^2$ and also at smaller, nearest-neighbor scales (Andrew and Underwood, 1992). The interaction between *C. rodgersii* and *H. rubra* in large barrens results in direct competitive exclusion of abalone. In experiments done in New South Wales and Tasmania, removal of *C. rodgersii* from patches of barrens resulted in an increase in the number of abalone (Andrew et al., 1998; Strain and Johnson, 2013). Conversely, the introduction of *C. rodgersii* into intact algal beds causes an avoidance-like behavioral change in *H. rubra* (Strain et al., 2009). The addition of *C. rodgersii* causes abalone to flee and seek shelter in cryptic habitats with potential negative effects on their growth and survival (Strain et al., 2009).

In manipulative experiments, *H. rubra* grew more slowly and had increased mortality in the presence of *C. rodgersii* compared with controls without sea urchins (Strain and Johnson, 2009). This was attributed to the sea urchin being a superior competitor by being a generalist herbivore while the abalone required specific algal food (Strain and Johnson, 2009). In enclosures with *C. rodgersii*, abalone showed reduced total and dry weights of stomach contents and increased mortality compared with controls (Strain and Johnson, 2009). Although strong evidence indicates that *C. rodgersii* has a negative impact on the dispersion and abundance of *H. rubra*, none indicates that the reverse is true. Increased density of *H. rubra* had no detectable effect on *C. rodgersii* (Strain and Johnson, 2009).

Competition for food may cause large abalone to move away from barrens, but shelter may be more important earlier in life. Andrew's (1993) results are consistent with a size-specific relationship between *C. rodgersii* and *H. rubra*. When shelter was provided in patches of barrens, densities of abalone were initially higher in the barrens than in *Ecklonia* forests but after 2.5 years, few abalone remained in the barrens. Grazing by *C. rodgersii* may also cause incidental mortality of juvenile abalone (McShane, 1991) and loss to predation by fishes and other predators due to the reduced structural complexity of barrens.

C. rodgersii co-occurs with *Heliocidaris erythrogramma* (Keesing, Chapter 30) and there is a negative association between the two species (Strain and Johnson, 2013). Removal of *C. rodgersii* from patches of barrens resulted in an increase in the density of *H. erythrogramma* (Strain and Johnson, 2013). *H. erythrogramma* forms extensive barrens in sheltered environments, but on open coasts where *C. rodgersii* barrens are prevalent, *H. erythrogramma* densities are lower and they appear to depend on drift algae (Ling et al., 2012). In New South Wales, *C. rodgersii* also co-occurs with the red urchin, *Heliocidaris tuberculata* and the two species are similar in size. Over the last 30 years the abundance of *H. tuberculata* has decreased due to overfishing by recreational and commercial fishers (M. Byrne, personal observation), resulting in concerns for the conservation of this species (New South Wales Department of Primary Industries, 2015). Removal of *H. tuberculata* may have released *C. rodgersii* from competition and certainly would have opened habitat for recruits. As *H. tuberculata* largely depends on drift algae and does not forage away from shelter like *C. rodgersii*, the removal of expansive populations of this species which did not recover is likely to have been another factor in the dominance of barrens in some locations in New South Wales (M. Byrne, personal observations).

In New Zealand *C. rodgersii* co-occurs with another barrens forming sea urchin, *Evechinus chloroticus*, but is more abundant at depths below this species (Cole et al., 1992). The ecological interaction between these species has not been documented.

3.5 Physical factors and global change

In southeast Australia, *C. rodgersii* lives in a climate change hot spot where above global average ocean warming and changes in ocean circulation are altering the distribution of this sea urchin and associated biota (Johnson et al., 2011; Przeslawski et al., 2012). By 2050, local waters may increase by 4°C (relative to 1990) (Hobday and Lough, 2011) and this is being exacerbated by marine heatwaves (Babcock et al., 2019). It is not known how this fast warming will impact the ecology and population biology of *C. rodgersii*, although it is highly deleterious to *H. erythrogramma* (Harianto et al., 2018). Ocean acidification will make calcification and growth more difficult for both *C.* species due to decreasing saturation of carbonate minerals and energetic constraints (Dworjanyn and Byrne, 2018; Byrne and Fitzer, 2019).

FIG. 22.4 *Centrostephanus rodgersii* (*arrows*) and macroalgae stranded following a major storm, the east coast low (extratropical cyclone) that impacted the east coast of Australia in 2016. *Photo M. Byrne.*

C. rodgersii is most abundant on subtidal rocky reefs not subjected to influxes of fresh water. Mass mortalities of this species have been observed on shallow reefs along the New South Wales coast immediately after floods (Andrew, 1991). Severe storms on the open coast scour the benthos and can move large boulders around the reef. Stranded and crushed *C. rodgersii* are found after these storms (Fig. 22.4). The 2016 El Niño-driven east coast low (extra tropical cyclone) caused record level surge and waves along the New South Wales coast stripping extensive areas of kelp and other biota (M. Byrne, personal observation) including local populations of *C. rodgersii* (J. Smyth, personal communication). This was followed by recruitment of *H. erythrogramma* to the area and, 3 years later, *C. rodgersii* has not returned to the patches from where it was removed. In Tasmania, *C. rodgersii* appears to be restricted to deeper water due to high swells and the whiplash effect of large kelps in shallow (to depths of ~10m) water (Johnson et al., 2005).

4 Reproduction

4.1 Reproductive cycle

The sexes are separate in *Centrostephanus* species although hermaphrodites are occasionally encountered (0.9% of *C. rodgersii*) (King et al., 1994; Thilakarantha, 2017). Sexual maturity of *C. rodgersii* is reached at 40–60-mm test diameter (King et al., 1994; Pecorino et al., 2013a). Small sea urchins (male and female test diameter 30–50mm and 50mm, respectively) can be induced to spawn but their gametes are not reliably fertile. Males may thus reproduce at an earlier age than females (King et al., 1994). Mature females spawn many small (diameter = 110–120 μm) eggs. Reproductive output increases with size but this relationship is variable (Byrne and Andrew, 2013).

Throughout its range, *C. rodgersii* undergoes peak spawning in the austral winter from late June/July to August, based on gonad indexes (Byrne et al., 1998; Ling et al., 2008; Pecorino et al., 2013a). Similarly, the gonad index of *C. tenuispinus* peaks in July followed by a July–August spawning period (Thilakarantha, 2017). For *C. rodgersii*, Byrne et al. (1998) found synchronous gonad development along 7° latitude, indicating that gametogenesis and spawning are cued by exogenous factors present in all the populations studied. Increased gametogenesis in May coincides with decreasing day length and mature gametes are not reliably released until mid-June. Initiation of spawning occurs around the winter solstice. Control of reproduction in *C. rodgersii* by photoperiod and/or lunar cues is similar to other *Centrostephanus* species and diadematid sea urchins in general (Pearse, 1972; Kennedy and Pearse, 1975; Pearse and Cameron, 1991).

The winter spawning period may last only a month in northern New South Wales, with complete spawn-out by July (O'Connor et al., 1978; Byrne et al., 1998). Spawning will occur for a longer period if sea temperature remains cool (S. Dworjanyn, personal communication). The longest spawning period (5–6 months), as indicated by gonad histology, occurs in the southern temperate region. On the south coast of New South Wales spawning may continue through November due to prolonged gamete storage. Peak spawning in Tasmania occurs in August although induction of gamete release through November indicates prolonged low-intensity spawning (Ling et al., 2008). In New Zealand, *C. rodgersii* spawns from July to September (Pecorino et al., 2013a).

4.2   Habitat-related patterns

As characteristic of other sea urchins, gonad growth in *C. rodgersii* varies in response to food quantity and quality and population density (Byrne et al., 1998; Blount, 2004). Reproductive output of *C. rodgersii* is greater in macroalgal than barrens habitat (Byrne et al., 1998; Blount and Worthington, 2002; Ling et al., 2008; Ling and Johnson, 2009). At some locations, gonad yield from fringe sea urchins may be double compared to that for barrens sea urchins (Byrne et al., 1998; Blount, 2004). In response to an experimental, 66% reduction in density, the gonads of barrens sea urchins increased by 200% relative to those from unmanipulated barrens (Blount, 2004).

Although *C. rodgersii* in kelp forests produce more gametes, they occur more patchily. Allee effects may be important in populations where low density of spawning individuals reduces the chances of fertilization. In contrast, sea urchins in barrens may have greater reproductive success due to the greater probability of fertilization from aggregated but less fecund sea urchins.

5   Development and larval ecology

5.1   Echinopluteus transversus

Centrostephanus larvae are characterized by long postoral arms, an evolutionary modification associated with loss of the other arm pairs seen in more typical sea urchin echinoplutei (Wray, 1992). Across the Echinoidea, the two-armed larva of the Diadematidae are unique and appear to have evolved only once (Wray, 1992). As the postoral arms grow, the larva develops a two-armed profile (Fig. 22.5). It was some decades before the identity of this larval type, called *Echinopluteus transversus* by Mortensen (1921), was determined. The anterolateral arms remain small and the posterodorsal and preoral arms do not develop. These larvae are suggested to be designed for long distance dispersal (Soars et al., 2009; Soars and Byrne, 2015; Rendleman and Pace, 2018).

In contrast to typical eight-armed echinoplutei, *C. rodgersii* larvae do not exhibit phenotypic plasticity in larval arm growth in response to food variation (Soars et al., 2009). This difference may be due to the constraint of having only two arms for swimming and feeding (Soars et al., 2009). Larval nutrition does, however, influence the appearance of larval *C. rodgersii*. Larvae fed a low ration or starved have thinner arm epithelia compared to those fed a high food ration (Byrne and Andrew, 2013). A recent study of *C. coronatus* provides a physiological basis for the long planktonic duration and possible teleplanktonic dispersal capabilities of *Centrostephanus* larvae (Rendleman and Pace, 2018).

5.2   Temperature tolerance of development

The thermal window for the development of *C. rodgersii* has been investigated from near its northern range limit in New South Wales to its mid-range in Sydney, its southern limit in Tasmania, and in northern New Zealand (Ling et al., 2008;
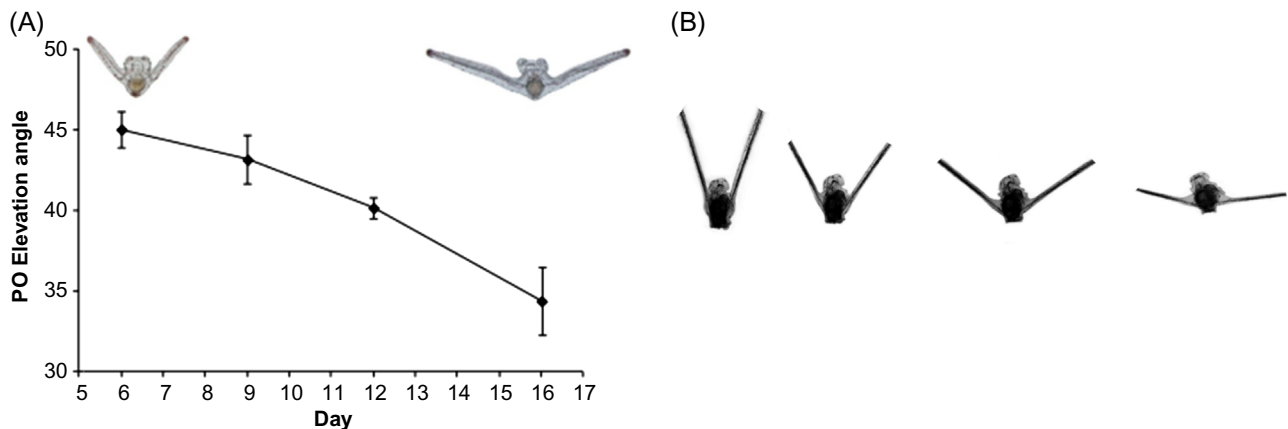

FIG. 22.5 (A) The two-armed *Echinopluteus transversus* of *C. rodgersii*. The elevation angle of the arms reduces along with growth, potentially as a means to control position in the water column. (B) Advanced larvae have well-developed muscles at the base of their arms and the larvae can move their arms through ∼180°. Scale bars = 100 μm. *Panel (A) From Soars, N.A., Byrne, M., 2015. Contrasting arm elevation angles of multi- and two-armed sea urchin echinoplutei support Grünbaum and Strathmann's hydromechanical model. Mar. Biol. 162, 607–616. Panel (B) Photo N. Soars.*

Pecorino et al., 2013b, 2014; Hardy et al., 2014) where spawning is initiated at temperatures of 20–21°C, 16–17°C, 11–12°C, and 16–17°C, respectively (Pecorino et al., 2013b). At warmer latitudes, the temperature range for successful larval development is 17–24°C (Pecorino et al., 2013b) while in cooler climes in Tasmania is 12–18°C (Ling et al., 2008). As might be expected due to thermal imprinting of gamete development (Byrne, 2011), the lower thermal limit for development is higher at warmer latitudes, ranging from 15°C in the north to 13°C near the mid-part of the range and 12°C in Tasmania. This indicates thermal plasticity in *C. rodgersii* development and thermal acclimatization of local populations across isotherms.

The 12°C developmental thermal threshold for the Tasmanian population approximates the maximum winter temperature and this is suggested to have been important in the success of immigrant larvae in establishing *C. rodgersii* populations (Ling et al., 2008). As sea temperatures will continue to increase in southeast Australia and in New Zealand, these regions are likely to become increasingly more favorable for the development of *C. rodgersii*. This increases the probability that local populations will become increasingly self-seeding (Ling, 2013; Pecorino et al., 2013b).

5.3   Development time

The larvae grow in size to be visible to the naked eye with >1.2 mm long arms and 3–4 mm in diameter from arm tip to arm (Huggett et al., 2005; Soars and Byrne, 2015). As they develop, the larvae exhibit a marked reduction in the angle of elevation of the arms (Fig. 22.5), a morphology modeled to confer high swimming speed and weight-bearing capacity (Grünbaum and Strathmann, 2003). The lowering of the arms with development is likely to help maintain the larvae in a favorable position in the water column as they increase in weight and form the juvenile (Soars and Byrne, 2015). Long arms at low angles would reduce sinking speed and may be a trait to remain in the water column (Emlet, 1983), facilitating long distance dispersal. Intriguingly, advanced *Centrostephanus* larvae can flex their arms through a ~180° angle and appear to "flap their wings" (Fig. 22.5). This capability is likely to influence the swimming and settlement mechanics of these larvae.

Development time of *C. rodgersii* is variable and is strongly influenced by temperature and food regime. The time for well-fed larvae to reach metamorphic competence has been reported to be 30 days near the northern range edge of *C. rodgersii* (Mos and Dworjanyn, 2016) and 77 days at this temperature reported elsewhere (Swanson et al., 2012). At 17–19°C competence was not reached for 3 months in the small number of larvae that were reared (n = 5) (Huggett et al., 2005). The larvae of *C. rodgersii* are resistant to low food conditions with larvae in no-food treatments being alive after 47 days (Soars et al., 2009), indicating that they may be able to use alternative food sources (e.g., dissolved organic material, bacteria). Resilience to low food levels would facilitate long distance dispersal.

The larvae of *C. rodgersii* settle and metamorphose in response to algal species from the habitat of adults (e.g., *Corallina officinalis*, *Laurencia* sp., *Amphiroa anceps*, *Sargassum linearifolium*) and in response to histamine produced by algae (Swanson et al., 2012). Depending on larval nutrition and duration of feeding, newly settled juveniles are 500–650 μm diameter (Huggett et al., 2005; Mos and Dworjanyn, 2016).

5.4   Effects of climate change stressors

Studies of the effects of near-future ocean acidification and warming on the early life history of *C. rodgersii* indicate that fertilization is resilient to these stressors (Byrne et al., 2010; Pecorino et al., 2014). A quantitative genetics study showed that this depended on the male–female pair (Foo et al., 2012). This study provided evidence that early development of *C. rodgersii* may have a capacity for adaptation in the face of selection by ocean change stressors. An unanticipated effect of acidification, at levels commensurate with near future change, is the marked reduction in the egg jelly coat of *C. rodgersii* with implications for sperm activating and attracting compounds in this structure that are important for fertilization (Deaker, 2016; Deaker et al., 2019).

Ocean acidification at levels projected for southeastern Australia by 2100 (pH 7.8) have a negative effect on larval development in *C. rodgersii* with slowed growth and abnormal skeleton development (Doo et al., 2012), as observed in many echinoplutei (Byrne, 2011; Byrne et al., 2013). Observations of small larvae with short arms have significant implications for *C. rodgersii*, because the long arms of larva have key roles in feeding, swimming and likely also defense (Allen, 2008; Soars et al., 2009). Larval success may be a bottleneck for persistence of populations in a changing ocean, particularly due to enhanced acidification of the more southerly parts of its range as colder higher pCO$_2$ waters with low mineral saturation expand northward in the Southern Ocean. Beyond the direct effect of climate change on *Centrostephanus* species, climate change, in particular marine heatwaves is causing the demise of kelp forests on both the east and west coasts (Babcock et al., 2019). This will have negative flow-on effects for these sea urchins.

6   Growth and age

As characteristic of the phenotypic plasticity in sea urchins (Ebert, 1996; Russell, 1998), *C. rodgersii* adjusts body growth with food availability (Blount, 2004; Ling and Johnson, 2009). This species reaches a maximum size in macroalgal habitats compared with barrens urchins and different ecomorphs occur in these habitats (Blount, 2004; Ling and Johnson, 2009). Sea urchins in macroalgal habitat have thicker tests, shorter spines, and faster growth rates, than while those from barrens (Blount, 2004; Ling and Johnson, 2009). Barrens *C. rodgersii* also have relatively larger jaws (Ling and Johnson, 2009), an indication of food limitation (Ebert, 1980). In New South Wales, a study of 32 sites along the coast indicated that *C. rodgersii* in barrens were generally ≤80-mm test diameter, while those from nearby macroalgal habitats were generally ≥ 90-mm test diameter (Blount, 2004). Experimental reductions in density by as little as 33% cause growth rates of the remaining *C. rodgersii* to double (Blount, 2004).

Growth of *C. rodgersii* in New South Wales, Tasmania, and New Zealand has been estimated using mark recapture techniques and direct aging using validated growth lines visible on the demipyramids and tetracycline injections to tag the skeleton (Ebert, 1982; Blount, 2004; Ling et al., 2009a; Pecorino et al., 2012) and by cohort analysis (Andrew, 1991, 1993). Despite variability between studies in different regions, overall trends are similar.

In New South Wales, following recruitment, *C. rodgersii* grows quickly reaching 35–40-mm test diameter after 1 year with a growth rate estimated to be 4–6 mm every 67 days (Andrew, 1991, 1993) and with a 50-mm test diameter estimated by year 2. A mark-recapture studies indicated that growth rates are variable depending on habitat, site, and food availability, with 80- and 100-mm test diameter sea urchins being 5–9 years old and 12–25 years old, respectively (Blount, 2004). Modal size *C. rodgersii* (test diameter = 70–90 mm) are estimated to be 4–10 years old (C. Blount and N. Andrew, unpublished data). The largest sea urchins found (test diameter >110-mm test diameter) may be up to 20 years old. Longevity is estimated to be 25–30 years. Although growth is faster at Sydney than at Eden (∼350 km to the south), maximum age shows little difference between these localities (C. Blount and N. Andrew, unpublished data) nor between fringe and barrens habitats (Blount, 2004).

In Tasmania, mark-recapture studies indicate that *C. rodgersii* reaches a test diameter of ca. 50 mm in 4–5 years followed by slower growth with a maximum test diameter of 114 mm within 25–35 years (analysis of data in Ling et al., 2009a by Pecorino et al., 2012).

The mark-recapture study of *C. rodgersii* in New Zealand indicated the sea urchins were 3–10 years old (Pecorino et al., 2013a). In this study, depending on the model used, *C. rodgersii* is estimated to reach a maximum growth rate of 17.7–23.8 mm year^{-1} at 1.5–3.0 years old followed by a decrease in growth rate to reach a test diameter of 10–13 mm in their fifth year, reaching 85-mm test diameter. This is followed by growth to a test diameter of 126 mm between 15 and 20 years. Comparison of estimated growth rates in Tasmania and New Zealand indicate similar growth to year 1. Thereafter, growth is faster in the New Zealand population, a difference suggested to be influenced by the warmer (3–4°C) water temperature in New Zealand (Pecorino et al., 2012).

7   Fishery and resource management

In New South Wales, the fishery for *C. rodgersii* has remained small for 20 years and in 2015, the harvest was estimated to be 75–78 tons landed weight (value ∼$100,000) (New South Wales Department of Primary Industries, 2015). The fishery in Tasmania is expanding and in 2019 passed 550 tons (J. Keane, personal communication). The yield of *C. rodgersii* roe is greatest in autumn. Roe quality and size is determined by density-related availability of macroalgae (Byrne et al., 1998) and so the harvest is largely taken from kelp habitat and not from barrens (Worthington and Blount, 2003; Norwood, 2012).

The abundance of *C. rodgersii* in Tasmania is prompting fishery interest with a focus on the possibility that harvest might reduce the impact of the destructive grazing of this species on macroalgae and the negative effects on associated commercial species such as abalone (J. Keane, personal communication). Incentives for increasing harvests in Tasmania are thus overtly part of a strategy to limit the ecological effects of *C. rodgersii*, including subsidized costs from affected fisheries such as that for abalone to improve commercial viability (op. cit.). Such approaches are integrated with other measures such as culling of sea urchins on selected reefs (Tracey et al., 2015) and catch reductions in the rock lobster fishery. Use of the fishery to facilitate kelp recovery on widespread barrens and in deeper water appears limited (Tracey et al., 2015).

The history of major sea urchin fisheries has been one of explosive growth followed by overfishing and often collapse (Andrew et al., 2002). The choices confronting policy makers in *C. rodgersii* fisheries offer a twist on standard fishery

thinking. If a broad ecosystem approach is taken, overfishing of sea urchins to increase the productivity of near shore reefs and the abundance of abalone is a rational management strategy. The legitimacy of this management objective is, however, dependent on the conclusion that the current dominance of the barrens habitat is a result of overfishing predators and that the current stable state of *C. rodgersii* habitat does not reflect any historic conditions. Andrew et al. (1998) advocated comanagement of the abalone and sea urchin fisheries on a rotational basis to increase the productivity of both. Such a scheme would require management at smaller scales and a stronger institutional environment for comanagement and integration of management plans among currently distinct fisheries. In essence, this approach would require reefs to be managed as a mosaic of distinct but inter-connected patches within a seascape (*sensu* Jones and Andrew, 1992).

8   Conclusion

The invasion of *C. rodgersii* in Tasmania offers a unique natural experiment that is providing important insights into the dynamics of temperate rocky reefs and important associated fisheries. In Tasmania and New South Wales, the ecological dynamics of subtidal rocky reefs are given prominence because they support commercially important fisheries for rock lobsters and abalone and, to a lesser extent, fishes. The differences and commonalities between these systems beg the question as to whether New South Wales offers a glimpse of what Tasmania may become, with a degraded abalone fishery, transformed reefs and a rebuilding rock lobster fishery. The unfolding story of the invasion of Tasmanian reefs by *C. rodgersii*, in turn should prompt a reanalysis of the ecology of reefs in New South Wales. Is the fact that half the shallow subtidal reefs are barrens habitat a "new normal" state that does not reflect the historical configuration of this ecosystem?

In response to a changing ecosystem, the research frontier for *C. rodgersii* is shifting toward larger-scale problems that address the resilience of reefs (e.g., Ling and Johnson, 2012). In Tasmania, what interventions will allow the system to cope and adapt? Could rock lobster populations increase to a level that would be ecologically significant, yet still support a viable fishery? In New South Wales, if the current state of the system is considered undesirable what mix of governance institutions and interventions will shift it into a trajectory that will lead to a different configuration? In many respects this evolution of research echoes that observed in other species of sea urchins (Moreno et al., 2007; Johnson et al., 2012).

As in other ecosystems undergoing profound climate-driven change (e.g., the Great Barrier Reef, Hughes et al., 2017), and the strong likelihood of hysteretic ecological processes, we speculate that attempts to restore the reefs of eastern Tasmania to their pre-*Centrostephanus* state, desirable as that may be, is a quixotic enterprise due to the increase in extreme climate events (Babcock et al., 2019). Interventions in the ecology of these reefs (*sensu* Hobbs et al., 2011) presents many challenges ranging from the moral hazards associated with intervening in nature to understanding the limits of what is possible over such large areas of reef. The strong body of work on human and ecological drivers, thresholds, and the ecological feedbacks on Tasmanian reefs (op. cit.) provides a strong foundation for addressing these challenges. New management objectives will be required, some of which will mean manipulating ecosystems and human behaviors to avoid thresholds in ecological variables in, among other species, sea urchin abundance, rather than optimizing yields in a classical fisheries sense. New institutional relationships will be required among researchers, policy makers, and the fishing industry as they grapple with potential alternative futures for these reefs. It is perhaps not too fanciful to suggest that lessons may be learned from other small-scale fisheries, including those in the developing world and in social-ecological systems with more flexible institutions (Berkes, 2003, 2009; Andrew et al., 2007; Moreno et al., 2007; Mahon et al., 2008; McClanahan et al., 2009).

Acknowledgment

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