FRDC FINAL REPORT

ESTABLISHMENT OF THE LONG-SPINED SEA URCHIN (*Centrostephanus rodgersii*) IN TASMANIA: FIRST ASSESSMENT OF POTENTIAL THREATS TO FISHERIES

Craig Johnson, Scott Ling, Jeff Ross, Scoresby Shepherd and Karen Miller

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Project Summary

PRINCIPAL INVESTIGATOR: Prof. Craig R. Johnson

The pattern of distribution of the long-spined sea urchin *Centrostephanus rodgersii* over ca. 40 y in the Kent group, Bass St., suggests initial establishment in the mid 1960s with subsequent expansion of populations to its current status as the dominant invertebrate on shallow subtidal rocky reef. On the east coast of Tasmania, *C. rodgersii* is most abundant in the vicinity of its location of initial discovery in 1978, but it occurs throughout the east coast between Eddystone Pt in the north and Recherche Bay in the south. Barrens habitat, supporting high densities of sea urchins but largely devoid of macroalgae, occurs extensively in the Kent group and at several sites on the northern half of the Tasmanian east coast, but declines with increasing latitude and does not occur south of the Tasman Peninsula. At the southern extent of barrens habitat on the open coast, barrens are incipient and occur as small patches in macroalgal beds. Evidence suggests that the barrens habitat in the Kent group and on the open rocky coast of Tasmania is formed by grazing of *C. rodgersii* and not by *Heliociaris erythrogramma*, another sea urchin that occurs on these barrens. This is largely because there is a significant positive relationship between *C. rodgersii* density and extent of barrens but not between *H. erythrogramma* density and extent of barrens, and because *H. erythrogramma* is not know to form barrens on exposed coast. These collective patterns suggest that the incursion of *C. rodgersii* into Tasmanian waters was from the north, and that spread on the east coast of Tasmania propagated from an 'epicentre' in the vicinity of St Helens in the northeast. We suggest that the initial incursion was via larvae transported from NSW in the East Australian Current, which has increasingly influenced the east coast of Tasmania over at least the past 4-5 decades. The lack of any genetic differentiation among *C. rodgersii* populations in NSW, the Kent group and the east coast of Tasmania is consistent with this view.

On the east coast of Tasmania, there is a clear negative relationship between the abundance of *C. rodgersii* and the density of commercially fished abalone (*Haliotis rubra*) and rock lobster (*Jasus edwardsii*). The density of abalone is significantly lower

on barrens habitat than in adjacent macroalgal beds at the same depth and on the same substratum type. We conclude that abalone and rock lobster are unlikely to occur in commercial quantity on *C. rodgersii* barrens. Given these findings, the spatially patchy distribution of existing extensive barrens, and particularly if existing incipient barrens (consisting of small barrens patches scattered through seaweed beds) develop to become extensive barrens, then a stronger focus on spatial management of fisheries on the east coast of Tasmania may be warranted.

In Tasmanian waters, large continuous tracts of *C. rodgersii* barrens do not develop in shallow water (2-10 m) as occurs in NSW, but largely occur within a depth range of ca. 10-20 m in the Kent group, and ca. 15-35 m on the east coast of Tasmania. Barrens habitat is more prevalent on boulder substratum than other types of consolidated reef, extending to cover >75% of the seafloor on this substratum at some sites, and averaging ca. 33% cover on boulder substratum across all sites in Tasmania where incipient barrens occur. Given these collective observations, and estimates that boulders comprise ca. 55% of consolidated reef in depths ≤18 m and 34% of consolidated reef to ca. 40 m depth, barrens habitat could potentially expand to account for ca. 50% of rocky reef on the east coast of Tasmania, as currently occurs in the Kent group and NSW. This scenario would have serious implications for abalone and rock lobster fisheries on this coast. However, the capacity to predict future patterns of barrens habitat requires better understanding of the mechanisms that initiate barrens formation and that determine the position and dynamics of boundaries between barrens and macroalgal-dominated habitat. Given these considerations, and evidence worldwide of the connection between fishing of sea urchin predators and formation of sea urchin barrens, we suggest that management intervention to limit the spread of *C. rodgersii* barrens in Tasmania is warranted.

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Background

Range extensions of species raise important questions about the underlying mechanisms and the effect of the new species on the structure and dynamics of the receiving community (Davis et al. 1998). Moreover, understanding the mechanisms of range expansion and concomitant impacts on ecologies is important in assessing whether management responses are possible or desirable. Range extension may arise as a result of changes in the environment so that areas previously physically or ecologically unsuitable become habitable, or by changes in dispersal patterns, or both. Environmental change encompasses shifts in the physical environment, usually associated with climate change (Hughes 2000; Walther et al. 2002; Parmesan & Yohe 2003; Beaugrand 2004; Chevaldonné and Lejeusne 2004), and alteration of ecological dynamics through changes in patterns of competition and trophic interactions (Davis et al. 1998; Walther et al. 2002; Alheit and Niquen 2004). Changes in dispersal patterns include the far reaching effects of anthropogenically mediated dispersal, which is effecting unprecedented rates of global redistribution of marine species (Vitousek et al. 1997; Carlton and Geller 1993; Carlton 1999; Bax et al. 2001). Whatever the facilitating mechanism, a crucial question is the impact of the 'new' species on the recipient community. This will depend on the strength of interactions with resident species, and on the specificity of habitat requirements of the newly establishing species.

Because of their capacity to overgraze and trigger a shift from dense and diverse macroalgae beds to sea urchin 'barrens' habitat largely devoid of macroalgae, few organisms have had as much impact on shallow temperate reef systems worldwide as sea urchins (Lawrence 1975; Chapman and Johnson 1990; Jackson et al. 2001; Steneck et al. 2002). Denuding reefs of macroalgae realises significant loss of physical structure with concomitant effects on biota (Tegner and Dayton 2000), and approximately a 100-fold reduction in rates of primary production (Chapman 1981) with flow on effects to secondary production (Duggins et al. 1989). The transition to urchin barrens is particularly problematic because, unlike other herbivores that overgraze, sea urchins are able to maintain populations on barrens (Johnson and Mann 1982) where they feed on

microalgae, non-geniculate coralline algae and occasional drift plants. It follows that range extensions of sea urchin species capable of forming barrens habitat can pose a potential threat to the integrity of reef communities within the new range.

In Australia, no other sea urchin has as large a role in the ecology of shallow reef communities as the long-spined sea urchin (*Centrostephanus rodgersii*). In central and southern New South Wales this species maintains barrens habitat over ~50% of the area of shallow reef, which amounts to several thousand hectares (Andrew and O'Neill 2000). The important role of this sea urchin is demonstrated in removing *C. rodgersii* from barrens habitat, which results in rapid regeneration of macroalgae algae, but notably this requires removing virtually all animals and not just a portion of them (Andrew 1991; Andrew & Underwood 1993; Hill et al. 2003). The indirect effects of the grazing of *C rodgersii* ostensibly affect some commercial species since, over several spatial scales, there is a negative relationship between densities of the sea urchin and the commercially important abalone, *Haliotis rubra* (Shepherd 1973; Andrew & Underwood 1992; Andrew et al. 1998).

Historically, *C. rodgersii* in Australia has been largely restricted to the coast of New South Wales, but in recent decades the range of this species has extended southwards. It was first recorded on the east coast of Tasmania in 1978 (Edgar 1997). The overall aim of the work reported here is to assess the potential threat of *C. rodgersii* to the integrity of shallow reef systems in eastern Tasmanian waters, and to the important abalone (*Haliotis rubra*) and rock lobster (*Jasus edwardsii*) fisheries that these reefs support. The Tasmanian abalone fishery, which supplies ca. 25% of the global market, has a landed annual value of *ca*. AUD $100 M, while the value of the rock lobster industry is *ca*. $50 M annually (ABARE 2004). To achieve this broad goal we addressed several more specific aims: (1) to determine patterns in the establishment of *C. rodgersii* and formation of *C. rodgersii* barrens in the Kent group of islands in Bass Strait (the strait separating Tasmania from mainland Australia) and on the east coast of Tasmania; (2) to consider this information and patterns of genetic variation between populations in New South Wales, the Kent group and east coast of Tasmania to infer likely mechanisms

underpinning the southward extension of the species' range; and (3) to examine the relationships between *C. rodgersii* density, and extent of *C. rodgersii* barrens, with habitat features (depth, substratum type and algal community composition), and with abundances of abalone and rock lobster.

As a result of both accelerated climate change and anthropogenically mediated introductions, the range boundaries of marine species are increasingly labile and, as a result, the ecology of marine systems face unprecedented potential for change (Carlton and Geller 1993; Carlton 1999; Walther et al. 2002; Parmesan & Yohe 2003). This is the first work to report on the range extension of a temperate sea urchin and assess the ecological consequences of its incursion.

Need

The impact of the long-spined sea urchin in forming extensive barrens habitat on shallow rocky reef in NSW, and the absence of abalone fisheries on urchin barrens in NSW is unequivocal. The establishment of this species and its commencement to form barrens habitat on the east coast of Tasmania is cause for concern for fisheries based on shallow reef systems. Thus, the work proposed here is crucial to assess whether the capacity of this species to destructively graze seaweeds in Tasmania parallels that observed in NSW. It is clearly evident from work on other systems that sea urchins may have dissimilar ecological roles and impacts in similar systems but in different regions (e.g. Foster 1990; Estes and Duggins 1995).

The Tasmanian abalone and rock lobster industries are worth *ca*. AUD $100M and $50M p.a. respectively before processing (ABARE 2004). If the impact of this sea urchin on the east coast of Tasmania increases to the scale of that observed in NSW, then there is likely to be significant and negative impact on these industries and others based on shallow rocky reef systems. Under these circumstances, current management systems based on size and quota restrictions will not secure the sustainability of these fisheries on the east coast of Tasmania at their current levels.

If the proposed work indicates that the potential for impact by the urchin is large, given that barrens formation in Tasmania may be at an early stage, it may be possible to elucidate and implement management actions to remedy the situation. This will require further research to identify the mechanism(s) triggering destructive grazing of seaweeds by the urchins.

Objectives

1. Determine the distribution of *C. rodgersii* on the east coast of Tasmania.
2. Determine the distribution of *C. rodgersii* barrens on the east coast of Tasmania.
3. Compare the standing stock of black lip abalone (*Haliotis rubra*) and southern rock lobster (*Jasus edwardsii*) in barrens habitat with that in adjacent seaweed beds.

Methods

Genetics

Allozyme electrophoresis was used to determine whether recent populations of *Centrostephanus rodgersii* in Tasmania displayed lower levels of genetic variation relative to mainland populations, as might be expected if Tasmanian populations arose from a single founder event and received little gene flow from other populations. Sixty animals were collected from each of Bass Pt, New South Wales (lat 34° 35' S, long 150° 54' E; August 2000); south side of East Cove, Deal Is, Bass St. (lat 39° 28.4' S, long 147° 18.4' E; June 2000), and Fortescue Bay, Tasmania (lat 43° 8.5' S, long 148° 0.0' E; October 2000 and April 2001). Samples of gonad (free of other tissue) were excised from live animals, snap frozen in liquid nitrogen, and stored at –80 deg C. Frozen samples from Deal Is were held in liquid nitrogen for transport until transferred to the storage facility. Frozen samples from NSW were transferred by air on dry ice prior to storage at –80 deg C.

An initial screening was undertaken on animals from Fortescue Bay and Bass Pt to identify enzyme systems suitable for further analysis. Approximately 0.25 g of frozen gonad tissue was ground in an equal volume of deionised water, and the homogenate centrifuged at 4°C (Eppendorf 5417R) at 10,000 rpm for three minutes. Aliquots (10 µl) of the supernatant from each sample were drawn off for electrophoresis on cellulose

acetate gels using two buffer systems (tris-glycine at 200V and 1.5 mA / plate, and tris-citrate at 150V and 5 mA / plate).

Samples were screened initially for 18 enzyme systems. Enzymes were stained using histochemical staining as outlined in Herbert & Beaton (1999) and Richardson *et al.* (1986). The enzyme systems tested were: aspartate amino transferase (AAT, EC 2.6.1.1), alcohol dehydrogenase (ADH, EC 1.1.1.1), aconitase (ACON, EC 4.2.1.3), adenylate kinase (AK, EC 2.7.4.4), arginine phosphokinase (APK, EC 2.7.3.3), fumerate hydratase (FUM, EC 4.2.1.2), glycerol-3-phosphate dehydrogenase (GPDH, EC 1.1.1.8), glucose-6-dehydrogenase (G6DH, EC 1.1.1.49), hexokinase (HEX, EC 2.7.1.1), isocitrate dehydrogenase (IDH, EC 1.1.1.42), lactate dehydrogenase (LDH, EC1.1.1.27), malate dehydrogenase (MDH, EC 1.1.1.37), Malate dehydrogenase (ME, EC 1.1.1.40), mannose phosphate isomerase (MPI, EC 5.3.1.8), phosphoglucomutase (PGM, EC 2.7.5.1), 6-phosphoglucanate dehydrogenase (6PGDH, EC 1.1.1.44), phosphoglucose isomerase (PGI, EC 5.3.1.9) and xanthine dehydrogenase (XDH, EC 1.2.1.37).

Of the 18 enzyme systems assessed in the initial survey, five (ADH, AK, GPDH, LDH and 6PGDH) were eliminated from further investigations due to failure to produce detectable banding. Of the remaining 13, seven (AAT, APK, IDH, MDH, MPI, PGM, PGI) provided clearly interpretable and consistently repeatable patterns. Of these, three (APK, IDH, MDH) were monomorphic. The remaining four enzyme systems (AAT, MPI, PGM, PGI) were selected for use in the primary study.

MPI, PGM and PGI were all run in the tris-glycine buffer (pH 8.5) and provided one polymorphic locus each. AAT demonstrated two loci in the tris-citrate buffer system (pH 7.0), but only one was consistently interpretable and polymorphic. Electrophoretic runs using the tris-glycine buffer were carried out at room temperature over 30 minutes, while those using tris-citrate were run at 4 deg C for 65 minutes. Protocols for cellulose acetate electrophoresis were after Richardson *et al.* (1986). From each of the three collection sites, gonad tissue from 60 individual animals was analysed. Each gel contained individuals from various sites, and several animals were analysed on several different

plates, to account for mobility variations among samples and sites. In scoring the gels, the most common allele at each locus in the Fortescue Bay samples was nominated as 100 (100%). All other alleles were scored according to their mobility relative to the dominant allele for each locus.

To examine the genetic relationship between the Tasmanian, Kent Group and mainland populations of *Centrostephanus rodgersii*, allelic diversity and heterozygosity among the three sites was compared using BIOSYS (Swofford & Selander 1981). Populations recently established via a founder event are likely to exhibit both a reduced number of alleles as well as reduced levels of heterozygosity (heterozygote deficits) compared to long-established populations from within the main range. Each population was also tested for departures from the levels of heterozygosity expected for single-locus Hardy-Weinberg equilibria using exact tests (Elston & Forthofer 1977), and Wright's fixation index (*f*) used to determine the nature of any departures from Hardy-Weinberg equilibrium whereby positive values of *f* represent heterozygote deficits and negative values of *f* represent heterozygote excesses.

The genetic relationship among sites was described by Nei's Unbiased genetic distance (D), calculated using BIOSYS (Swofford & Selander 1981). The possibility of subdivision between the mainland and Tasmanian populations of *C. rodgersii* was also examined by calculating F_{ST} (as θ, Wier & Cockerham 1984). Mean F_{ST} among sites (± SE) was calculated by jacknifing over loci, and departures from panmixis (i.e. $F_{ST} = 0$) were tested using the 95% confidence intervals of F_{ST}, calculated by bootstrapping over loci using the software package TFPGA (Miller 2000).

Surveys of sea urchins and barrens habitat, Kent Group

Surveys in 1974 and 1981

Counts of echinoids in East Cove (Table 1) were undertaken in May 1974 and in March 1981 by one of us (Shepherd). The diver swam along three straight-line transects normal to the shore and along curved transects parallel to the shore at fixed depths of 5, 10 and 15 m. On each transect normal to the shore, the diver swam down the slope to the

seaward edge of the reef and returned to shore along a parallel line displaced 5 m from the outward-line. The transects at constant depth were ca. 350 m in length. On each transect swim, the diver recorded the numbers of sea urchins (*C. rodgersii* and *Heliocidaris erythrogramma*) within 1 m of the line for each 2-minute interval of swimming time. The extent of sea-urchin barrens, sizes of algal patches within the barrens, and the boundaries of macroalgal patches of *Macrocystis angustifolia*, *Phyllospora comosa* and *Ecklonia radiata*-fucoid communities were measured and recorded. Data from timed swims were converted to estimates of density, using the calibration of diver swimming speed applied in abalone studies (Shepherd 1985). By this calibration, the diver swam 40 m and covered 40 m^2 in each two minutes. Data were recorded on a map from which contours were constructed. Maps were then digitised and mean densities calculated by integrating within contour bands. Measures of variance were not calculated from contour maps since variances are entirely dependent on the size of nominal sampling units used to 'sample' the map.

In both 1974 and 1981, qualitative observations of *C. rodgersii* were also recorded during spot dives at a range of sites at Deal Is, Dover Is and Erith Is (Table 1). On these dives, divers searched intensively for *C. rodgersii* along straight-line transects normal to the shore from shallow water (ca. 2 m) to the sand-edge of the reef.

In these surveys, *C. rodgersii* barrens were recorded as Type I (under- and overstorey both removed) or Type II (understorey removed, but overstorey of *Ecklonia radiata* and large fucoids largely intact).

In 1974 dives were in Murray Pass (to 50 m), Winter Cove (to 30 m) and Little Squally Cove (to 50 m) at Deal Is, and on the southern end of Erith Is (to 30 m). In 1981, spot dives were more extensive and undertaken at the northern side of East Cove, Garden Cove, Winter Cove, and Squally Cove at Deal Is, on the northern and southern sides of West Cove at Erith Is, and at sites on the NE and NW coasts of Dover Is (Table 1).

Surveys in 2000

Quantitative surveys were undertaken on the southern and northern shores of East Cove, and in Winter Cove at Deal Island, and on the NE Coast of Dover Is in June 2000 (Table 1). At each site, four belt transects were laid 50-150 m apart, normal to the shore and extending from ca. 3 m depth to the sand edge or to a maximum depth of 18 m. Divers worked to 1 m on each side of each transect, recording the percentage cover of different substratum types, percentage cover of algal species or guilds, percentage cover of *C. rodgersii* barrens, and counts of all sea urchins (*C. rodgersii*, *H. erythrogramma*), abalone (*Haliotis rubra*, *H. laevigata*) and rock lobsters (*Jasus edwardsii*) in consecutive 5 m sections of transect. Most brown and green algae were identified to species, while understorey reds were treated as an assemblage. Algae recorded in the survey are listed in Appendix 1.

The extent of *C. rodgersii* barrens was also recorded during spot dives commencing at ca. 2 m depth at Little Squally Cove to 30 m, and on the northern side of West Cove to 14 m depth. Similar observations were made on a drift dive in Murray Pass between lat. 39° 27.76’ S, long. 147° 18.74’ E and lat. 39° 28.02’ S, long: 147° 18.56’ E, in which divers moved between 2-30 m depth.

The time series from 1974-2000 indicates that the occurrence of *C. rodgersii* in the Kent group had changed from the animal occurring sparsely within a restricted distribution to become the dominant invertebrate spread widely throughout the group. An important question is whether this pattern might arise from one or a small number of settlement events, or from a series of many recruitment events (from either closed or open recruitment). Because age distributions might throw some light on this question, a total of 298 *C. rodgersii* were collected randomly from barrens habitat between 10-15 m on the south side of East Cove for ageing. Effort was made to search crevices to locate smaller non-emergent animals, but boulders were not moved in searching. On return to the surface, the test diameter of each animal was recorded, their jaws and lantern apparatus removed, labeled and frozen for further processing, and the gonads of 60 animals representing a large size range were excised and stored in liquid nitrogen for genetic

analysis (see above). Jaws were removed from lanterns, bleached for 24 h in a 4% solution of bleach, and then any organic tissue removed before drying. The total length of jaws were measured, and ridges on jaws counted under a dissecting microscope aided by strong side-illumination. Blount (NSW Fisheries, unpub. data) has validated that jaw ridges are a strong proxy for age.

Surveys of sea urchins and barrens habitat, Tasmania east coast

There were three broad components of this work, namely to ascertain the spatial extent of *Centrostephanus rodgersii* on the east coast of Tasmania, to estimate the cover of *C. rodgersii* barrens on the east coast, and to compare the standing stocks of abalone and lobsters inside and outside *C. rodgersii* barrens.

Distribution of C. rodgersii populations

The spatial distribution of *Centrostephanus rodgersii* on the east coast of Tasmania was estimated using a spatially hierarchical sampling design based on 13 primary sites between Eddystone Point and Recherche Bay on the east coast (Fig. 6). Primary sites were separated by ca. 25-30 km along the linear coastline (i.e. ignoring embayments and estuaries). Within each primary site there were three sub-sites (ca. 0.3-0.5 km apart), and within each subsite four belt transects were surveyed by divers. Belt transects were set perpendicular to the shore, extending from ca. 3 m depth to a maximum depth of 18 m or a maximum total length of 100 m if the maximum seaward depth was less than 18 m. Because reef topography varied among sites, sub-sites and individual transects within sub-sites, the surveyed length of each transect was variable. On each transect line, a pair of divers worked to 1 m each side of the line, and for each 5 m section of the transect recorded depth; percentage cover of substratum types; percentage cover *C. rodgersii* barrens habitat; abundance of sea urchins (*C. rodgersii* and *H. erythrogramma*), rock lobster (*J. edwardsii*) and abalone (*H. rubra*); and the percentage cover of algal species or guilds. Algal cover was estimated to the nearest 5 % for each 5 x 1 m section, while species occupying less than 5 % cover were recorded as being present. Species of red algae were recorded as a single guild, as were filamentous brown and green algae. Our

grouping of *Zonaria* spp. comprised *Z. tuneria*, *Z. spiralis*, *Z. angustata*, and *Homeostrichus olsenii*. Species recorded in the survey are listed in Appendix 1.

Habitat classified as *C. rodgersii* barrens was characterised as largely lacking foliose macroalgae and obviously supporting locally abundant *C. rodgersii* individuals. Areas of grazed substratum could be discerned unambiguously. The substratum was classified either as flat rock shelves (>5 m effective diameter; the presence of cracks or crevices was noted), very large boulders (>2.5 m and < 5 m diameter), large boulders (>1 m and <2.5 m diameter), small boulders (>0.2 m and <1 m diameter), cobble (>0.1 m and < 0.20 m diameter), pebble (>0.01 m and < 0.10 m diameter), gravel (< 0.01 diameter), or sand.

Further information on the distribution of *C. rodgersii* in Tasmania was obtained in partnership with the community group SeaCare Australia, which conducted a survey of 'sightings' among recreational, commercial and scientific divers. Divers were provided with a clear description and diagram of *C. rodgersii* to enable unambiguous identification, and with a data sheet on which to record their observations, which included estimates of abundance, habitat type, substratum type, depth and location. Most sightings in new areas have been confirmed by experienced scientific divers from the Tasmanian Aquaculture and Fisheries Institute.

Distribution of C. rodgersii barrens

The spatial extent of *C. rodgersii* **'**barrens**'** was estimated by surveying rocky reef with a towed underwater video system. Sampling using video transects was performed at the same sites and sub-sites as for the diver-based surveys (see previous section). Two video transects normal to the shore and two transects parallel with the shore were conducted at each subsite. The perpendicular transects covered depths from 1 to 45 m, while parallel transects were within a depth range of 15 to 20 m. In most cases, perpendicular tows spanned the width of reef from the shore to the reef fringe/sand edge. Parallel tows were conducted for 20-30 minutes or approximately 1 km in length (straight-line distance from tow start point), but tow speed varied depending on weather conditions and reef

topography. Thus, at each site, ca. 6-7 km of inshore rocky reef was surveyed for barren habitat using this method, with the entire survey covering > 80 km of reef.

The video camera system was a scaled down version of the system developed by Barker et al. (1999). The camera was mounted inside a positively buoyant protective cage with an attached chain to provide stability and ensure that the camera and frame floated 1-2 m above the sea floor. This system enabled towing the camera across rocky reef with rough topographic relief so that the camera remained a similar distance off the sea floor regardless of depth, providing a field of view ca. 3-4 m wide depending on surge and topography. The camera system was linked to (1) an onboard video recorder to capture the image, date, time, position and depth; (2) a real time monitor; and (3) computer which logged the depth under the boat (from an electronic depth sounder) and position (from a GPS) of the vessel at 4 s intervals, and comments input by the operator. Note that data on depth and position related to the boat, while the camera was on a tow line 40-55 m behind the boat. In the laboratory, the video footage was examined in detail to classify habitat types, which was recorded against the logged data. In this way, the total distance of each video transect tow, and the proportion of each transect that was classified as *C. rodgersii* barrens and other habitat types was estimated from the logged GPS coordinates. In the event of poor GPS signals (e.g. at base of large cliffs), position was back-calculated by interpolating between fixes determined from good satellite coverage.

Substratum types were resolved as either ‘unclassified reef ‘ if the substratum type was unclear (usually where macroalgal cover prevented a clear view of the substratum) or, where the substratum could be discerned, ‘flat rock’ with little apparent relief, ‘boulder reef’, ‘cobble’, ‘gravel’, ‘pebble’, or ‘sand’. Habitat types denoted either *C. rodgersii* barrens, or habitat dominated by particular canopy-forming species.

Habitat was classified as sea urchin barrens when the understorey was completely denuded, and the overstorey occupied <15% cover. We recognized four categories of sea urchin barrens habitat: Type 1 barrens denotes continuous barrens habitat in the camera field of view for > 10 m, while the other 3 categories are different types of ‘patchy’

incipient barrens, where a patch was defined as a section of reef that was not continuously barren for 10 m. Type 2 barrens was defined as patchy barren where barrens covered > 40% of the bottom; Type 3 barrens defined patchy barrens in which barrens occupied between 20 - 40% cover; while Type 4 barrens referred to patchy barren where barren cover was < 20% cover.

Effect of C. rodgersii barrens on standing stocks of abalone and rock-lobster

Abalone (*H. rubra*) and rock-lobster (*J. edwardsii*) populations were compared on *C. rodgersii* barren and in adjacent algal-dominated habitat at the same depth and on the same substratum type at three sites (Elephant Rock, 41° 15.30' S, 148° 20.37' E; St Helens Is, 41° 20.95' S, 148° 20.15' E; Mistaken Cape, 42° 38.86' S, 148° 9.70' E). At Elephant Rock and St Helens Is, the barrens are extensive and well established Type 1 barrens, while at Mistaken Cape the barrens in 8-14 m are incipient Type 4 barrens, comprising small barren patches in the algal bed. Note that while there are extensive barrens in deeper water (>18 m) at Mistaken Cape, at these depths working time is limited and it was difficult to locate intact macroalgal beds on equivalent substrata. Sampling involved four 50 x 2 m belt transects set within the 15 – 18 m depth strata in each habitat type at each site. The belt transects were surveyed by divers as outlined above.

Analyses

Because rocky reef was the habitat of interest, non-reef substratum (i.e. sand cover) was factored out of all analyses. To avoid bias from different lengths of transects or sections of transects (e.g. within depth or substratum categories), means are weighted accordingly.

All univariate statistical analyses were undertaken using the SAS® software (v. 6.12) with the exception of quantile regressions which were performed using the 'R' statistical package. For ANOVAs, data were checked for conformity to assumptions of homoscedasticity and normality. Where data were heteroscedastic, the transformation to stabilise variances was determined by the relationship between group standard deviations and means (Draper & Smith 1981). Transformations are expressed in terms of the

untransformed variate *Y*. Multiple range tests were conducting using the Ryan-Einot-Gabriel-Welsch (REGW) procedure.

Patterns in the distribution of *C. rodgersii* on the east coast were analysed using a nested analysis of variance (ANOVA), with factors of site and subsite-nested-within-site, and the dependent variable describing mean density (individuals m^{-2}) on replicate transects. The cover of barrens habitat was analysed in the same way, with the dependent variable describing the percentage of each transect that was *C. rodgersii* barrens.

In analysing the significance of differences in any dependent variable among depths, it is necessary to recognise that different depths within the same transect are not independent. Accordingly, we analysed these data using split plot designs. Thus, in analysing data from the Kent group where replicate diver transects were taken at several sites, the ANOVA model comprised main effects of Site and Depth, a nested effect of Transect-within-Site, and interactions of D*S and D*T(S), with corresponding error mean squares as $MS_{T(S)}$, MS_{S*D}, $MS_{within\text{-}cells}$, $MS_{D*T(S)}$, and $MS_{within\text{-}cells}$ respectively. For the main survey on the east coast of Tasmania the design was more complex because there were 3 subsites (abbreviated SS) within each site. In this case the appropriate model recognised main effects of S and D, nested effects of SS(S) and T(SS), and interactions D*S, D*SS(S) and D*T(SS), with corresponding error mean squares $MS_{SS(S)}$, MS_{D*S}, $MS_{T(SS)}$, $MS_{within\text{-}cells}$ error, $MS_{D*SS(S)}$, $MS_{D*T(SS)}$ and $MS_{within\text{-}cells}$ respectively.

Comparisons across different substratum types could adopt a similar approach to the analysis of the effects of depth because measures made on different substratum types within transects are also strictly not independent. However, because some substrata were not represented on particular transects, the analysis was simplified to treat mean values (of the dependent variables associated with particular substrata) across all transects within a subsite as the base level of replication. Thus, because subsites are treated as the replicates, only differences among sites and substratum types were considered in these analyses. In examining the effects of substratum type on independent variables we included in the analysis only those 5*2 m ‘plots’ on each transect that were dominated by

a particular substratum type. A dominant substratum was defined arbitrarily as that occupying >60% of the plot. Note that we obtained qualitatively identical results in other analyses (not presented here) based on data derived by defining the dominant substratum as >70% and >80% of each 5*2 m area.

Multivariate analyses were based on the PRIMER 5 (v. 5.2.9) software (Clarke & Warwick 2001), and used the nMDS, ANOSIM, BIOENV, RELATE and SIMPER routines (details are provided in the results section). Algal community data were analysed by generating a multivariate vector of the mean percentage cover of each species for each subsite.

Results

Long-term changes in *Centrostephanus rodgersii* populations in the Kent Group, Bass St. 1974-2000

Space-time patterns in sea urchin abundance

In 1974 the distribution of *C. rodgersii* in the Kent Group was limited. It was recorded only on the eastern side of Murray Pass but not at two other sites on the western side of Murray Pass, or at sites elsewhere on the eastern (Winter Cove), southern (Squally Cove) and western (Little Squally Cove) sides of Deal Is (Table 1). There was evidence of the initial stages of development of barrens habitat on the south side of East Cove, with destructive grazing of small patches of understorey (Table 2). By 1981, the overall density of *C. rodgersii* at this site had not changed (Table 1), although the animals were more aggregated and largely restricted to depths > 10 m where most of the reef was devoid of macroalgae (Table 2). This pattern in the depth distribution of the sea urchins and associated barrens habitat at East Cove was similar in 2000 (Table 2), and reflected the distribution of *C. rodgersii* and barrens at other sites (Figs. 1a,c).

In 1981, there was still no evidence that *C. rodgersii* occurred at Erith Is on the western side of Murray Pass, although it was recorded in Murray Pass at Dover Is, where patchy barrens were already evident (Table 1). In 1981 the distribution around Deal Is was patchy, since no animals were found on the northern side of East Cove or in Squally Cove, while the urchin was recorded at Garden Cove and at Winter Cover, and patchy barrens were evident at the latter site between 10-15 m (Tables 1,2).

By 1993, *C. rodgersii* was recorded at 8 of 9 sites in the Kent Group (Table 1; data from Barrett & Edgar 1993). In 2000 this species was clearly the dominant invertebrate at all 7 sites visited, and *C. rodgersii* barrens were virtually continuous between ca. 10-18 m depth at most sites, while patchy barrens were evident between 5-10 m (Table 1, Fig. 1a,c). Macroalgae recorded on ‘continuous’ barrens were largely restricted to the top surfaces of large boulders whose topographic relief extended above the local seafloor

level. Notably, by 2000 a wide variety of ages was represented in the population, although the shape of the estimated age-frequency curve indicates that significant recruitment may be sporadic (Fig. 2).

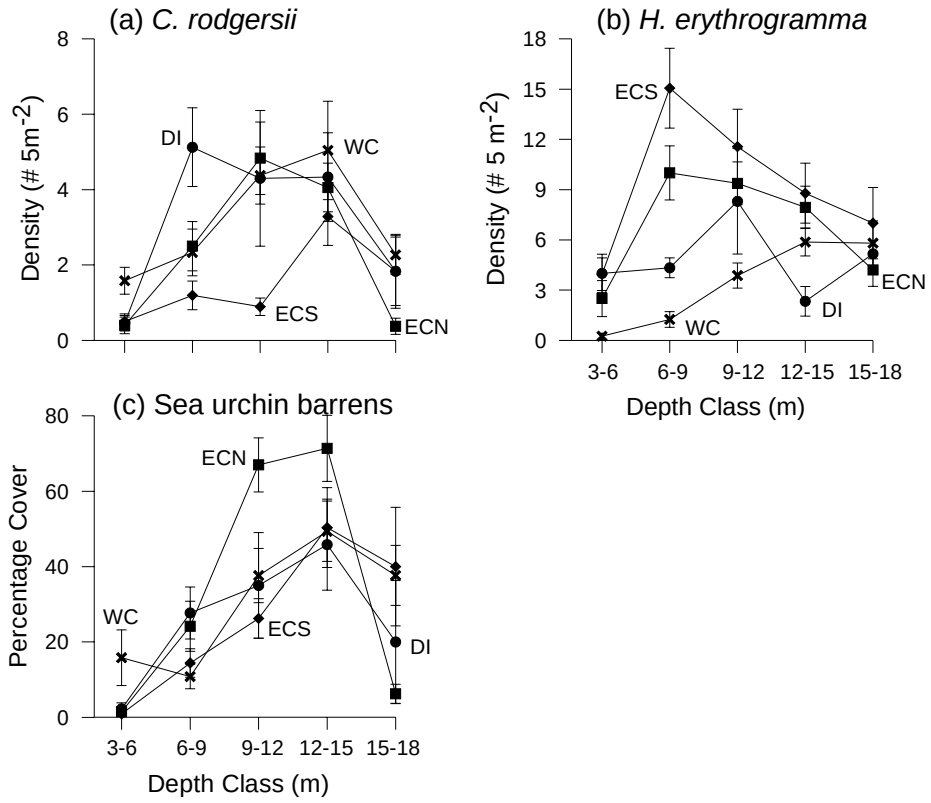


Figure 1. Mean density (±SE) of *C. rodgersii* and *H. erythrogramma* and percentage cover of sea urchin barrens at all sites surveyed in the Kent Group in 2000, by depth. DI = Dover Is; ECS = East Cove south; ECN = East Cove north; WC = Winter Cove.

Table 1. Abundance of *C. rodgersii* 1974-2000 in the Kent Group, Bass St.

Site	Location	Abundance of *C. rodgersii*			
		1974	**1981**	**1993**[1]	**2000**
Erith Is					
Barrett #9	Lat 39° 26.70' S Long 147° 16.56' E	ns	ns	0	ns
Barrett #10	Lat 39° 26.78' S Long 147° 17.57' E	ns	ns	0.14 m^{-2}	ns
Barrett #1	Lat 39° 26.53' S Long 147° 17.74' E	ns	ns	0.035 m^{-2}	ns
Barrett #12	Lat 39° 26.97' S Long 147° 17.97' E	ns	ns	0.215 m^{-2}	ns
West Cove (N)	Lat 39° 27.33' S Long 147° 18.17' E	0	0	ns	PB TI (7-10 m) EB TI (10-15 m)
West Cove (S)	Lat 39° 27.60' S Long 147° 17.96' E	ns	0	ns	ns
SE Corner	Lat 39° 27.72' S Long 147° 17.96' E	0	ns	ns	0
Dover Is					
NE	Lat 39° 27.91' S Long 147° 17.74' E	ns	PB TI	0.87 m^{-2}	0.646 m^{-2} PB TI (6-8 m) EB TI (8-14 m)
NW	Lat 39° 27.85' S Long 147° 17.17' E	ns	R, NB (18-25 m)	ns	ns
Deal Is					
East Cove (N)	Lat 39° 28.14' S Long 147° 18.57' E	ns	0	0.34 m^{-2}	0.526 m^{-2}
East Cove (S)	Lat 39° 28.37' S Long 147° 18.55' E	0.054 m^{-2} PB TII (10-12 m)	0.055 m^{-2} EB TI (10-15 m)	ns	0.257 m^{-2} PB TI (6-11 m) EB TI (11-14m)
Murray Pass (NE)	Lat 39° 27.91' S Long 147° 18.62' E	R, NB (8-20 m)	ns	0.21 m^{-2}	PB TI (6-10 m) EB TI (10-18m)
Garden Cove	Lat 39° 27.08' S Long 147° 19.75' E	ns	P, NB (12-20 m)	ns	ns
Barrett #3	Lat 39° 27.69' S Long 147° 20.72' E	ns	ns	0.13 m^{-2}	ns
Winter Cove	Lat 39° 28.52' S Long 147° 21.20' E	0	PB TII (10-15 m)	0	0.678 m^{-2} PB TI (3-10 m) EB TI (10-18 m)
Squally Cove	Lat 39° 29.36' S Long 147° 20.38' E	0	0	ns	ns
	Lat 39° 29.60' S Long 147° 20.56' E	ns	ns	1.99 m^{-2}	ns
Little Squally Cove	Lat 39° 29.00' S Long 147° 18.44' E	0	ns	ns	0 (2-9m) PB TI (9-17 m) EB TI (17-21 m) PB TI (21-28m) P NB (28-32 m)

Notes: [1]These data are from Barrett & Edgar (1993) who conducted surveys at 5 m depth (these data are presented to provide a more complete time course, and because of the obscurity of the original report). TI=Type I barrens (devoid of under- and overstorey macroalgae); TII = Type II barrens (barren understorey but overstorey largely intact). *C. rodgersii* abundance codes: 0 = no animals observed and no barrens, R = rare, P = present, NB = no barrens, PB = patchy barrens, EB = extensive barrens. Numbers without parentheses refer to densities (no. m^{-2}); numbers in parentheses, e.g. (10-15 m), refer to depths. ns = not surveyed.

Table 2. Mean densities of *C. rodgersii* (*C. ro*), *H. erythrogramma* (*H. er*) and percentage cover of sea urchins barrens by depth, at East Cove (south), Deal Is., 1974-1981. Barrens are distinguished as TI (understorey and overstorey both absent) and TII (understorey absent but canopy present) in 1974 and 1981, but only TI barrens were recorded in 2000. [1]Area surveyed represents the entire area of the contour map, but 100% of this area was not searched. [2]Area surveyed represents total area of belt transects in which 100% of the area was searched.

	1974					1981					2000				
Depth (m)	**[1]Area (m^2)**	***C. ro* # m^{-2}**	***H. er* # m^{-2}**	**TI %**	**TII %**	**[1]Area (m^2)**	***C. ro* # m^{-2}**	***H. er* # m^{-2}**	**TI %**	**TII %**	**Depth (m)**	**[2]Area (m^2)**	***C. ro* # m^{-2}**	***H. er* # m^{-2}**	**TI %**
0-10	48423	0.04	0.51	0	0.1	53576	0.01	0.57	2.5	0	3-6	110	0.10	0.79	0.90
											6-9	180	0.23	3.01	14.40
10-15	25201	0.09	0.90	0	9.5	27397	0.15	1.02	75.9	17.0	9-12	140	0.18	2.31	26.25
											12-15	70	0.66	1.76	50.36
>15	4960	0.00	0.54	0	0	3606	0.13	0.84	88.8	11.5	15-18	30	0.37	1.40	40.00

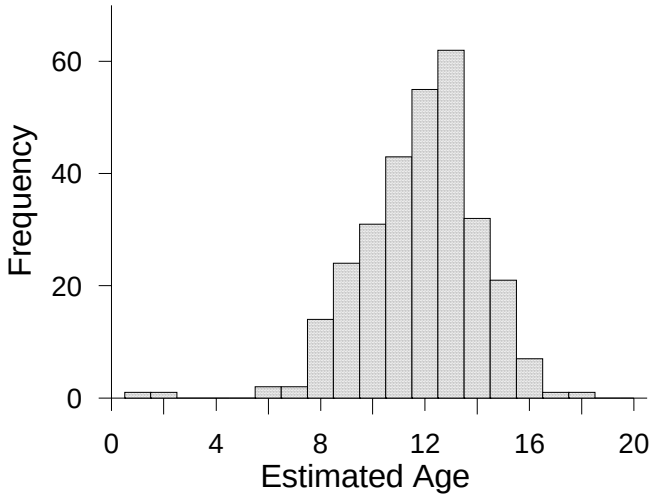


Figure 2. Age-frequency plot for *C. rodgersii* at East Cove, Kent group, June 2000. *N* = 298. Age is estimated from ridge lines on jaws, a technique validated by C. Blount, unpub. data.

The pattern of spatial variation in the distribution of both species of sea urchins and barrens habitat was broadly similar in that all showed significant differences among transects within sites depending on depth, or alternatively, differences among depths depending on the transect (Table 3). At a larger spatial scale, the pattern across depth ranges in the distribution of each species and of sea urchin barrens was broadly similar across the different sites (Table 3, Fig. 1). However, the pattern of depth distribution of

the two sea urchins were distinctly different. At sites where it was most abundant, *H. erythrogramma* was most abundant between 6-12 m, while *C. rodgersii* and barrens habitat were most abundant at deeper depths (9-15 m) (Fig.1). Not surprisingly then, the relationship between *C. rodgersii* and *H. erythrogramma* was negative at a scale of 10 m^2 among sites of high local abundance (Fig. 3a), and there was a clear positive relationship between *C. rodgersii* density and the extent of barrens habitat (Fig. 3b), but not between *H. erythrogramma* density and the extent of barrens (Fig. 3c).

Table 3. Significance of spatial variation in the density of *C. rodgersii* and *H. erythrogramma*, and in the percentage cover of barrens habitat, in the Kent Group, Bass St., from surveys conducted in 2000. Significant effects at α=0.05 are in bold. Abbreviations are D=depth; S=site; T= transect; parentheses indicate nested effect. *P* values of 0.0001 indicate probabilities < 0.0001.

Variable →			*Centrostephanus rodgersii*		*Heliocidaris erythrogramma*		% cover of barrens	
Transformation →			$\sqrt{Y}$		$\log(Y + 0.01)$		no transformation	
Source	**Error Term**	**d.f.**	***F***	***P***	***F***	***P***	***F***	***P***
Site	T(S)	3,12	1.14	0.371	1.09	0.390	0.23	0.876
Transect(Site)	Error	12,309	9.53	**0.0001**	6.95	**0.0001**	7.45	**0.0001**
Depth	D*S	4,12	3.68	**0.035**	5.67	**0.008**	5.01	**0.013**
Depth*Site	D*S(T)	12,31	1.33	0.250	0.99	0.481	1.12	0.378
Depth*Transect(Site)	error	31,309	3.89	**0.0001**	2.76	**0.0001**	5.40	**0.0001**

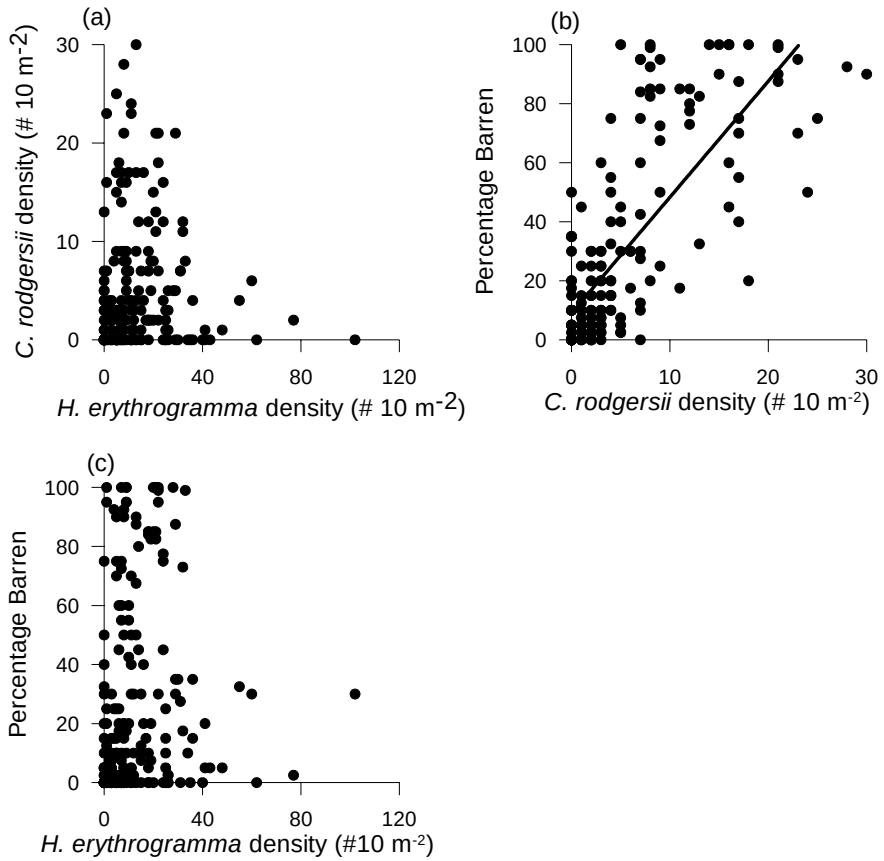


Figure 3. Relationships between (a) the abundance of *H. erythrogramma* and *C. rodgersii*, (b) cover of barrens habitat and *C. rodgersii*, and (c) cover of barrens habitat and *H. erythrogramma* across all sites and depths surveyed in the Kent Group in 2000, at a scale of 10 m^2.

Relationship between C. rodgersii and algal community composition

MDS analysis did not reveal strong patterns in the algal community across depths and sites (Figs. 4a,b). The broad pattern from the MDS showed overlap in algal community composition in 10 m^2 areas across all depth classes, but also showed that variability in the algal community increased with depth (Fig. 4a). There was no evidence of distinct differences in algal community composition among sites (Fig. 4b).

In recognizing that the algal assemblage is potentially influenced by both depth and *C. rodgersii* grazing, we conducted RELATE and BIOENV analyses to examine correlations between the algae and these two variables (excluding 10 m^2 areas >90% barrens). The

correlation between *C. rodgersii* density and overall algal community structure across depths and transects was poor (Fig. 4c) and not significantly different from zero (PRIMER RELATE procedure, ρ=0.006, *P*=0.441, 4999 permutations, algae based on Bray Curtis similarity, square-root transformation; *C. rodgersii* based on Euclidean distance, square-root transformation). In terms of single species, patterns among depth-transect combinations in the combined effects of depth and *C. rodgersii* density were most closely correlated with patterns in *Phyllospora comosa* and *Sargassum heteromorphum*, although the correlations were low (BIOENV, Spearman correlation = 0.16 for both species). *P. comosa* was the only species selected in each of the 10 'best' correlations of combinations of 5 algae with *C. rodgersii* density and depth. *P. comosa* was largely restricted to shallow depths (mean cover = 37.1%±9.5 SE and 14.8%±5.9 SE at depths 3-6 and 6-9 m respectively; <1.5% cover at all other depths), as was *S. heteromorphum*, although the latter species was not a prominent member of the flora (maximum cover was 1.7%±0.6 SE at 6-9 m). *P. comosa* was identified in the SIMPER analysis as one of the species that typify the macroalgal assemblage at 3-6 m, and was the most important species to distinguish algal communities at 3-6 m depth from those in all other depth ranges measured (Table 4). While not all shallow sites supported *P. comosa*, the association of this species with shallow water is clearly evident (Fig. 5a). Given low densities of *C. rodgersii* in shallow water (Fig. 1a), it is not surprising that the relationship between *P. comosa* and *C. rodgersii* density is a marked step function (Fig. 5a), while upper surfaces of relationships between the other abundant species of large brown algae and *C. rodgersii* density are more continuous (Fig. 5b-d). Other than *P. comosa*, the species *Cystophora monilifera*, *Xiphophora chondrophylla* and *Sargassum verruculosum* were most important in distinguishing between algal communities at different depths (Table 4).

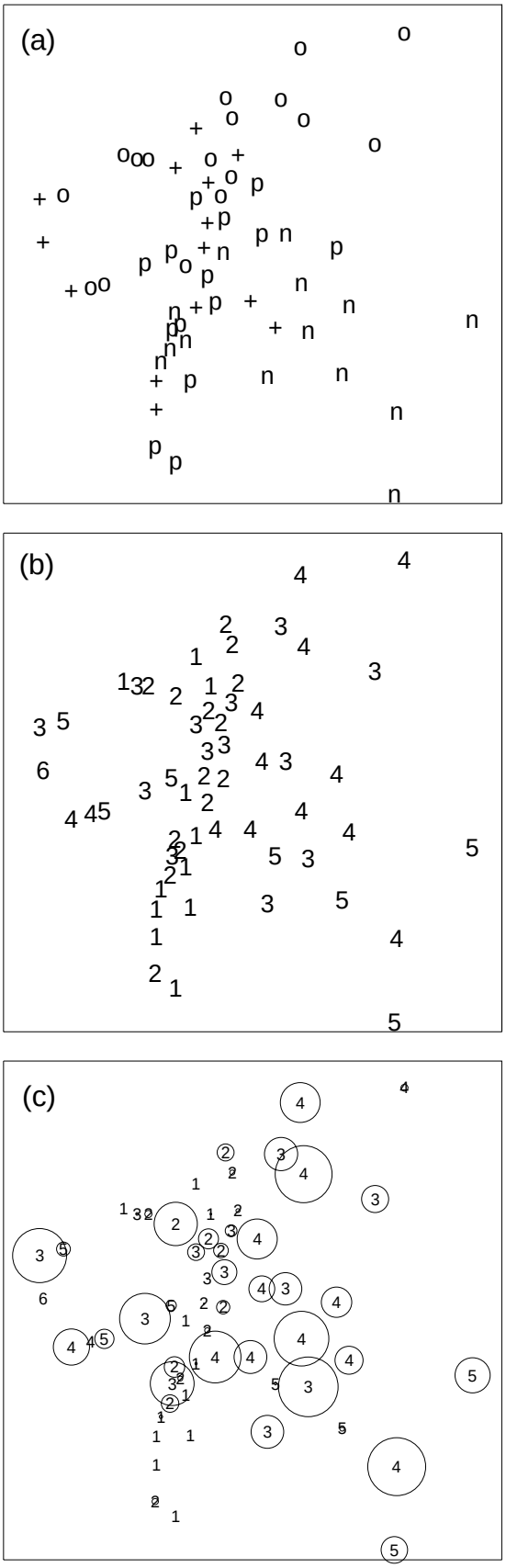


Figure 4. MDS plot based on mean macroalgal community composition on rocky reef habitat in each depth stratum at each transect and site, Kent Group 2000 (4^{th} root transformation, Bray Curtis dissimilarity; stress = 0.21). (a) MDS indicating sites (+ = NE Dover Is.; n = East Cove (north); o = East Cove (south); p = Winter Cove); (b) MDS indicating depths (1 = 3-6 m; 2 = 6-9 m; 3 = 9-12 m; 4 =12-15 m; 5 = 15-18 m); (c) MDS indicating depths (as above) superimposed with a bubble plot representing percentage cover of *C. rodgersii* barrens.

Table 4. Results of SIMPER analysis comparing algal community composition on rocky substratum among depths (Kent Group, 2000). The diagonal gives the % contribution of species to the average Bray Curtis similarity (4^{th} root transformation) within groups, and the mean % cover of identified species (in parentheses), for each depth class. The off-diagonal shows the % contribution of species to the average dissimilarity between groups. Only algae contributing >10% of total similarity or >7% dissimilarity, or where the ratio of mean:standard deviation ≥1.4 for similarities or dissimilarities (indicated by *), are included. For similarities within groups, ratios of mean:SD ≥1.4 identifies species 'typical' of particular depth classes. For dissimilarities between groups, ratios ≥1.4 identify algae that best discriminate between two depth classes. Data are based on mean % cover of algae within transects. '% cont.' = percentage contribution; (% cov.) = percentage cover. *E. radiata = Ecklonia radiata*; *P. comosa = Phyllospora comosa*; *X. chondro. = Xiphophora chondrophylla*; *S. verrucul. = Sargassum verruculosum*; *C. monilifera = Cystophora monilifera*; *C. moniliformis = Cystophora moniliformis*; *C. obscura = Caulerpa obscura*.

	Depth Class (m)									
Depth Class (m)	**3-6**	% cont. (% cov.)	**6-9**	% cont. (% cov.)	**9-12**	% cont. (% cov.)	**12-15**	% cont. (% cov.)	**15-18**	% cont. (% cov.)
3-6	*E. radiata* *	24.6% (16.2%)	*P. comosa*	10.7%	*P. comosa* *	12.6%	*P. comosa* *	13.8%	*P. comosa* *	12.9%
	P. comosa	20.5% (37.1%)	*S. verrucul.* *	8.6%	*S. verrucul.*	7.3%	*E. radiata*	7.1%	*X. chondro.* *	6.8%
	C. monilifera	10.9% (5.9%)								
	X. chondro.	10.4% (4.9%)								
6-9			*E. radiata* *	23.0% (12.9%)	*P. comosa*	8.4%	*P. comosa*	8.5%	*C. monilifera* *	8.1%
			C. monilifera *	15.9% (7.9%)	*S. verrucul.*	7.3%	*C. monilifera* *	6.5%	*S. verrucul.*	7.7%
			S. verrucul.	12.8% (14.1%)			*X. chondro* *	6.0%	*P. comosa*	7.7%
			X. chondro. *	12.7% (3.1%)					*X. chondro.* *	6.7%
9-12					*E. radiata*	19.8% (8.1%)	*E. radiata*	7.4%	*C. monilifera* *	7.8%
					C. monilifera *	18.3% (6.7%)	*S. verrucul.*	7.1%	*E. radiata*	7.6%
					S. verrucul.	12.5% (7.5%)			*C. obscura*	7.1%
					C. moniliformis	10.6% (3.0%)			*S. verrucul.*	7.0%

(continued …)

Table 4 (continued)

	Depth Class (m)			
Depth Class (m)	**12-15**	% cont. (% cov.)	**15-18**	% cont. (% cov.)
12-15	*S. verrucul.*	22.3% (3.5%)	*E. radiata*	9.5%
			C. obscura	8.8%
	E. radiata	21.8% (9.5%)	*C. moniliformis*	7.3%
			S. verrucul.	7.3%
	C. monilifera	13.5% (1.7%)		
15-18			*E. radiata*	29.5% (15.6%)
			C. obscura	19.1% (8.2%)
			reds	10.5% (4.3%)

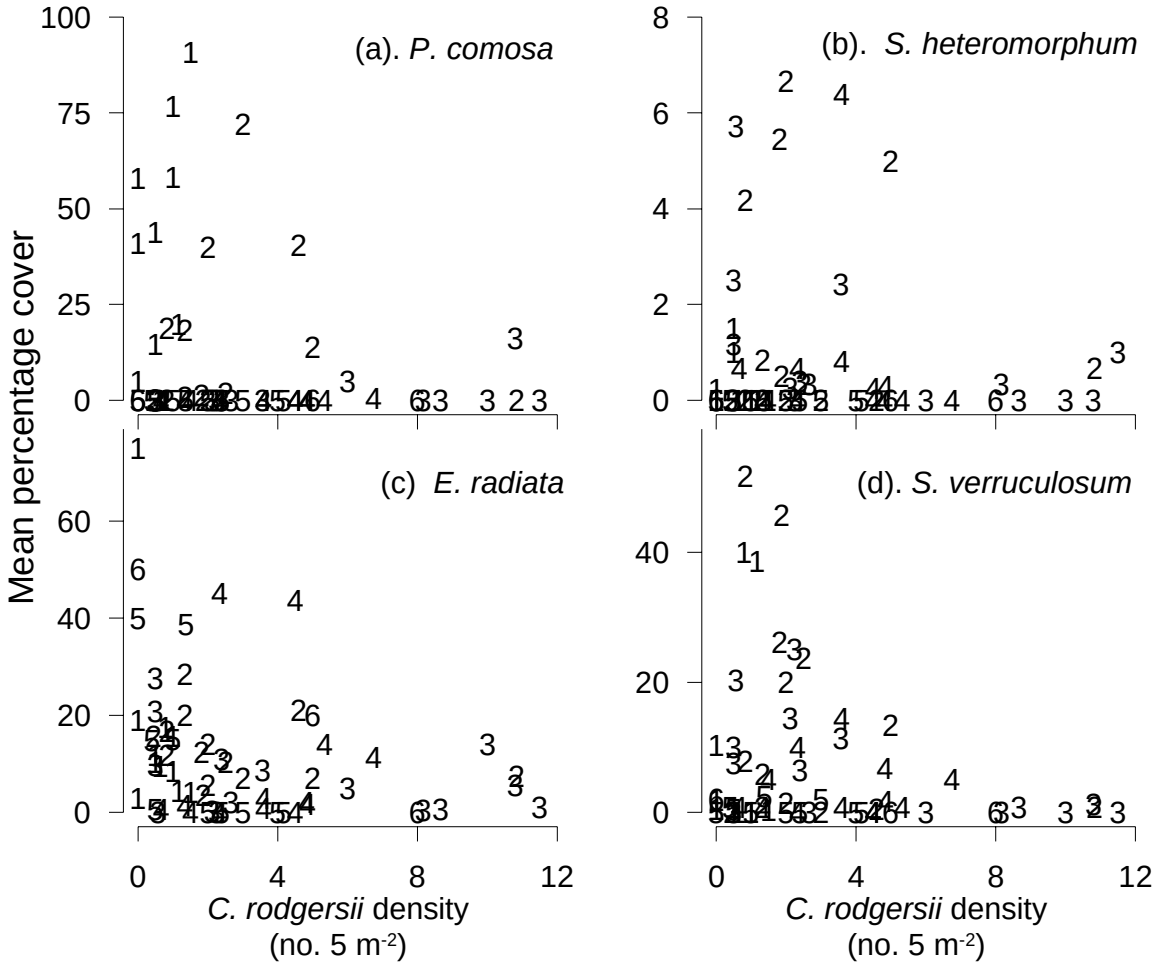


Figure 5. Relationship between cover of abundant canopy-forming brown algae and density of *Centrostephanus rodgersii* on rocky substrata, Kent Group 2000. Algae are (a) *Phyllospora comosa*, (b) *Sargassum heteromorphum*, (c) *Ecklonia radiata*, and (d) *Sargassum verruculosum*. Single species *P. comosa* and *S. heteromorphum* best correlate with depth and the extent of *C. rodgersii* barrens; abundances of *P. comosa*, *E. radiata* and *S. verruculosum* were most important in distinguishing algal community structure among depths. Labels on points refer to depth classes: 1 = 3-6 m, 2 = 6-9 m, 3 = 9-12 m, 4 = 12-15 m, 5 = 15-18 m, 6 = >18 m.

Distribution of *C. rodgersii* on the east coast of Tasmania

Distribution across sites

Diver surveys recorded *C. rodgersii* at all sites between Eddystone Pt (site 1) and SW Tasman Peninsula (site 10) (Figs. 6a,b), although only a single specimen was recorded at the latter site. While *C. rodgersii* was not observed on transects at Bruny Is or further south, it was recorded by other divers (through the SeaCare survey, confirmed by scientific or abalone divers) as far south as Recherche Bay (Fig. 6b). Highest abundances were recorded at St Helens, with a trend of declining abundances southward. However, densities are highly variable across a range of spatial scales. Considering only those sites where >1 sea urchins were recorded in our survey (i.e. sites 1-9 between Eddystone Pt and Fortescue Bay respectively), there is significant variability in sea urchin density among sites (nested model II ANOVA, transformation = $Y^{0.159}$, $F_{8,18} = 4.674$, $P = 0.003$), but not among subsites within sites ($F_{18,81} = 1.596$, $P = 0.081$). In this analysis, a greater amount (29.8%) of the total variance was attributable to variation among sites (~10^4 m) than among subsites (9.1% of total variance; ~10^3 m), while variation among transects within subsites (~10^2 m) accounted for most (61.1%) of the total variance.

Distribution across depths

Pooling across sites (and therefore subsites) where *C. rodgersii* was recorded at >1 m^{-2} (i.e. sites 1-9), the urchin was most abundant at depths >9 m over the depth range considered in the diving surveys (0-18 m) (Fig. 7a). This trend is significant (1-way model I ANOVA, transformation = ln(Y+0.001), $F_{4,111} = 2.63$, $P = 0.038$), despite the high standard errors which reflect considerable variations in the density of *C. rodgersii* among sites and subsites (Appendix 2). The analysis by pooling is valid since there is no evidence of a depth*site interaction (split plot Model III ANOVA; transformation = ln(Y+0.01); depth*site, error = depth*subsite-within-site: $F_{24,46}$= 1.03, $P = 0.45$), or depth*subsite-within-site interaction (depth*site-within-subsite, error = transect*depth*subsite-within-site: $F_{46,109}$= 1.03, $P = 0.45$), despite significant differences in urchin abundance across sites (site, error = subsites-withn-site: $F_{8,18}$= 2.69, $P = 0.038$) and subsites (subsite, error = transects-within-subsite: $F_{18,81}$= 2.07, $P = 0.014$).

Distribution by substratum type

Pooling across depths and sites, there was a significant (1-way model I ANOVA, transformation = ln(Y+0.001), $F_{3,74}$ = 4.84, P = 0.004) trend of higher densities of *C. rodgersii* on large (>1 m and <2.5 m diameter) and very large (>2.5 m and < 5 m diameter) boulders than on other substratum types (Fig. 7b). Despite large differences among sites in the overall density of *C. rodgersii* (Appendix 3), the pattern of utilisation of substratum types was consistent across sites (2-way Model II ANOVA; transformation = ln(Y+0.001); substratum-type*site interaction, $F_{23,43}$= 1.17, P = 0.324; substratum-type, $F_{3,23}$= 5.03, P = 0.008; site, $F_{8,73}$= 3.87, P = 0.002). No *C. rodgersii* were encountered in 5*1 m plots in which cobble, pebble, gravel or sand substrata were the dominant substratum.

Relationship between C. rodgersii and algal community composition

Across those sites where *C. rodgersii* was detected (Sites 1-9), the pattern of similarity among all transect-depth combinations in algal community structure correlated significantly with the pattern of similarity determined from *C. rodgersii* density (PRIMER RELATE procedure, 999 permutations, Spearman correlation, ρ=0.084, P=0.008; algae based on Bray Curtis similarity, square root transformation; *C. rodgersii* based on Euclidean distance, square root transformation). Notably, across sites where *C. rodgersii* was detected, patterns in algal community structure among transect-depth combinations were more strongly correlated with depth (PRIMER BIOENV, Spearman correlation = 0.26; algae based on Bray Curtis similarity, square root transformation; depth based on Euclidean distance, no transformation) than with *C. rodgersii* density (PRIMER BIOENV, Spearman correlation = 0.09; algae based on Bray Curtis similarity, square root transformation; *C. rodgersii* based on Euclidean distance, square root transformation). For the principal canopy-forming species, the relationship between *C. rodgersii* density and cover of *Ecklonia radiata* and *Phyllospora comosa* was poor, while the presence of the sea urchin was mutually exclusive of any significant cover of *Durvillaea potatorum* and *Carpoglossum confluens* (Fig. 8).

Considering all 13 sites, the correlation between the pattern of similarity in algal community structure among transect-depth combinations and the pattern of similarity based on depth alone was also highly significant (RELATE procedure, 4999 permutations, Spearman correlation, ρ=0.186, *P*=0.0002; algae based on Bray Curtis similarity, square root transformation; depth based on Euclidean distance, no transformation). Despite this, correlations between the pattern of similarity among transect-depth combinations described by depth and patterns of similarity based on particular algae or combinations of algae were low. BIOENV analyses showed that the highest Spearman rank correlation with depth for individual species was only 0.16 for *Ecklonia radiata* and *Carpomitra costata*, and 0.13 for *Caulerpa flexilis* (see also Fig. 9). For combinations of 4 and 5 species of algae, *E. radiata*, *Lessonia corrugata* and *Durvillaea potatorum* were the three species that were consistently represented in the 10 highest correlations with depth (the highest Spearman rank correlation for combinations of five species with depth was 0.265; see Fig. 8). Unlike the case for the Kent group, the relationship between depth and abundance of *Phyllospora comosa* was poorly defined (Fig. 9).

Given the strong influence of depth on algal community structure, that the distribution of *C. rodgersii* was also depth-dependent, and because not all depth classes were represented at each site or transect, we standardised for the effect of depth by analysing the relationship between algal community composition and *C. rodgersii* density within a restricted depth range (8-15 m). All transects at all 13 sites covered this range. Within this depth range, there were highly significant differences among sites and subsites in algal community composition (nested ANOSIM based on Bray Curtis matrix, square root transformation, 4999 permutations, *P*<0.0001 for both). Notably, differences in the composition of algae among sites reflected a gradient of change with latitude (PRIMER seriation test, ρ=0.43, *P*<0.001), which is clearly reflected in the associated MDS plot (Fig. 10). This change is, in part, associated with crossing the boundary between the Freycinet and Bruny bioregions (Fig. 10). Among those sites (1-9) where *C. rodgersii* was recorded, despite large variations in algal community structure among sites and subsites, the correlation between patterns among transects in *C. rodgersii* density and

patterns in algal community structure is poor (Fig. 9) and not significantly different from zero (PRIMER RELATE procedure, 999 permutations, Spearman correlation, ρ=0.066, P=0.136; this relationship was not improved by including all 13 sites in the analysis). The marked difference in this result and the significant correlation indicated between *C. rodgersii* density and algal community structure when all depths are considered reflects that both the density of *C. rodgersii* and algal community structure vary with depth. When variability due to depth is removed, there is no evidence of any relationship between *C. rodgersii* density and algal community structure.

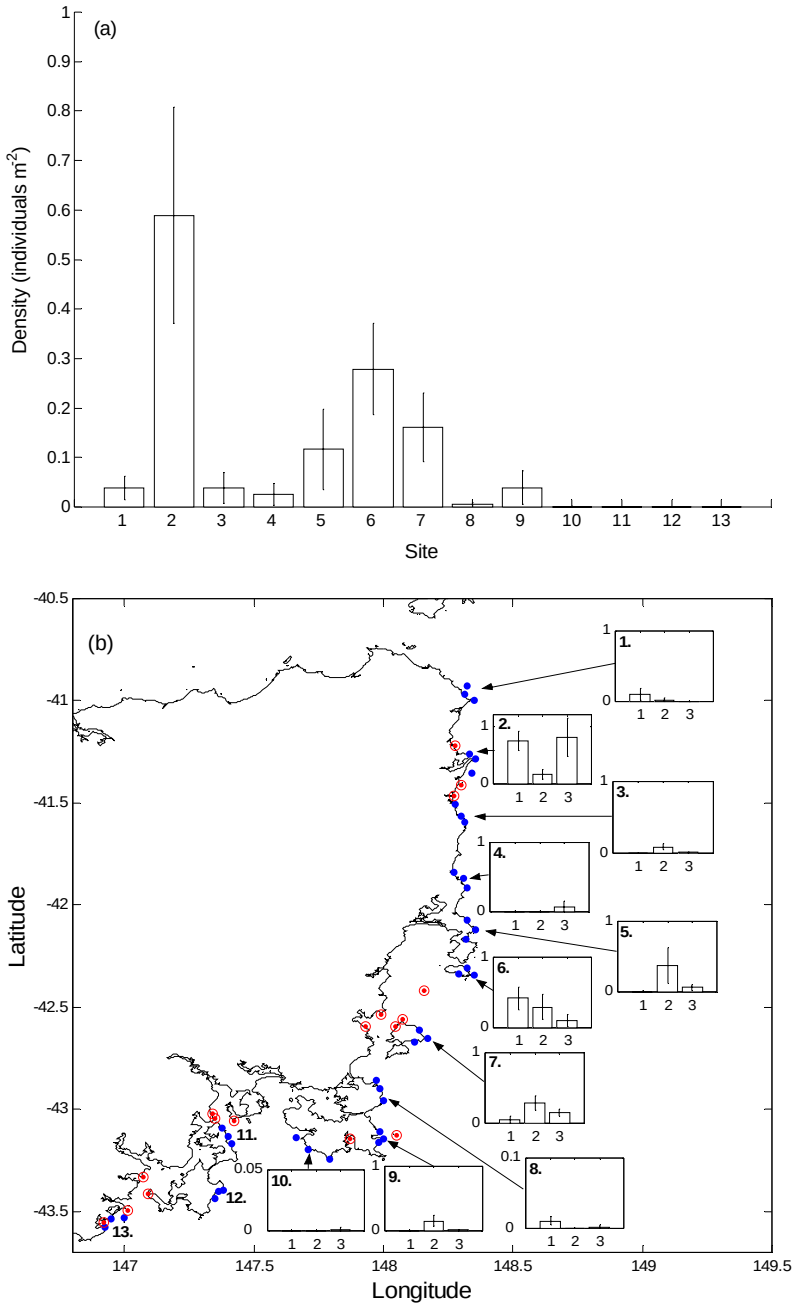


Figure 6. Mean density (per m^2) of *C. rodgersii* at each (a) site (±SE based on subsites as replicates) and (b) subsite (±SE based on transects within subsites as replicates) on the east coast of Tasmania. In (b), blue marks indicate positions of dive transects, and red circles indicate sites where *C. rodgersii* has been recorded as present but which were not part of the formal survey. Site codes are 1=Eddystone Pt, 2=St Helens, 3=Ironhouse Pt, 4=Bicheno, 5=Cape Tourville, 6=Schouten Is, 7=Maria Is, 8 =NE Forestier Peninsula, 9=Fortescue Bay, 10=SW Tasman Peninsula, 11= North Bruny Is, 12=South Bruny Is, 13=Recherche Bay.

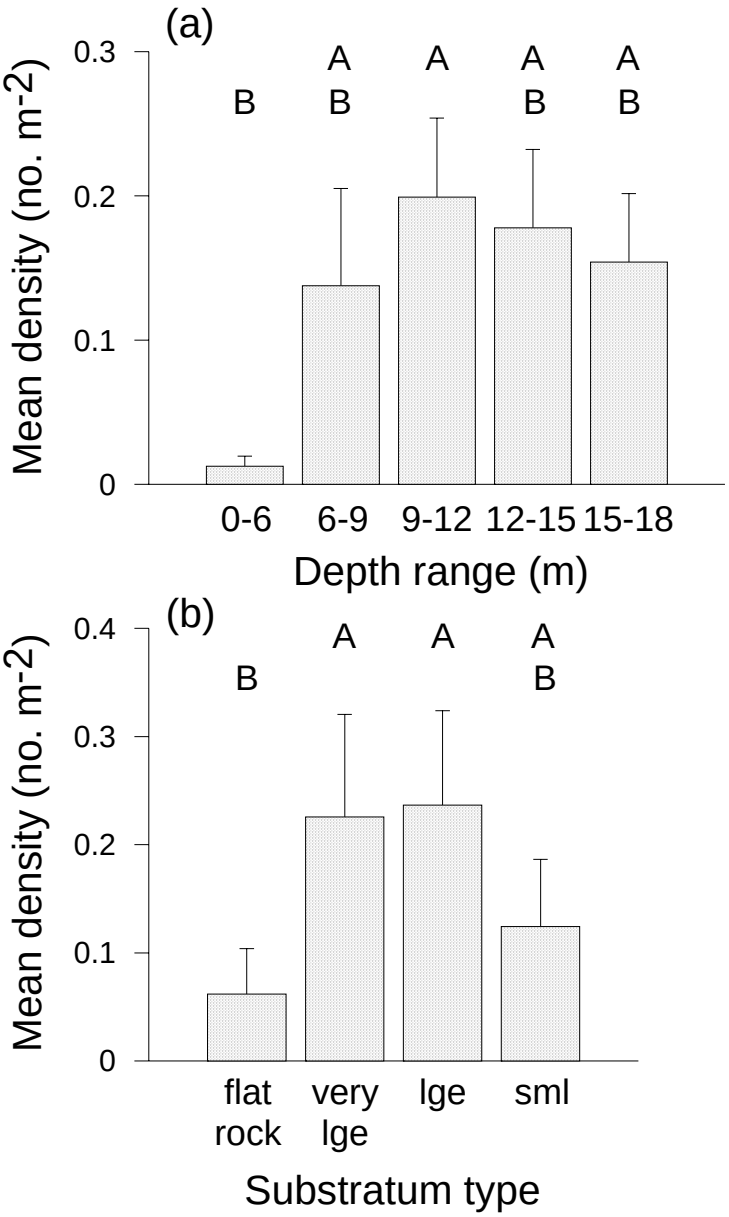


Figure 7. Patterns in the distribution of *C. rodgersii* (pooled across sites 1-9) with (a) depth and (b) dominant substratum type, based on diver surveys to 18 m depth. No sea urchins were found in quadrats dominated by other substratum types (cobble, pebbles, gravel or sand, which accounted for 2.1%, 0.6%, 0.6% and 6.0% of the total substratum across all 9 sites respectively). Dominant substratum type is that covering >60% of a 5*2 m plot. Note that qualitatively identical results were obtained using dominance criteria of >70% and >80% of the quadrat area, and using 5*1 m quadrats. Letters A/B indicate REGW-groupings in multiple range tests following ANOVA. Abbreviations: very lge = very large boulders; lge=large boulders; sml=small boulders (see Methods for definitions). Data are means +SE.

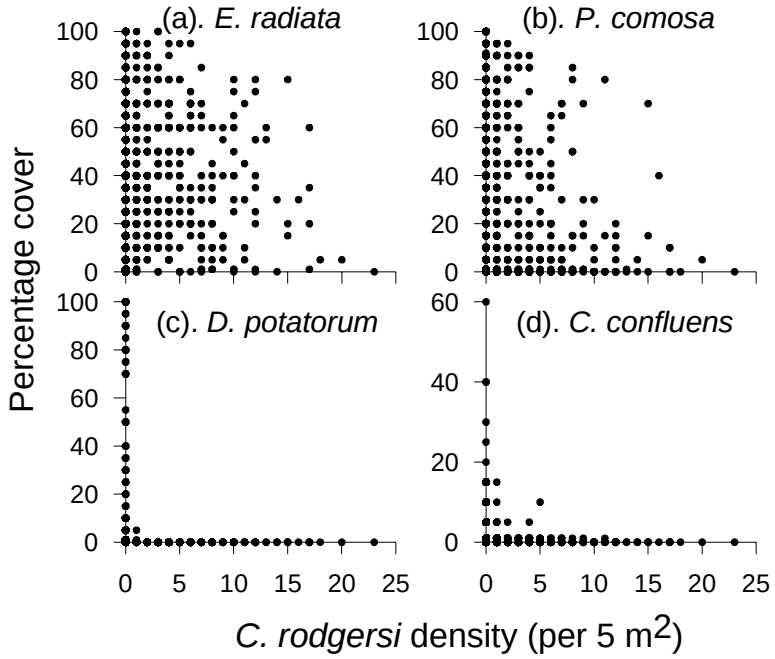


Figure 8. Relationship between cover of the main canopy-forming algae and density of *C. rodgersii* in 5 m^2 plots, sites 1-9. On the east coast, *Durvillaea potatorum* (c) usually develops in a distinct zone above *Phyllospora comosa* (b), while *Ecklonia radiata* (a) grows in a broad zone beneath *P. comosa*. *Carpoglossum confluences* (d) can form locally dense patches, usually within the shallower portion of the *E. radiata* zone.

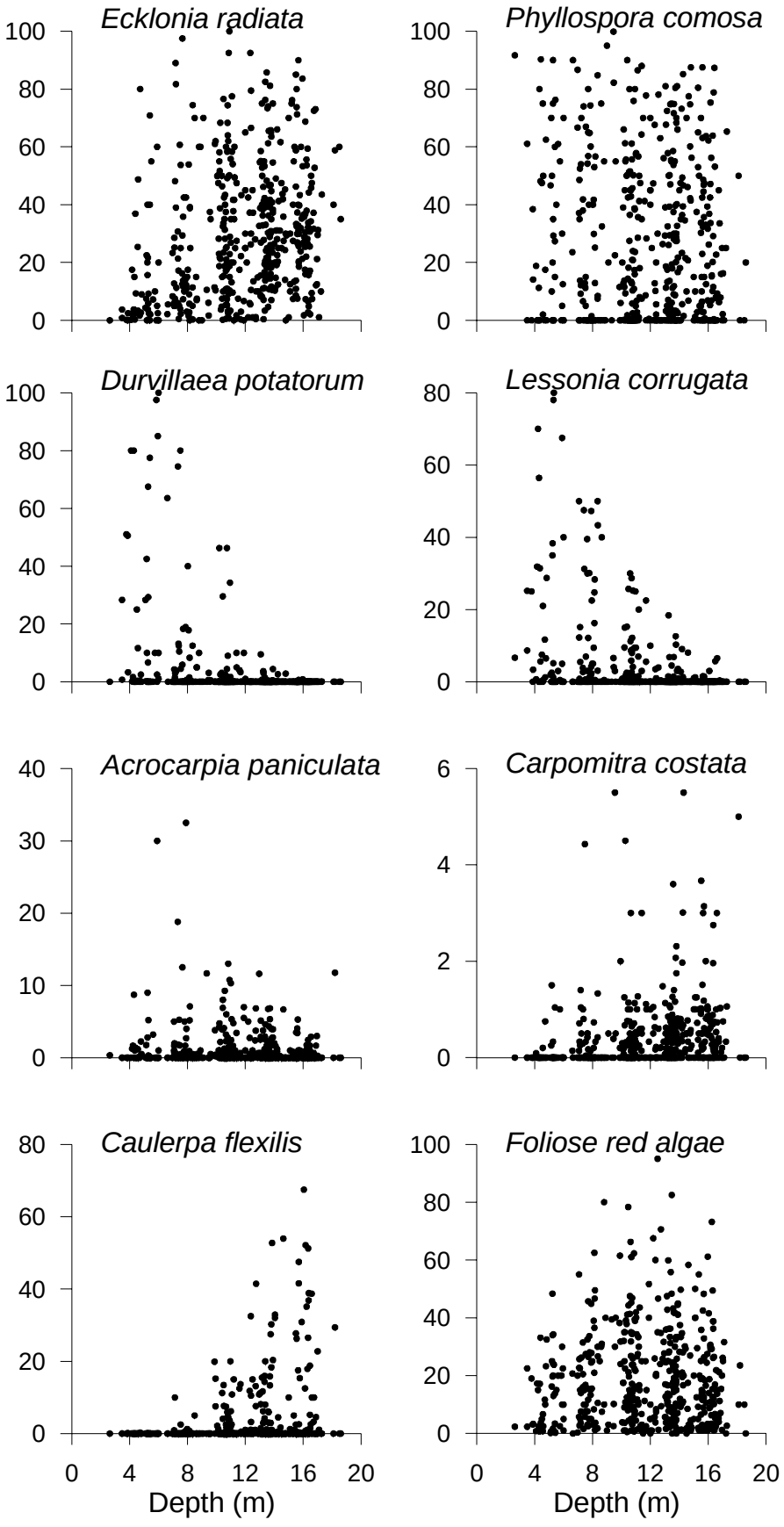


Figure 9. Relationship between algal cover and depth across all sites for the most abundant species and species identified as best correlating with depth in the BIOENV analysis. Each point represents mean cover across a 3 m depth stratum (3-6 m, 6-9 m, … , 15-18 m) on a single transect, and depth is calculated as the mean of all 10 m^2 'quadrats' within the depth stratum on the transect.

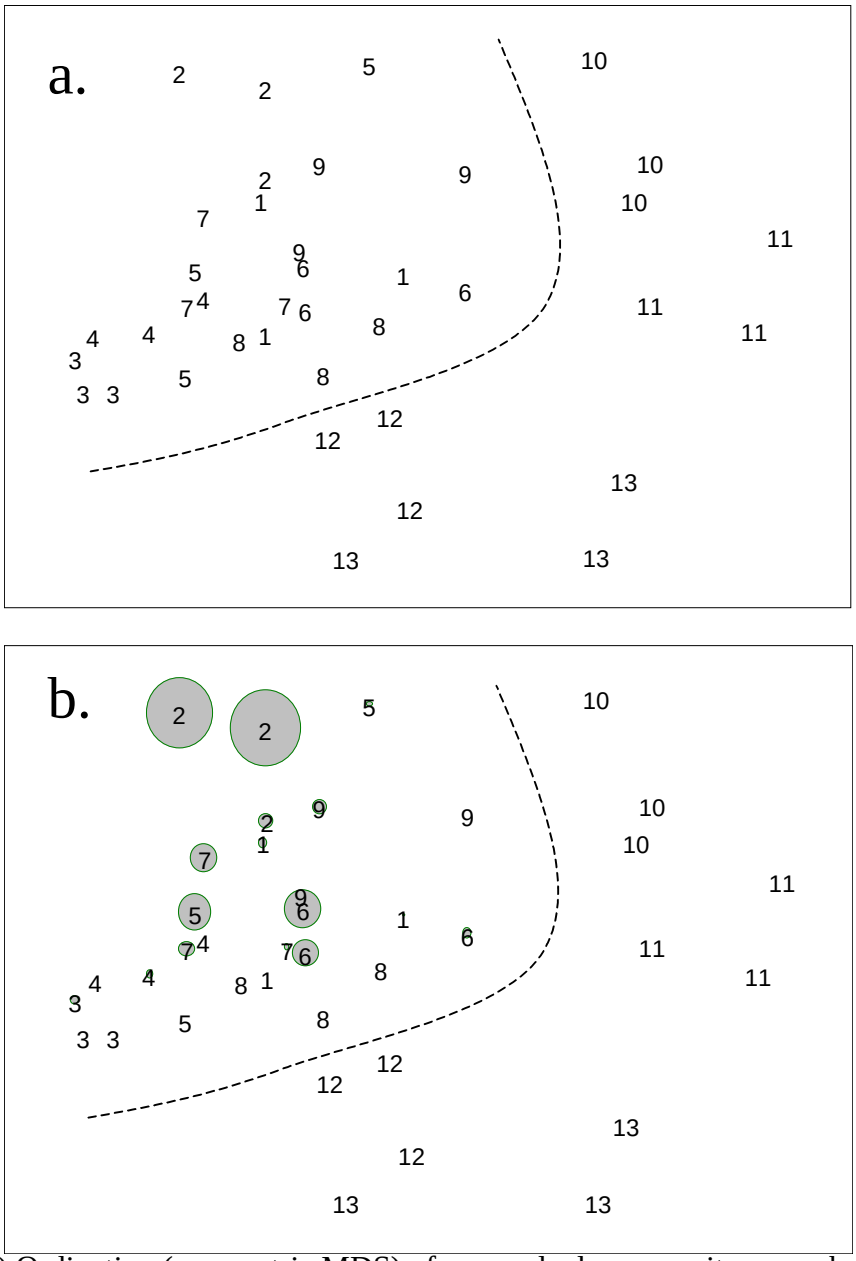


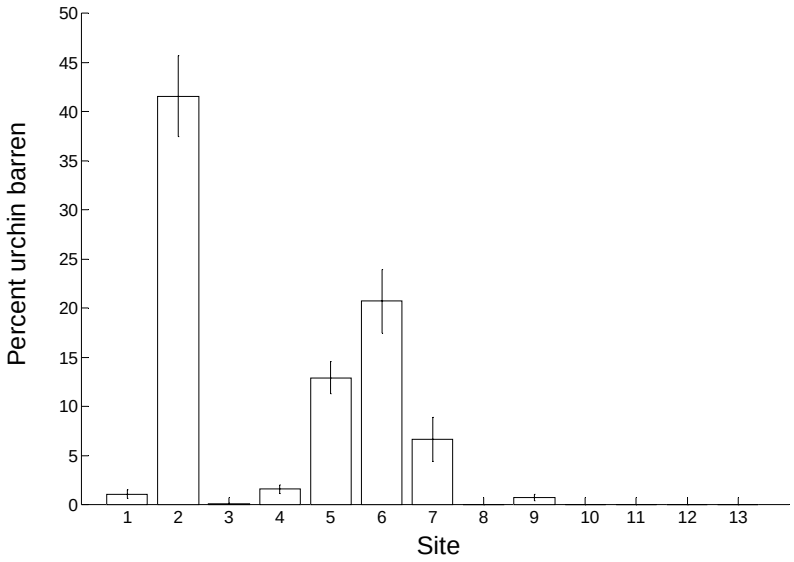
Figure 10. (a) Ordination (non-metric MDS) of macroalgal community on rocky substrata in depths 8-15 m across sites and subsites (based on Bray-Curtis dissimilarity matrix obtained from square root transformed data), and (b) the ordination overlaid with a bubbleplot of *C. rodgersii* density. The dotted line separates sites where >1 *C. rodgersii* were recorded (left hand side) from those where only a single animal (site 10) or no specimens (sites 11-13) were found. It also separates east coast sites (1-9) from those in the southeast (10-13) to the west of 147° 50' E. Sites 8-13 are in the Bruny Bioregion while sites 1-7 are located in the Freycinet Bioregion. Minimum stress for the ordination = 0.15. Site codes (1-13) are as in Figure 6.

Distribution of *C. rodgersii* barrens on the east coast of Tasmania

Patterns in the distribution of barrens habitat determined from >80 km of towed underwater video were broadly similar to patterns of variability in *C. rodgersii* density (Fig. 11). All analyses of *C. rodgersii* barrens are restricted to those sites (1-9) at which >1 animals were found. Pooling across all four categories of *C. rodgersii* barrens, there was significant variation among sites and subsites in the distribution of barrens (Fig. 11; nested Model II ANOVA, transformation = $Y^{0.1}$; sites, $F_{8,18} = 14.7$, $P < 0.001$; subsites $F_{18,79} = 1.15$, $P = 0.326$). Most (53.8%) of the variation was evident at the largest spatial scale (~10^4–10^5 m = among sites) and smallest scale (~10^2 m; 44.5% of total variance explained by variation among transects within subsites). Differences among subsites within sites (scale ~10^3 m) accounted for very little (1.7%) of the total variation. This reflects that there are large differences in the amount of barrens habitat among sites and that, at sites where barrens do occur, barrens occur patchily at scales of 10^1-10^2 m and in most cases are not yet coalesced to form continuous barrens along large sections of coastline as occurs in the Kent Group. However, within sites, the spatial pattern of barrens formation is remarkably consistent over scales 0.3-0.5 km.

Considering the different types of sea-urchin barrens we recognised, which reflect a range of stages in barrens formation between incipient barrens (Type 4) and extensive well-established barrens (Type 1), it is clear that the most extensive barrens occur in the vicinity of St Helens (site 2), although large tracts of barrens are also evident at Schouten Is (site 6) (Fig. 12). Incipient and intermediate stages of barrens formation were also most extensive off St Helens and at Schouten Is that at other sites, but were also commonly encountered of Cape Tourville (site 5), Maria Is (site 7), and occur at Fortescue Bay (site 9) (Fig. 12).

(a)



(b)

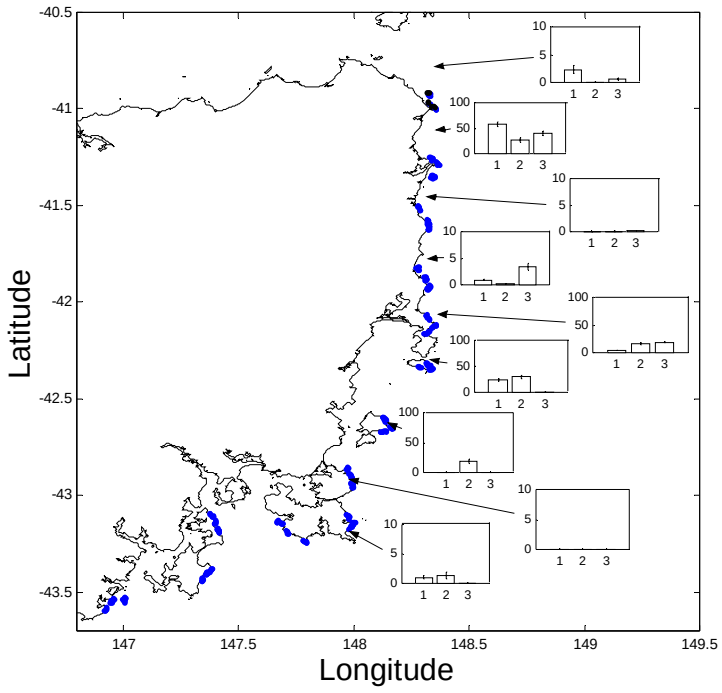


Figure 11. Mean cover of *C. rodgersii* barrens on rocky reef at each (a) site (±SE based on subsites as replicates) and (b) subsite (±SE based on transects within subsites as replicates) on the east coast of Tasmania determined from video transects. All types of barrens (see Methods) are pooled. In (b), blue marks indicate positions of transects. Site codes are as in Fig. 6.

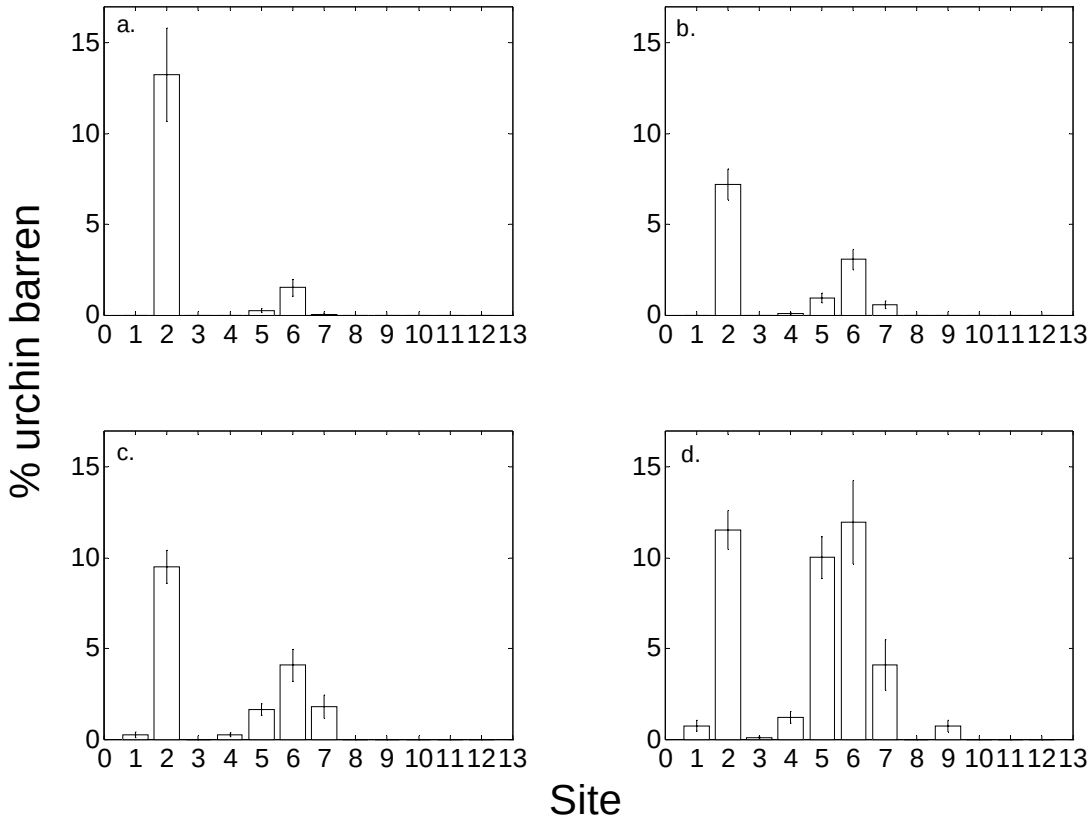


Figure 12. Extent of (a) continuous (Type 1) *C. rodgersii* barrens, and various stages of incipient barrens ((b) Type 2, (c) Type 3, and (d) Type 4; see methods for definitions) across all sites. Data are means ± SE based on subsites as replicates (i.e. pooling across transects). Site codes are as in Fig. 6.

Similar to patterns of density, the broad patterns in the distribution of barrens indicated that this habitat is most extensive in deeper (15-30+ m) water with greatest prevalence in the depth range 20-25 m (Fig. 13a), and in habitats dominated by boulders rather than by other kinds of rocky substratum (Fig. 13b). Analyses showing that differences in the extent of barrens on the three abundant substratum types (unclassified reef, boulders and flat rock) were not consistent among sites (2-way Model III ANOVA, transformation = $Y^{0.26}$, site*substratum: $F_{16,80} = 3.38$, $P = 0.0004$; analysis based on weighted means across transects within subsites), and that differences in the extent of barrens among depths were not consistent among sites (split plot Model III ANOVA, transformation = $Y^{0.23}$, site*depth: $F_{30,60} = 1.94$, $P = 0.014$), reflect that there was virtually no *C. rodgersii* barrens at some sites. The pattern of increasing cover of barrens habitat with depth is

most prominent on boulder substratum (Fig. 13 c). However, it is not possible to assess whether the most extensive barrens (which occur at depths >18 m) reflects *C. rodgersii* density, since diver surveys of density were limited to shallower (≤18 m) depths.

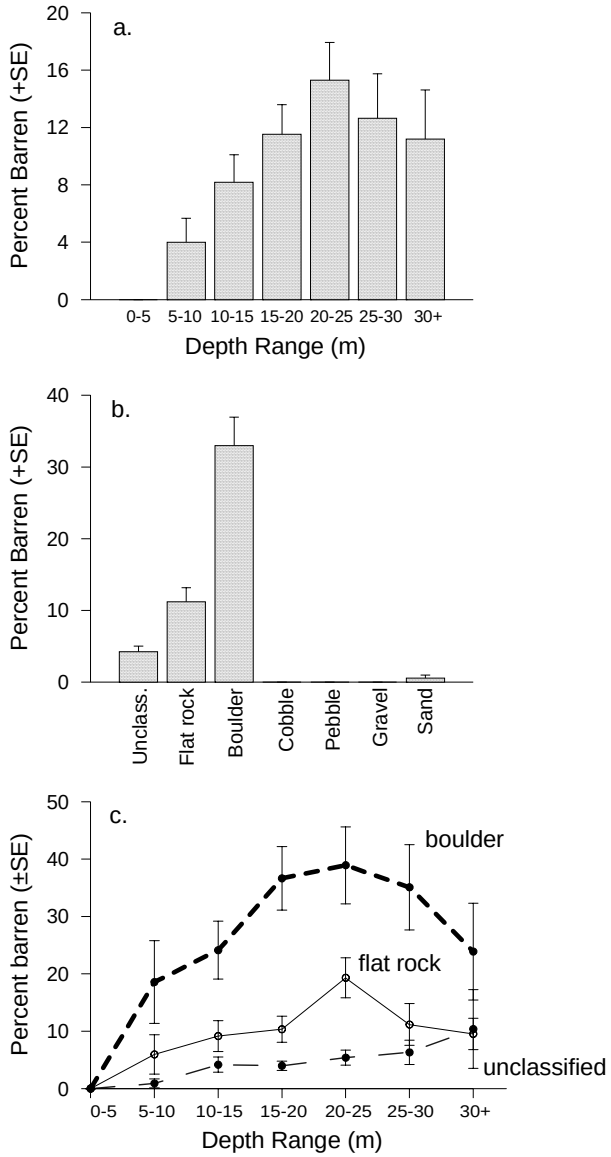


Figure 13. Distribution of *C. rodgersii* barrens determined by video transects across sites 1-9 dependent on (a) depth and (b) substratum type. In (c) the distribution of barrens by depth is given for the main substratum types encountered. 'Unclass.' = unclassified reef substratum (this arises when the substratum type cannot be clearly interpreted); sand refers to patchy reef where >60% of the substratum is sand. Barren Types1-4 are pooled in this analysis. The relative cover of hard substratum types encountered in the video survey was 49.2% unclassified reef; 32.4% flat rock; 18.1% boulder substratum; 0.04% cobble reef; 0.06% pebble reef; 0.2% gravel reef.

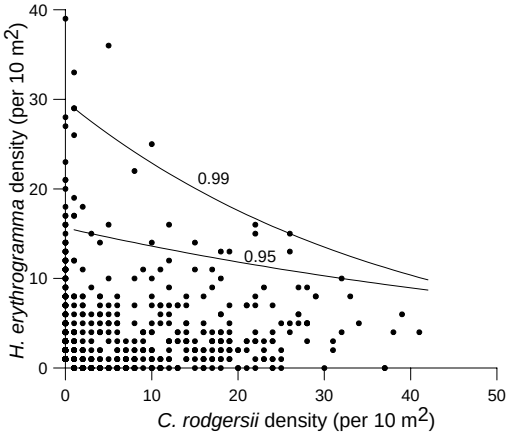
We interpret the sea urchins barrens we encountered as formed and maintained by grazing of *C. rodgersii* and not *Heliocidaris erythrogamma* on the basis of the relationship between *C. rodgersii* and *H. erythrogamma,* and between *C. rodgersii* and *H. erythrogamma* and the extent of barrens habitat. These relationships were qualitatively identical to those evident in the Kent Group, namely that the two sea urchins are negatively correlated where they occur abundantly (Fig. 14a), and that there exists a clear positive relationship between the extent of barrens habitat and *C. rodgersii* abundance (Fig. 14b), but not between the extent of barrens and abundance of *H. erythrogramma* (Fig. 14c).

Relationship between *C. rodgersii* and commercial species

The black lip abalone (*Haliotis rubra*) and southern rock lobster (*Jasus edwardsii*) are the two most valuable commercial species associated with shallow rocky reef in Tasmanian waters. Pooling data across sites 1-9, it is clear that both commercial species show a significant negative relationship with *C. rodgersii* (Figs. 15a,b). The nature of this relationship is a triangular 'factor ceiling' distribution, suggesting that other factors also influence abundances of *H. rubra* and *J. edwardsii*, but that *C. rodgersii* density sets an upper limit to abundances of these commercial species.

At 'paired' sites (St Helens Is, Elephant Rock and Mistaken Cape at Maria Is) where abalone density was compared on *C. rodgersii* barrens and in adjacent macroalgal beds at the same depth and on the same substratum type, abalone abundance was consistently higher in the kelp beds than in adjacent Type 1 barrens habitat at St Helens Is and Elephant Rock (Fig. 16). On these barrens, abalone do not occur in commercial quantities. At Mistaken Cape where the *C. rodgersii* barrens at 15-18 m depth are largely incipient Type 4 barrens, abalone densities were similar inside and outside the grazed patches (Fig. 16). Similar analyses were not possible for rock lobster because abundances of this species were low in all habitats examined at these three sites.

(a)



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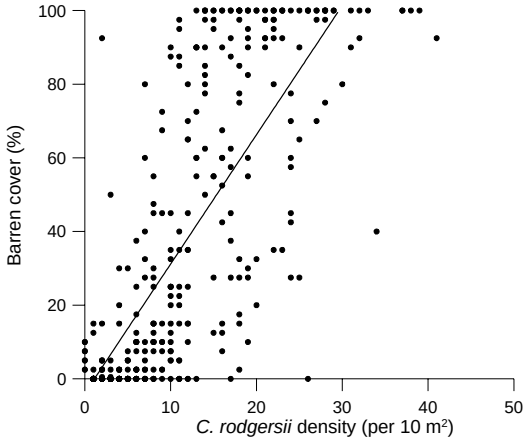


(c)

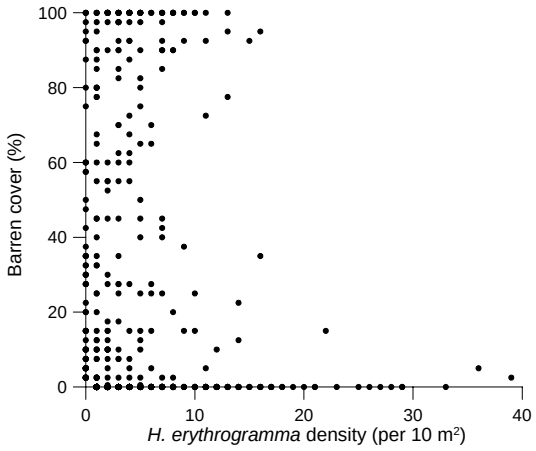
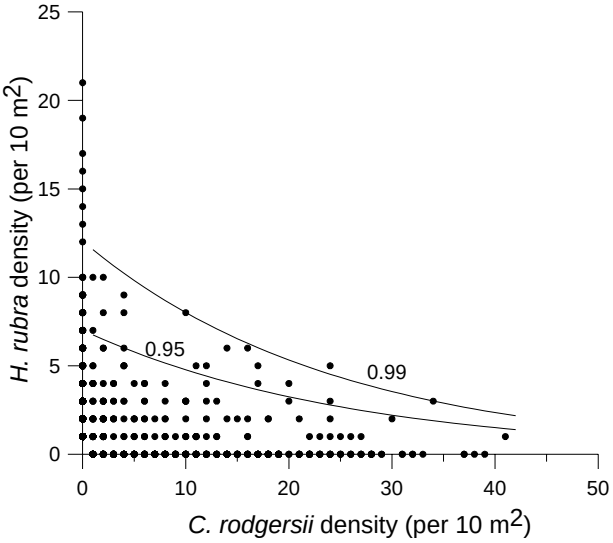


Figure 14. Relationships between (a) the abundance of *H. erythrogramma* and *C. rodgersii*, (b) cover of barrens habitat and *C. rodgersii*, and (c) cover of barrens habitat and *H. erythrogramma* at sites 1-9 in depths ≤18 m (at a scale of 10 m^2). In (a), lines for the 99^{th} and 95^{th} quantiles are given: 99^{th} quantile, y = exp(-0.0264 x +3.394), P<0.0001; 95^{th} quantile, exp(-0.014 x +2.751, P=0.056. In (b), y = 3.51 x – 3.87, P<0.0001.

(a)



(b)

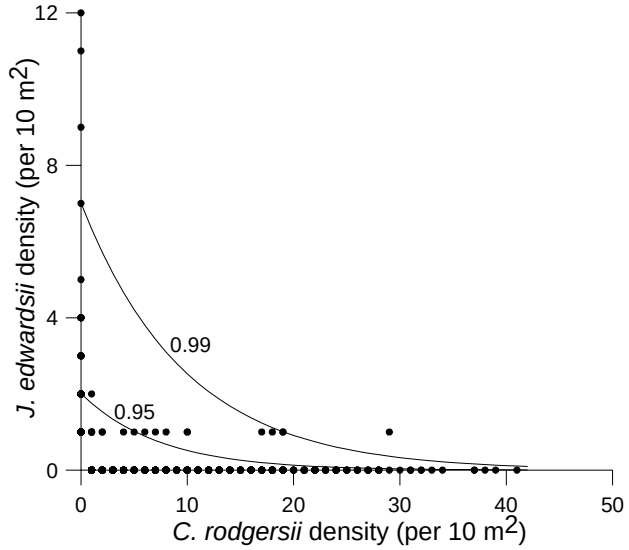


Figure 15. Relationship between abundances of *C. rodgersii* and (a) *H. rubra* and (b) *J. edwardsii* at a scale of 10 m^2 across sites 1-9. Quantile regressions (95^{th} and 99^{th} quantiles) reveal significant negative relationships in both cases. In (a), 99^{th} quantile, $y = \exp(-0.040\ x + 2.489)$, $P < 0.0001$; 95^{th} quantile, $y = \exp(-0.038\ x + 1.947)$, $P = 0.0016$. In (b), 99^{th} quantile, $y = \exp(-0.102\ x + 1.947)$, $P = 0.0001$; 95^{th} quantile, $y = \exp(-0.136\ x + 0.698)$, $P < 0.0001$.

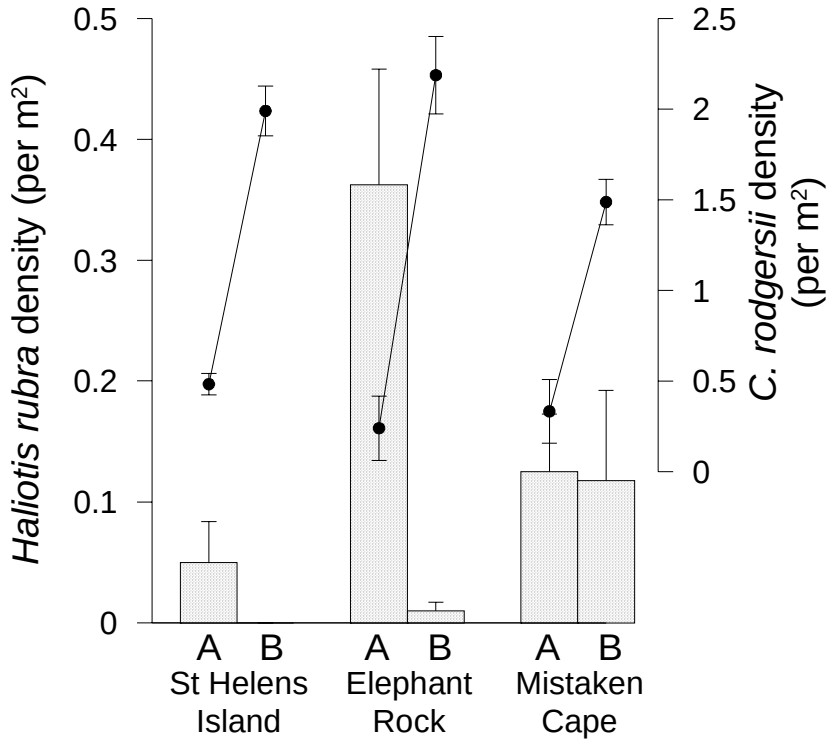


Figure 16. Comparison of densities of abalone (*H. rubra*, bar chart, left hand axis) and sea urchins (*C. rodgersii*, line chart, right hand axis) in macroalgal habitat (A) and in adjacent *C. rodgersii* barrens (B) at 15-18 m depth at St Helens Is, Elephant Rock, and Mistaken Cape. At St Helens Is and Elephant Rock barrens are Type 1, while at Mistaken Cape barrens are largely Type 4. ANOVA indicated that abalone are significantly less abundant on Type 1 barrens habitat than in adjacent sites supporting dense macroalgal cover (Model III 2-way ANOVA: transformation = $Y^{0.19}$; habitat (=fixed), $F_{1,1} = 264.4$, $P = 0.039$; site (= random) $F_{1,12} = 11.51$, $P = 0.005$; habitat*site, $F_{1,12} = 0.18$, $P = 0.677$). At Mistaken Cape, differences in abalone abundances inside and outside of small patches of barrens were not significant (Model I 1-way ANOVA: no transformation; habitat, $F_{1,6} = 0.01$, $P = 0.935$).

Genetic relationships among *C. rodgersii* populations, NSW to Tasmania

Overall, the genetic structure of populations of *C. rodgersii* from the three locations was very similar, and showed no evidence that Tasmanian populations may have established through a single founder event or that they remain isolated from other populations. All three populations had high levels of allelic diversity (mean number of alleles per site was 5.3-5.8; Table 4), with most alleles, including the rare ones, occurring in all three populations. The only exceptions were the two rare alleles Pgm^{40} and Mpi^{40} which were absent from the Fortesque Bay sample (Table 4). Genetic differences between the three populations were minor, with both Nei's genetic distance and pairwise F_{st} values reflecting the close similarities in all populations (Table 6). In addition there was no evidence of genetic subdivision among the three sites (mean F_{st} = -0.0009, 95% CI = –0.0047 – 0.0034).

The levels of single-locus heterozygosity closely matched expectations for Hardy-Weinberg Equilibrium in all populations. Of 12 single-locus tests across the 4 loci, we found 7 cases of heterozygote deficits and 5 heterozygote excesses (Table 5). Only two of these differed significantly from expectations under assumptions of random mating (heterozygote deficits at *Aat* and *Mpi* in the Deal Island population; Table 4). However, if the nominal level (α=0.05) is corrected to control for compounding of Type I errors due to multiple tests, then none of the loci in any population deviates significantly from Hardy-Weinberg expectations. In sum, the genetic analyses indicate clearly that, despite evidence of heterozygote deficit in some alleles in the Bass Strait population, the three populations are remarkably genetically similar, and there is no evidence of founder effects or any other mechanism that has realised limited gene flow between these populations.

Table 4. Allele frequencies and summary statistics of polymorphic loci estimated for populations at Bass Pt (NSW), Deal Is (Kent Group, Bass Strait), and Fortescue Bay (SE Tasmania). Loci are glucosephosphate isomerase (*Gpi*), aspartate amino transferase (*Aat*), phosphogluco mutase (*Pgm*), and mannose phosphate isomerase (*Mpi*). *N* indicates sample size.

Locus	**Allele Frequency**		
Allele (relative mobility)	**Bass Pt NSW**	**Deal Is Bass St**	**Fortescue Bay**
Gpi			
(*N*)	60	60	58
60	0.033	0.008	0.009
80	0.308	0.300	0.241
100	0.625	0.667	0.716
120	0.025	0.017	0.026
140	0.008	0.008	0.009
Aat			
(*N*)	60	57	54
90	0.058	0.079	0.028
100	0.908	0.904	0.954
110	0.033	0.018	0.019
Pgm			
(*N*)	51	53	58
40	0.039	0.028	0.000
60	0.157	0.170	0.112
80	0.206	0.245	0.198
100	0.343	0.406	0.500
120	0.176	0.132	0.155
140	0.078	0.019	0.034
Mpi			
(*N*)	46	46	54
40	0.011	0.022	0.000
60	0.076	0.109	0.093
70	0.022	0.022	0.009
80	0.283	0.261	0.231
90	0.087	0.054	0.028
100	0.283	0.326	0.352
110	0.054	0.000	0.019
120	0.141	0.141	0.222
140	0.043	0.065	0.046
Mean alleles per locus (SE)	5.8 (1.3)	5.5 (1.0)	5.3 (1.0)
Mean heterozygosity per locus:			
Direct count (SE)	0.519 (.151)	0.441 (.140)	0.430 (.134)
[1]Expected HdyWbg (SE)	0.571 (.149)	0.544 (.141)	0.492 (.152)

[1]Expected mean heterozygosity assuming Hardy-Weinburg equilibrium.

Table 5. Estimated deviations from Hardy-Weinberg equilibrium for each locus in each population expressed as Wright's Fixation Index (*f*). For this index, positive values indicate heterozygote deficits, while negative values indicate heterozygote excesses. The significance of deviations from expected frequencies of alleles assuming Hardy-Weinberg equilibrium, based on Fisher exact tests after pooling of rare alleles, is given in parentheses (data are *P* values). Significant deviations (shown in bold) are based on α=0.05. Note that after adjusting the nominal significance level by the Dunn-Sidak method (α_{new}=0.0043) to control for compounding of Type I error in conducting 12 simultaneous tests, none of the test results indicate significant deviation from Hardy-Weinberg equilibrium. Locus abbreviations as for Table 4.

Population	**Locus**			
	Gpi	***Aat***	***Pgm***	***Mpi***
Bass Pt (NSW)	0.057 (0.785)	0.315 (0.063)	-0.061 (0.350)	0.186 (0.731)
Deal Is (Bass St)	-0.003 (1.0)	0.505 (**0.005**)	-0.063 (1.0)	0.447 (**0.044**)
Fortescue Bay (SE Tasmania)	0.196 (0.0192)	-0.036 (1.0)	-0.025 (0.796)	0.222 (0.070)

Table 6. Summary of genetic distance between populations based on Nei's (1978) unbiased genetic distance (above the diagonal), and F_{st} (Weir and Cockerham 1984) (below the diagonal).

Population	Bass Pt NSW	Deal Is Bass St	Fortescue Bay SE Tasmania
Bass Pt (NSW)	***	0.000	0.004
Deal Is (Bass St)	-0.0062	***	0.000
Fortescue Bay (SE Tasmania)	0.0052	-0.0018	***

Discussion

Patterns of range extension of *C. rodgersii* in Tasmanian waters

Broadscale patterns of incursion in time and space

Over nearly 40 years of observation (1974-2000) in the Kent group, the pattern of distribution of *C. rodgersii* is consistent with that of an invading population. In 1974 the sea urchin was observed at only 2 sites in close proximity in Murray Pass of a total of 7 sites visited on Erith Is and Deal Is, while ca. 3 decades later in 1993 this species was recorded at all but one of 9 sites surveyed, and in 2000 all 7 sites visited were characterised by extensive cover of *C. rodgersii* barrens. On this basis, it seems likely that the species might have established in the Kent group in the mid-late 1960s, and over 4 decades expanded to become the ecologically dominant invertebrate on shallow reefs at most sites on these islands.

The pattern of temporal change in *C. rodgersii* populations observed in the Kent group may assist interpretation of spatial patterns in the distribution of the species on the east coast of Tasmania. On this coast, the population has also expanded greatly in the 3 decades since the first animals were observed in the north east in the vicinity of St Helens in 1978. The current broad distributional trend shows highest densities near St Helens with populations declining to the south. South and west of Tasman Peninsula (sites 11-13), we did not detect any animals in our surveys, although other divers have confirmed sightings along the coast to Recherche Bay in the far south. This pattern is consistent with the population spreading from an ‘epicentre’ in the north east, although there are alternative possibilities to account for the latitudinal pattern in abundance.

Two important queries that arise from these observations concern the nature of the mechanism(s) that facilitated establishment of populations south of their previous range in the first place, and whether there has been ongoing recruitment to the Tasmanian populations. Given that *C. rodgersii* larvae are planktotrophic with an estimated planktonic phase of ca. 8 weeks (Andrew and Byrne 2001), the most plausible scenario is that larvae were transported from Australian mainland populations by the south flowing

southwest Pacific boundary current, the East Australian Current (EAC). In Tasmanian latitudes EAC influence is largely a summer phenomenon, with eddies propogating from the main stream off the shelf break and moving westwards to collide with the coast (Ridgway and Dunn 2003 provide a summary of EAC behaviour). Although the onset of spawning of *C. rodgersii* is in winter (June), the duration of spawning is extended in southern New South Wales (NSW) populations, continuing for 5-6 mo (Byrne et al. 1998). Thus, it is possible that the timing of the summer southwards extensions of the EAC and larval production in NSW are coincident. Given that the EAC has been a long term feature of the eastern seaboard of the continent, why has the southwards range extension of this species occurred only recently? It is very likely that the frequency, magnitude and duration of southwards incursions of the EAC has increased over the past 60 years as evidenced by trends of increasing salinity and temperature off the east coast of Tasmania (Harris et al. 1987; K. Ridgway, CSIRO, pers. comm.) and, in particular, greater rates of increase in salinity in summer than in winter (Fig. 17). These elevated salinities are a characteristic signature of EAC water mass (K. Ridgway, CSIRO, pers. comm.). Indeed, the chemistry of deepwater octocorals, which provides a relatively direct proxy of water temperatures, indicates that poleward extension of the EAC commenced ca. 200 years ago (Thresher et al. 2004).

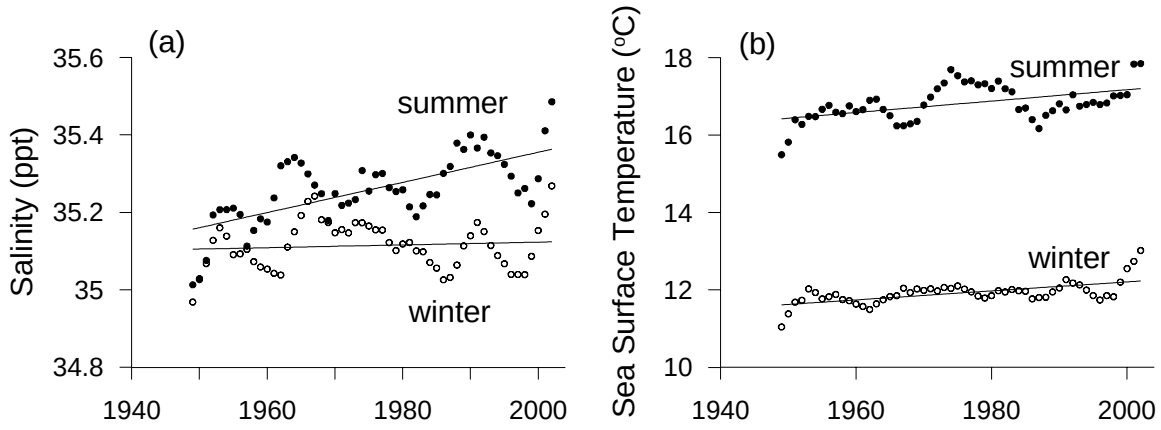


Figure 17. Trends in 5 y running average of sea surface (a) salinity and (b) temperature in summer (February and March) and winter (August and September) off Maria Is., central east coast of Tasmania,1944-2002. Data from CSIRO.

Assuming that larval transport initiated the establishment of *C. rodgersii* in Tasmanian waters, our genetic results do not support the possibility that Tasmanian populations of *C. rodgersii* originated from a single founder event, or remain isolated from mainland populations. There was no evidence of reduced levels of genetic diversity in Tasmanian populations compared with mainland populations, and heterozygosity matched expectations of random mating in all populations. However, genetic structure in the Fortescue Bay population is more different to that of the NSW sample than to the Kent group population. This suggests that there may be some degree of isolation by distance, but to properly examine this will require more work at a finer scale of genetic resolution. The occurrence of a wide distribution of age classes (1-18 y) in the Kent group (Fig. 2), and observations of a wide range in size classes off the Tasmanian coast (C. Johnson, pers. comm.), indicate that recruitment to the Tasmanian populations has been ongoing. However, the age distribution from Deal Is suggests that recruitment is not consistent among years, with episodic events of successful recruitment. Similar patterns in recruitment are known for this species in NSW (Andrew and Underwood 1989: Andrew and O'Neill 2000), and for other sea urchins with planktotrophic larvae in the northern hemisphere (Ebert and Russell 1988; Tegner et al. 1992). While it is not possible from our data to distinguish between self recruitment in Tasmanian populations and recruitment as a result of larval transport from NSW populations, we note that Tasmanian animals demonstrate a normal gonadal cycle and produce viable gametes (S. Ling, unpub. data), so that an element of self recruitment seems highly likely.

Consistent patterns in the distribution of *C. rodgersii* in Tasmania were that, over the depth range of diver-based surveys (to 18 m depth), densities tended to be greater in deeper water (9-15 m in the Kent group, 9-18 m east coast of Tasmania) than at shallower depths. The distribution of barrens habitat below 18 m (Fig. 13a) suggests that peak densities may extend through to 25 m depth. In both Bass Strait and the east coast of Tasmania, peak mean densities at the scale of subsites (transects as replicates) were ca. ≤ 1 m^2. These patterns differ from those in NSW where mean densities at the same spatial scale are typically 2-4 times greater (Andrew 1991; Andrew and Underwood 1992; Hill et al. 2003), and where high densities and extensive barrens occur commonly in shallow

water 2-10 m depth (Andrew & Constable 1999; Hill et al. 2003). The tendency for peak densities of *C. rodgersii* to occur at greater depths in Tasmanian waters than in NSW is unlikely to be a function of wave exposure alone, since the pattern is also evident at relatively sheltered sites such as East Cove and Winter Cove at Deal Is in the Kent group, and on the inside of St Helens Is off the east coast of Tasmania. One possibility is that the sweeping action of particular algal species whose fronds lie on the substratum limits sea urchin abundance in shallow water, and that these species are more common in Tasmania than NSW. The capacity of dense patches of particular macroalgae to limit invasion by sea urchins from adjacent barrens habitat is well documented (Konar and Estes 2003). Candidate species include *Durvillaea potatorum, Carpoglossum confluens* and *Phyllospora comosa*, all of which dominate in dense patches or zones in shallow water in Tasmanian waters but are not widespread in NSW (note that although dense patches of *C. confluens* occur in Tasmania, they are not widespread). We rarely recorded any *C. rodgersii* in 5*1 m plots dominated by *D. potatorum* or *C. confluens* (Fig. 8), but the relationship is not so clear for *P. comosa*. While in the Kent group there was some evidence of a 'step' in the relationship between *P. comosa* and urchin density above ca. 30% cover of this alga (Fig. 5), there was no evidence of abrupt boundaries of urchin density associated with cover of *P. comosa* on the Tasmanian coast. The possibility that particular algae may influence the small scale distribution of *C. rodgersii* warrants critical testing using manipulative experiments. After controlling for the effect of depth, there was no evidence that *C. rodgersii* was associated (positively or negatively) with particular community assemblages of algae.

Formation of *C. rodgersii* barrens habitat

Because both *C. rodgersii* and the smaller *Heliocidaris erythrogramma* are capable of forming barrens habitat, and that both sea urchins co-occurred at all sites in this study, it needs to be ascertained whether the grazing activity of either or both species is largely responsible for the barrens habitat we describe. There are several compelling reasons to indicate that the barrens habitat that now occurs on the exposed rocky coast of Tasmania, and which characterizes the rocky subtidal seascape of the Kent group, is due primarily to grazing by *C. rodgersii*. Across both regions of this study, we found a positive

relationship between the extent of barrens and densities of *C. rodgersii* (Figs. 3,14) but no similar relationship with *H. erythrogramma*, and a significant negative relationship between the two sea urchin species. In Tasmania *H. erythrogramma* is known to form barrens only in relatively sheltered bays, usually on a smaller spatial scale than those reported here, and usually characterised by significant accumulation of sediment (Valentine and Johnson 2005; C. Johnson, pers. obs.). These features are distinctly different to those of the barrens habitat we describe in the present work. Given our observations and those of others who have examined grazing by *C. rodgersii* in New South Wales (e.g. Andrew 1991; Andrew & Underwood 1993; Andrew and O'Neill 2000; Hill et al. 2003), we conclude that the widespread barrens habitat in the Kent group and on the open Tasmanian coast is a direct result of the grazing activity of *C. rodgersii*.

There is a clear difference in the depth distribution of *C. rodgersii* barrens in NSW and Tasmania. In Tasmania extensive barrens occur below 10-15 m depth, while in shallower water small patches of barrens habitat may occur but rarely do these patches coalesce to form larger areas of virtually continuous barren habitat such as occurs in NSW, where extensive barrens habitat occurs commonly at depths as shallow as 2-5 m (Andrew and Underwood 1993; Hill et al. 2003; C. Blount, pers. comm.). In Tasmania, the greatest extent of barrens was at depths 20-30 m, while in NSW *C. rodgersii* densities decline notably at depths >20 m (Andrew and Constable 1999). Another notable difference is that, in Tasmania, *C. rodgersii* densities on extensive barrens are typically 25-50% of those on barrens habitat in NSW (cf. Andrew and Underwood 1989, 1992, 1993).

The broad spatial pattern of declining cover of barrens habitat moving southwards along the Tasmanian east coast is consistent with a gradual southward propogration of *C. rodgersii* populations, and a lag of several decades between initial establishment and formation of extensive barrens habitat. What is less clear are the mechanisms that realise the large variation in extent of barrens cover at scales of 10^1 m (within transects), 10^2 m (between transects) and 10^3 m (between subsites within sites). It is unclear why barrens cover is so patchy at these scales, both in Tasmania and NSW. This highlights that the mechanisms for the transition from macroalgal bed to barrens habitat, and the dynamics

of the boundary between macroalgal bed and barrens, are poorly understood (Andrew 1993; Konar and Estes 2003; Hill et al. 2003). It is clear that there is a threshold density to initiate destructive grazing of macroalgae (Hill et al. 2003), and that the density necessary to create barrens is greater than that necessary to maintain barrens (Andrew 1989; Hill et al. 2003). Given much lower densities on barrens habitat in Tasmania, the threshold density to initiate barrens may be lower in Tasmania than in NSW.

Andrew (1993) examined the relationship between the availability of crevices providing cover for *C. rodgersii*, sea urchin densities and grazing, and concluded that the availability of shelter for the urchins was a sufficient condition to initiate barrens formation. However, this does not explain why areas of barrens habitat and dense macroalgal bed, with a sharp boundary between them, are found at the same depth and across the same substratum type (e.g. Fig. 16). Although *C. rodgersii* barrens in Tasmania are mostly on boulder substratum that provides ample shelter in crevices, at some locations there are expansive areas of barrens on flat rock without obvious places for sea urchins to shelter so that they remain exposed during the day. In NSW, the boundary between *C. rodgersii* barrens and dense macroalgae appears to be relatively stable (Andrew 1994; Hill et al. 2003), and it seems likely that discontinuities in substratum type (Andrew 1993), and perhaps the sweeping motion of macroalage at these boundaries (Konar and Estes 2003), may contribute to maintaining this stability.

In Tasmania, the extent of *C. rodgersii* barrens has clearly been increasing since this sea urchin was first recorded in the 1970s. The extent to which the barrens habitat may expand, and the dynamics of barrens boundaries will remain uncertain until more is known about the mechanisms triggering the onset of barrens formation and determining the stability of boundaries between barrens and macroalgae. Notably, in line with observations of *C. rodgersii* in NSW (Andrew 1993; Hill et al. 2003), we see no evidence in Tasmania of the complex behaviours demonstrated by strongylocentrotid species in the northern hemisphere which are important in effecting transitions, in both directions, between dense macroalgal cover and barrens habitat (Bernstein et al. 1981, 1983; Harrold and Reed 1985; Vadas et al. 1986). Barrens habitat seems to be particularly likely to

develop on boulder substratum, perhaps because of the complexity of crevices available for shelter (Andrew 1993). In the area of St Helens we found that ca. 75% of boulder substratum was characterised by *C. rodgersii* barrens. Over the entire coast, diver based surveys to 18 m depth estimated that 55.3% of reef was boulder substratum, while the video surveys identified 34.3% of discernable consolidated reef as boulders. On this basis, and given that barrens also form on other types of consolidated reef, it is possible that barrens habitat could expand to account for ca. 50% of inshore reefs, as occurs in the Kent group and NSW. This would have a dramatic impact on abalone and rock lobster fisheries in this region.

Why do *C. rodgersii* barrens form?

It is important to emphasise that the mechanisms underpinning the incursion of *C. rodgersii* into Tasmania may not be related to those underpinning the formation of barrens habitat by *C. rodgersii* in Tasmania, i.e. that the advent and establishment of *C. rodgersii* in Tasmania as a result of transport of larvae by the EAC and warming of east coast waters need not inevitably lead to barrens formation. A key question is to identify the mechanism(s) that lead to barrens formation. One potential candidate is that fishing has reduced populations of predators to the point where sea urchins densities can increase to the point where destructive grazing of seaweeds commences. Considerable attention has been given to the effects of fishing down predators on marine ecosystems in general (Jackson et al. 2001) and on kelp ecosystems in particular (Steneck 1997, 1998; Sala et al. 1998; Tegner & Dayton 2000). While mechanisms and dynamics are complex and often peculiar to particular systems, the general conclusion of this work is that overfishing of predators of sea urchins often results in increases in urchin populations with subsequent formation of urchin barrens.

Potential significant predators of *C. rodgersii* in Tasmania that are subject to fishing include rock lobsters (*Jasus edwardsii*) and reef associated fishes. Experimental and correlative evidence suggests a potentially important role of lobsters in limiting urchin populations in South Africa (Tarr et al. 1996; Mayfield et al. 2001), New Zealand (Andrew & MacDiarmid 1991; Babcock et al. 1999) and California (Tegner & Levin

1983). Moreover, recent experiments in Tasmania has shown that predation by legal-sized rock lobsters in the field is sufficient to prevent the urchin *Heliocidaris erythrogramma* from attaining densities sufficient to create barrens (Pederson 2003; Johnson et al. 2004). In all of these examples, the effect of lobsters on urchins is size-specific, with all lobsters preferring small urchins, while only large lobsters are able to consume large urchins. In Tasmania, only legal-sized lobsters have significant predatory impact on *H. erythrogramma* (Pederson 2003; Johnson et al. 2004). Since the biomass of legal-sized lobsters on the east coast of Tasmania in the recent past has been as low as 2-8% (depending on the area) of pre-fished biomass (Frusher 1997), this trophic link is essentially functionally eliminated in this system.

In other areas, benthic fishes appear to be important predators of sea urchins. In the Gulf of Maine, there is a strong case that overfishing of demersal scalefish has enabled urchin populations to increase and create extensive barrens (Witman & Sebens 1992; Vadas & Steneck 1995). Similarly, fish predation is sufficient to regulate urchin populations in California (Cowen 1983), and may have a role in New Zealand (Babcock et al. 1999). However, while wrasse are a key predator of invertebrates in the kelp-bed systems of southern Australia, urchins are a poorly preferred prey and only large fish prey on *H. erythrogramma* (Shepherd & Clarkson 2001), which is a notably smaller species than *C. rodgersii*. In Tasmania, experiments and large-scale surveys alike suggest that legal-sized lobsters are far more important as predators of *H. erythrogramma* on rocky reefs than are fishes (Pederson 2003; Johnson et al. 2004). Given the large size of *C. rodgersii*, and that both lobsters and *C. rodgersii* are nocturnal while wrasse forage only during the day, it is very likely that the same conclusion will be found in the case of *C. rodgersii*.

These ideas require critical testing. If the hypothesis is supported that fishing of rock lobsters has enabled *C. rodgersii* populations in seaweed beds to increase to the point of barrens formation, then the phenomenon of *C. rodgersii* barrens in Tasmania arises from an interaction between climate change (facilitating the establishment of *C. rodgersii* in Tasmania in the first instance) and fishing (enabling populations to expand). The genesis of both of these forcings is arguably anthropogenic.

Implication of barrens formation for commercial fisheries species

It is clear that extensive *C. rodgersii* barrens habitat in Tasmania is unable to support abalone (*Haliotis rubra*) and rock lobster (*Jasus edwardsii*) at levels suitable for commercial harvesting. Abalone densities were significantly lower on established barrens than in adjacent macroalgal habitat on the same substratum type and at the same depth, and there is a clear negative relationship between densities of *C. rodgersii* and that of abalone and rock lobster on the Tasmanian coast. Reduced secondary production on sea urchin barrens reflects that levels of primary production are ca. 100-fold lower than in macroalgal beds (Chapman 1981) and, in the case of abalone, the likelihood of direct competition with sea urchins for food and space. Evidence of potential competition between sea urchins and abalone (*Haliotis* spp.) includes significant negative associations between the two, which has been reported for *C. rodgersii* in Australia (Shepherd 1973; Andrew & Underwood 1992) , *Evechinus chloroticus* in New Zealand (Naylor & Gerring 2001), and *Strongylocentrotus franciscanus* in California (Karpov et al. 2001). Karpov et al. (2001) concluded that, although negative associations between abalone and *S. franciscanus* were also evident within macroalgal beds, competition between these species was most pronounced in habitats where macroalgae was scarce. Notably, experimental removals of *C. rodgersii* in NSW realised a 10-fold increase in abalone (Andrew et al. 1998), and similar results have been obtained with other species in California (Tegner & Dayton 2000). In New Zealand, addition of urchins (*E. chloroticus*) to kelp-beds realised dramatic reductions in abalone (*Haliotis iris*), while urchin removal resulted in small but significant increases in abalone (Naylor & Gerring 2001).

The ultimate impact of the incursion of *C. rodgersii* into Tasmania on the abalone and rock lobster fisheries will depend on the extent to which associated barrens habitat develop, and on the spatial overlap of barrens habitat with preferred areas of fishing. At this stage it is not possible to predict the expansion of barrens habitat, although the extent of incipient barrens we observed, particularly on boulder substratum, suggests that further expansion of extensive barrens is likely. The most extensive barrens occur between 15-30 m depth, and the majority are in depths ≥15 m. To the extent that much of the abalone

fishing occurs in depths <15 m, the direct impact on this fishery may be less than is indicated by the spatial extent of barrens habitat. However, as abalone become significantly depleted at some sites on the east coast (Tarbath et al. 2004), effort is likely to shift to deeper water. Rock lobster is fished throughout the depth range of barrens formation, but also in deeper water. It needs to be emphasised that the impact of barrens formation on both fisheries is two-fold in that the advent of barrens habitat not only represents area lost to the fishing, but since both fisheries are managed by a total allowable catch, increases in barrens habitat inevitably leads to greater fishing pressure in remaining habitat suitable for fishing. Given these effects and that development of extensive barrens is patchy in space, there is a case to consider more detailed spatial management of fisheries. Certainly if existing areas of incipient barrens develop into extensive barrens, then spatially explicit management of rock lobster and abalone fisheries may become an imperative on the east coast of Tasmania.

While the negative effect on abalone and rock lobster of the transition to barrens is clear, we have not examined whether increases of *C. rodgersii* in macroalgal habitat has any impact on these species. We found no difference in the density of abalone inside and outside of small patches of incipient barrens in macroalgal beds off Mistaken Cape, and no evidence that juvenile abalone obtain shelter from predators beneath the spine canopy of sea urchins as occurs in California and South Africa (Tegner & Dayton 1981; Tarr et al. 1996; Mayfield & Branch 2000).

Is incursion of *C. rodgersii* a management issue?

Any management response to the incursion of *C. rodgersii* into Tasmanian waters would sensibly focus on preventing further spread of barrens habitat and, possibly, rehabilitation of existing barrens. The two elements of preventing further expansion of *C. rodgersii* barrens and rehabilitating barrens pose distinctly different management issues. The question of whether a management response is warranted has both economic and philosophical elements. The economic issue is whether the cost of a management response is justified against the value of saved fisheries and the broader value of macrolagal beds to ecosystem functioning and to society. The philosophical issue is

whether barrens formation is a 'natural' phenomenon that should be allowed to run its course in the ebb and flow of ecological dynamics, or whether it is linked to anthropogenic activity which may justify management intervention.

The transition from productive macroalgal beds to poorly productive sea urchins barrens habitat has occurred in temperate waters worldwide. The common denominator underpinning this transition is fishing pressure on predators of sea urchins (Steneck 1997, 1998; Sala et al. 1998; Pinnegar et al. 2000; Jackson et al. 2001; Steneck et al. 2002; Tegner and Dayton 2000; Shears and Babcock 2003), although at specific sites there may also be other influencing factors (Pinnegar et al. 2000; Shears and Babcock 2003). If a similar role of fishing of *C. rodgersii* predators is demonstrated in Tasmania (see previous section on "Why do *C. rodgersii* barrens form?"), then there is a compelling case for management intervention. Our initial experiments show that legal sized rock lobsters are an important predator of *C. rodgersii* (S. Ling, unpub. data). While management decisions have already been implemented to increase the biomass of legal sized lobsters, it is unclear to what level this biomass is likely to build and whether it will have any effect on the population dynamics of sea urchins.

Management intervention to limit further expansion of *C. rodgersii* barrens in Tasmania is likely to be more tractable than any attempt to rehabilitate existing barrens. There are two reasons for this. First, large scale removal of sea urchins, particularly in deeper water, is difficult. Second, the density of *C. rodgersii* necessary to create barrens habitat is significantly greater than that needed to maintain barrens (Andrew and Underwood 1993; Hill et al. 2003). Thus, the transition to *C. rodgersii* barrens represents a classical ecological hysteresis and regime shift (Scheffer et al. 2001; Collie et al. 2004) to an alternative community configuration with high resilience stability.

For all of the reasons outlined, we suggest that a timely management response to the incursion of *C. rodgersii* in Tasmania is warranted. This will require identifying the mechanisms that trigger the onset of barrens formation and that determine the boundaries between barrens and macroalgal-dominated habitat.

Benefits and Adoption

Stakeholders to benefit from this work include those fisheries dependent on productive reef ecosystems in eastern Tasmania, *viz*. abalone (*Haliotis rubra*), rock lobster (*Jasus edwardsii*) and wrasse (*Notolabrus tetricus, N. fucicola*) fisheries; managers of Tasmanian rocky reef systems; and the general public with interests in ensuring the sustainability of healthy and properly functioning rocky reef systems.

The key benefits of the work have been to highlight to industry, managers and the general public (1) that *Centrostephanus rodgersii* represents a significant threat, both actual and potential, to the integrity of rocky reefs and the important fisheries they support on the east coast of Tasmania, and (2) the scale of the problem posed by *C. rodgersii* in Tasmanian waters.

Industry and relevant individuals in government have been made aware of this work through a series of presentations (e.g. in several research reviews; annual general meetings), and the general public through considerable exposure in mainstream media (radio, television and newspapers). Dissemination of the results in this way has generated significant discussion among scientists, industry representatives and managers. The work has been a catalyst for a major workshop to address (1) the status of *C. rodgersii* in Tasmania, (2) the need and potential for management intervention, and (3) priorities for future research. The workshop will occur in December 2005, and involve researchers, industry representative, and managers.

Further Development

The workshop to be conducted in December 2005 will examine the need and options for management responses to *C. rodgersii* in Tasmania. Irrespective of the outcomes of these discussions, results of the work presented here suggest that it would be sensible to continue to monitor expansion of the range of *C. rodgersii* in Tasmania (the range has extended considerably over the past decade, and continues to expand), and particularly to monitor changes in the extent of *C. rodgersii* barrens, since it is establishment of barrens

habitat that is of greatest concern to the integrity of rocky reef systems and the productivity of the fisheries they support.

If the extent of *C. rodgersii* barrens in Tasmania does not increase further, it may be that no management response is a cost effective option. However, given the extent of incipient barrens and apparent increases in both the range and local densities of *C. rodgersii* (data from the research presented here and subsequent observations), then it needs to be acknowledged there is a high likelihood of further increases in the extent of *C. rodgersii* barrens over the next decade. Given that barrens formation has a major effect on ecosystem integrity, that it effectively removes habitat from key fisheries, and that resultant transfer of fishing effort increases pressure on fisheries resources in remaining suitable habitat, then further increases in barrens are undesirable and present a case for management intervention. However, if responses to minimize further expansion of barrens are to be implemented, then a better understanding of the mechanism(s) underpinning barrens formation is required. Thus, an immediate priority for future research is to determine whether barrens formation arises largely as a result of the activity of sea urchins on existing barrens grazing at the border between barrens and seaweed habitat, or whether they form largely as a result of the activity of sea urchins residing in seaweed beds. Resolving this issue is important since it will identify the sub-population of animals that needs to be targetted in attempting to limit further expansion of barrens.

Another priority is to ascertain the nature of a feasible management response. Mounting evidence implicating the role of rock lobsters (*Jasus edwardsii*) as key predators of *C. rodgersii* requires critical testing. If rock lobsters prove to be important predators of *C. rodgersii*, then the instigation of trials involving translocation of large numbers of lobsters from deep water onto shallow reefs presents an important opportunity to examine the possibility of predator control of sea urchins by rock lobsters as a means to both prevent further development of barrens habitat and rehabilitate existing *C. rodgersii* barrens.

Planned Outcomes

The intended primary outcome of the work was to indicate whether a significant management response to the establishment of *C. rodgersii* in Tasmania is warranted. The research outlined here will inform a workshop attended by relevant stakeholders (researchers, representative of fisheries interests and managers) to address this issue in December 2005.

Conclusions

Available evidence suggests that the sea urchin *Centrostephanus rodgersii* first established in the Kent Group of islands in eastern Bass Strait in the late 1960s or early 1970s, and about a decade later on the north east coast of Tasmania. This significant range extension was likely effected by transport of larvae from more northern regions by the East Australian Current. Subsequent expansion of populations of the sea urchin in the Kent Group has resulted in formation of extensive sea urchins barrens, which now occur across *ca*. 50% of shallow rocky reefs in the area. The extent of barrens habitat on the east coast of Tasmania is much less, and barrens in this region are distributed very patchily. There is mounting evidence to suggest that population densities of *C. rodgersii*, and therefore barrens formation, might be controlled through predation by the southern rock lobster (*Jasus edwardsii*). If so, then the advent of *C. rodgersii* barrens in Tasmania results from the combined effects of climate change (affecting the EAC) and fishing (affecting population levels of the rock lobster). The notion of predator control of *C. rodgersii* populations requires critical testing.

In eastern Tasmania, rocky reef on the open coast dominated by boulders is particularly susceptible to become *C. rodgersii* barrens, ostensibly because of the amount of shelter provided to the sea urchins compared with other habitat types. However, barrens can form on any kind of rocky reef in depths to at least 40 m. Considering the range of *C. rodgersii* on the east coast, the current distribution of incipient barrens, and the distribution of bottom dominated by boulders, then there is the potential for *C. rodgersii* barrens to expand to occupy ca. 50% of shallow rocky reefs, as currently occurs in NSW

and the Kent Group. Commercial quantities of important fisheries resources such as abalone (*Haliotis rubra*), rock lobster and possibly wrasse (*Notolabrus* spp.) do not occur on *C. rodgersii* barrens in Tasmania. These circumstances warrant consideration of management responses to minimize risk of further development of *C. rodgersii* barrens, and perhaps rehabilitation of existing barrens. These responses may include more spatially explicit management of fisheries resources.

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Appendix 1. List of macroalgae recorded in the Kent group during surveys in 2000, and on the east coast of Tasmania in surveys 2001-02.

A. Kent group

Halopteris paniculata	*Sargassum heteromorphum*
Zonaria spp.	*Sargassum verruculosum*
Perithallia caudata	*Sargassum fallax*
Ecklonia radiata	*Sargassum vestitum*
Xiphophora condrophylla	*Sargassum lacerifolium*
Phyllospora comosa	*Sargassum* spp.
Sierococcus axillaris	*Codium harveyi*
Cystophora moniliformis	*Codium spp.*
Cystophora monilifera	*Caulerpa longifolia*
Cystophora retroflexa	*Caulerpa brownii*
Cystophora subfarcinata	*Caulerpa obscura*
Cystophora spp.	*Caulerpa flexilis*
Caulocystis uvifera	*Caulerpa vesiculifera*
Acrocarpia paniculata	*Caulerpa* spp.
	foliose red algae

B. East coast of Tasmania

Halopteris paniculata	*Sargassum verruculosum*
Dictyopteris sp.	*Sargassum fallax*
Zonaria spp.	*Sargassum vestitum*
Carpomitra costata	*Sargassum paradoxum*
Sporochnus sp.	*Sargassum* spp.
Perithallia caudata	*Chlanidophora microphylla*
Lessonia corrugata	*Ulva* spp.
Macrocystis pyrifera	*Chaetomorpha* spp.
Macrocystis angustifolia	*Cladophora* sp.
Ecklonia radiata	*Codium spp.*
Undaria pinnatifida	*Codium pomoides*
Durvillaea potatorum	*Caulerpa scapelliformis*
Xiphophora gladiata	*Caulerpa longifolia*
Phyllospora comosa	*Caulerpa trifaria*
Sierococcus axillaris	*Caulerpa brownii*
Carpoglossum confluens	*Caulerpa flexilis*
Cystophora platylobium	*Caulerpa geminata*
Cystophora moniliformis	*Caulerpa hodgkinsoniae*
Cystophora retorta	*Caulerpa cactoides*
Cystophora retroflexa	*Caulerpa* spp.
Cystophora spp.	filamentous green algae
Acrocarpia paniculata	filamentous brown algae
Sargassum varians	foliose red algae
Sargassum decipens	seagrass

Appendix 2. Mean density (no. m^{-2}) of *Centrostephanus rodgersii* at different depths across sites 1-9. Standard errors in curved parentheses (); number of replicate transects in square parentheses []; nd = no data (it was not always possible to work transects into shallow depths). 2-way Model II ANOVA (transformation = ln(*Y*+0.001)) showed no evidence of a depth*site interaction ($F_{30,73}$= 0.66, *P* = 0.898), but significant differences in density among depths ($F_{4,30}$= 5.13, *P* = 0.003) and sites ($F_{8,73}$= 3.85, *P* = 0.0008).

Site	Depth Range (m)				
	0-6	**6-9**	**9-12**	**12-15**	**15-18**
1. Eddystone Pt	nd	0.045 (0.045) [2]	0.085 (0.085) [2]	0.030 (0.013) [3]	0.013 (0.013) [3]
2. St Helens	0 (0) [2]	1.035 (0.135) [2]	0.493 (0.250) [3]	0.727 (0.255) [3]	0.53 (0.275) [3]
3. Ironhouse	nd	0.100 (0.100) [2]	0.007 (0.007) [3]	0.050 (0.045) [3]	0.027 (0.027) [3]
4. Bicheno	0 [1]	0 [1]	0.020 (0.020) [2]	0.010 (0.010) [3]	0.050 (0.050) [3]
5. Cape Tourville	0.050 (0.050) [2]	0.100 (0.100) [2]	0.263 (0.181) [3]	0.107 (0.078) [3]	0.073 (0.073) [3]
6. Schouten Is	0.020 (0.020) [3]	0.077 (0.062) [3]	0.470 (0.087) [3]	0.367 (0.134) [3]	0.353 (0.184) [3]
7. Maria Is	0.007 (0.007) [3]	0.017 (0.017) [3]	0.243 (0.209) [3]	0.270 (0.142) [3]	0.247 (0.075) [3]
8. NE Forestier Peninsula	0.005 (0.005) [2]	0.003 (0.003) [3]	0.010 (0.006) [3]	0.003 (0.003) [3]	0 (0) [3]
9. Fortescue Bay	0.003 (0.003) [3]	0.013 (0.007) [3]	0.103 (0.103) [3]	0.037 (0.022) [3]	0.093 (0.070) [3]

Appendix 3. Mean density (per m^2) of *Centrostephanus rodgersii* on different substratum types across sites 1-9, determined from dive transects. Standard errors in curved parentheses (); number of replicate transects in square parentheses []; nd = no data (not all substratum types were represented on all transects). 2-way Model II ANOVA (transformation = ln(*Y*+0.001)) indicated the absence of a substratum-type*site interaction ($F_{23,43}$= 1.17, *P* = 0.324) but significant variation in densities with substratum-type ($F_{3,23}$= 5.03, *P* = 0.008) and site ($F_{8,73}$= 3.87, *P* = 0.002).

Site	Substratum Type			
	flat rock	**very large boulders**	**large boulders**	**small boulders**
1. Eddystone Pt	0 (0) [2]	0.130 [1]	0.083 (0.060) [3]	0 (0) [2]
2. St Helens	0.640 (0.280) [2]	0.765 (0.765) [2]	0.827 (0.567) [3]	0.512 (0.209) [3]
3. Ironhouse	0.010 (0.006) [3]	0.200 (0.200) [2]	0.05 (0.05) [3]	0.155 (0.155) [2]
4. Bicheno	0 (0) [3]	0.365 (0.365) [2]	nd	0 (0) [2]
5. Cape Tourville	0.023 (0.023) [3]	0.040 (0.040) [2]	0.183 (0.159) [3]	0 [1]
6. Schouten Is	0.020 (0.020) [2]	0.300 [1]	0.383 (0.097) [2]	0 [1]
7. Maria Is	0 (0) [3]	0.180 (0.080) [2]	0.237 (0.162) [3]	0.100 [1]
8. NE Forestier Peninsula	0 (0) [3]	0.025 (0.025) [2]	0 (0) [2]	0.007 (0.007) [3]
9. Fortescue Bay	0 (0) [2]	0.015 (0.015) [2]	0.05 (0.036) [3]	0.010 [1]
Percentage of total substratum across all 9 sites	34%	14%	25%	17%

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