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Responses of intertidal invertebrates to rising sea surface temperatures in the southeastern Indian Ocean

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Introduction: The west coast of Western Australia (WA) is a global hotspot for increasing sea surface temperatures and marine heatwaves.

Methods: We used visual survey transects to compare mollusc and echinoderm populations on three coastal intertidal platform reefs on the Perth shoreline with two intertidal platforms at the west end of Rottnest Island (32°S) which are under the influence of the southward flowing Leeuwin Current.

Results: In 1983, temperate species dominated Perth coastal molluscan diversity, but the tropical mussel *Brachidontes sculptus* dominated density. Species richness on coastal platforms remained constant in 2007 and 2021, but total densities were lower in 2007 as *B. sculptus* declined; partial recovery occurred on coastal platforms in 2021. Tropical species were a significant component of mollusc diversity and density at Rottnest Island in 1982 and 2007. Total mollusc density declined by 98% at the island sites of Radar Reef and 86% at Cape Vlamingh and

total echinoderm density by 52% and 88% respectively from 2007 to 2021; species diversity also declined sharply.

Discussion: Tropical species have moved southward in WA subtidal environments, but tropical, temperate and WA endemic species all suffered losses of biodiversity and catastrophic declines in density of 90% or more on the two Rottnest Island intertidal platforms. Data presented here provide a sound basis for exploring the possible causes of the catastrophic mortality at the west end of Rottnest Island and monitoring for recovery.

KEYWORDS

Indian Ocean, climate change, marine heatwave, Leeuwin Current, sea surface temperatures, biogeography, molluscs, echinoderms

Introduction

Global warming is recognized as one of the critical environmental issues in marine ecosystems, and the pace of change is increasing (O'Hara et al., 2021). Ocean circulation patterns and water chemistry are being disrupted, including changes in marine temperatures, stratification, nutrient input, oxygen content and ocean acidification (Harley et al., 2006; Doney et al., 2012).

Warming ocean temperatures are occurring globally, but the phenomenon is uneven; some areas are warming more rapidly than others. Hobday and Pecl (2013) analyzed monthly sea surface temperatures (SST) for the five decades of 1950 to 1999, reporting 24 global hotspots of increasing SST either in warming rate or being in the top 10% of warming. A related phenomenon is marine heatwaves (Pearce et al., 2011) where SST increase markedly for short periods in a local area then return to more normal levels (Hobday et al., 2016; Oliver et al., 2021). Marine heatwaves increased in frequency by 34% from 2005 to 2016 and their duration by 17% (Straub et al., 2019), with further increases in frequency and temperature spikes predicted (Oliver et al., 2019). The physical and chemical changes in marine systems modify biological parameters such as calcification rates, community structures, larval transport patterns and species ranges (Harley et al., 2006; Doney et al., 2012; Poloczanska et al., 2016).

A key impact of ocean warming is that the ranges of tropical species are increasing towards the poles (Wernberg et al., 2011; Yamano et al., 2011; Baird et al., 2012; Hyndes et al., 2016; Hastings et al., 2020; Melbourne-Thomas et al., 2021). In Australia, of the 198 range shifts recorded, 87% were poleward (Gervais et al., 2021). Babcock et al. (2019) collated the effects of extreme climatic events over 45% of the Australian coastline in the short period of 2011 to 2017: coral bleaching over much of northern Australia; loss of seagrasses on both the east and west coasts through excessive rainfall and marine heatwaves; loss of kelp forests on the west coast through marine heatwaves; and loss of mangroves during droughts and unusually low sea levels during the 2016 El Niño event.

Studies on the west coast of Western Australia (WA), extending over 12° of latitude from North West Cape south to Cape Leeuwin, have been particularly important in elucidating the effects of climate

change on the marine environment. The region has the only poleward current on the west coast of a continent, the Leeuwin Current (Cresswell and Golding, 1980; Pearce and Walker, 1991; Pearce, 2007) which has naturally dispersed tropical species farther southward than they would otherwise occur. The lower west coast of WA is a global hotspot in warming SST which have risen ~0.6°C since 1951 (Pearce and Feng, 2007; Hobday and Pecl, 2013). The region has also recently experienced several marine heatwaves, the largest of which was in the summer of 2011 when temperatures were up to 3°C above average for about three months and inshore temperatures increased by up to 5°C for shorter periods (Pearce and Feng, 2013). The heatwave caused considerable changes in the subtidal marine flora and fauna along the entire west coast. Extensive temperate kelp beds contracted 100km to the south and were replaced by tropical and subtropical marine algae, invertebrates, corals and fishes (Pearce and Feng, 2013). The changed community structure altered key ecological processes, suppressing the potential recovery of kelp (Wernberg et al., 2011; Wernberg et al., 2013; Hyndes et al., 2016; Wernberg et al., 2016). Coral bleaching occurred along the entire west coast (Thomson et al., 2011; Abdo et al., 2012; Moore et al., 2012; Smale and Wernberg, 2012). Valuable scallop, crab, abalone, prawn and rock lobster fisheries were severely affected. Some, but not all, fisheries have since partially recovered (Caputi et al., 2019).

Most of the known adverse effects of the 2011 marine heatwave in WA occurred in subtidal environments. The exception was a small commercial fishery of the temperate abalone *Haliotis roei* which was wiped out on intertidal platforms at Kalbarri (27.7°S) near the northern limit of its range; it has not recovered (Hart et al., 2018; Caputi et al., 2019; Strain et al., 2020).

With increasing SST in the Perth region on the lower west coast of Western Australia (Pearce and Feng, 2007; Hobday and Pecl, 2013) and the southward expansion of subtidal species in the region as a result of marine heatwaves (Wernberg et al., 2011; Wernberg et al., 2013; Hyndes et al., 2016; Wernberg et al., 2016) we hypothesize that there would have been an increase in tropical invertebrates on intertidal platform reefs in the Perth region in recent decades. To test this hypothesis, we used visual transect surveys on molluscs and echinoderms collected over the 39 years from 1982 to 2021.

Materials and methods

Platform reef habitat

There is a series of rocky ridges in the shallow water marine environment of the Perth region; some are emergent, reaching heights of up to 60m above sea level while others remain subsurface. Limestone platforms along the continental shoreline and on islands range from a few metres to over 100m wide at Cape Vlamingh at Rottneest Island. The region is microtidal, a mixture of diurnal and semidiurnal tides; tidal ranges vary from a few centimetres to up to 1m. Rock platforms occur from tidal datum to about 1m above; many are at about 0.3m. The platform surface is generally flat, but highly dissected by channels and pools on some platforms. There is usually a low ridge, or rim, up to 0.2m high and 2m wide on the seaward margin or along channels that traps water in a shallow pool on the platform. As seawater drains from the platform at low tide it is replaced by waves crashing over the seaward rim or water emerging from fissures and blowholes in the rock surface (Wells and Walker, 1993).

Molluscs and echinoderms were investigated on five platforms in the present study: Cape Vlamingh and Radar Reef at the western end of Rottneest Island and three platforms along the Perth coastline (Cottesloe, Trigg Point and Waterman) (Figure 1).

Transect surveys

Visual surveys were made along transects 100m apart from the base of the inshore cliff to the seaward edge of the intertidal platforms

at Cape Vlamingh and Radar Reef in 1982. Every 5m all molluscs $\geq 5\text{mm}$ in their greatest dimension in a 1m^2 quadrat were identified and counted. There were six transects with 97 quadrats at Cape Vlamingh and six transects with 65 quadrats at Radar Reef (Figure 1). A similar series of transects from the shoreline to the seaward edge of the platform was made at the coastal sites of Cottesloe, Trigg Point and Waterman in the austral summer of 1982. Results of the 1982 surveys were summarised from Wells (1985).

In 1983 a major investigation was initiated on molluscs present on the coastal platforms to assess possible overexploitation, particularly of the abalone *Haliotis roei*. From 1983 to 1987 an intensive summer survey (January to March) was made of molluscs (and in 1986 echinoderms) on the platforms at Cottesloe, Trigg Point and Waterman. Each platform was divided into habitats based on macroalgal assemblages present (Figure 1). Four zones were defined at Cottesloe: inshore platform; inner *Sargassum* on the middle of the platform; outer *Sargassum* at the seaward margin of the platform; and an *Ecklonia* zone in slightly deeper water (approximately 1m; 32m^2). Three habitats were defined at Trigg Point and Waterman: an inshore platform with a diverse assemblage of macroalgae; *Sargassum* zone; and a seaward bare zone with only sparse macroalgal coverage (24m^2 each at Trigg Point and Waterman). Transects commenced at the northern end of each zone (Figure 1) and were sampled parallel to shore at 5-10m intervals depending on the size of the platform. Quadrats were searched in detail for all molluscs $\geq 5\text{mm}$. Data for each habitat were converted to average density for the overall platforms using estimates of the area of each habitat on each platform.

Molluscs and echinoderms on the Rottneest Island and coastal platforms were resurveyed in the summers of 2007 and 2021 using the

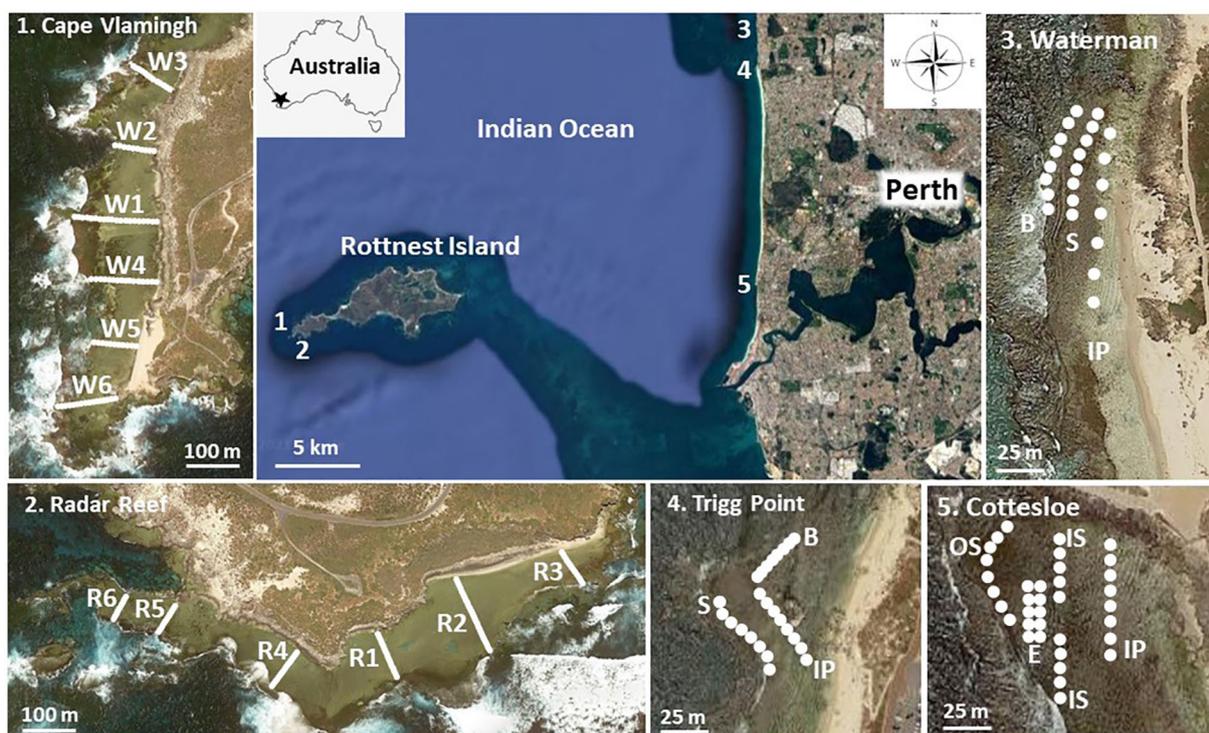


FIGURE 1

Map of the location of the study sites and transects at Rottneest Island and along the coastline of Perth, Western Australia. For the coastal platforms, habitat codes are IP inshore platform; S, *Sargassum*; B, bare; IS, inner *Sargassum*; OS, outer *Sargassum*; E, *Ecklonia*; Redrawn from Google (n.d.).

same methodology, except that quadrats were reduced from 1m² to 0.25m² to minimise the workload. As far as possible the same transects were used for each platform. The number of quadrats in each habitat on coastal platforms was increased from 8 to 10, so there were 40 quadrats (10m²) at Cottesloe and 30 quadrats (7.5m²) each at Waterman and Trigg Point. Statistical analysis indicated that the reduced quadrat size would possibly reduce the numbers of species recorded on each platform but should not affect estimates of density (Irvine et al., 2008).

Taxonomic and biogeographic determinations

All molluscs collected in the 1982–1983 surveys were taken to the Western Australian Museum, Perth, WA where they were sorted to species, identified using the museum collections and published literature and counted. Representative specimens of each species were deposited in the museum. As far as possible identifications were made in the field in subsequent years and the animals returned to the platform to minimize study impacts.

Biogeographic relationships (tropical, temperate and species endemic to WA) are based on published distributions and/or collections of the WA Museum. The dominant mussel on inshore platforms was previously identified as a WA endemic species, *Brachidontes ustulatus* (Wells and Bryce, 1986; Wilson, 2002), but it is now considered to be the tropical species, *B. sculptus* (Huber, 2010). The species names presented in Supplementary Tables 1 and 2 have been updated using the World List of Marine Species (WoRMS Editorial Board, 2022).

Data analysis

Data analysis was performed using R statistical software, version 4.0. Non-metric multidimensional analysis (nMDS) using Bray-Curtis distance to describe differences in mollusc and echinoderm community assemblages was performed using the Vegan R package (Dixon, 2003). ANOSIM was used to establish significance levels ($p < 0.05$) for changes in community assemblages between years, and between coastal versus Rottneest Island sampling sites. Heatmaps displaying mollusc density were restricted to the 16 most numerous species, with each individual species representing >1% of all individuals observed at any site for any given year. Echinoderm densities were restricted to the 9 most abundant species, with specimens with very low occurrence (<1%) or unidentified to species level presented as class aggregates. Hierarchical cluster analysis was performed using the Vegan R package (Dixon, 2003). Community diversity was estimated as species richness.

Sea surface temperature data (annual mean temperatures for southwestern Australia) were obtained from the Australian Bureau of Meteorology (available at: http://www.bom.gov.au/climate/change/#tabs=Tracker&tracker=timeseries&tQ=graph%3Dsst%26area%3Dsw%26season%3D0112%26ave_yr%3D10).

Results

Molluscs

Rottneest Island

In 1982, 53 mollusc species were collected and identified at two sites on the western end of Rottneest Island: 32 at Radar Reef and 44 at Cape Vlamingh (Table 1). Isolated individuals, mostly small juveniles, of 5 species at Radar Reef and 3 at Cape Vlamingh could not be identified. The total density of molluscs was 130.8 ± 17.9 ind/m² at Radar Reef and 135.0 ± 14.8 ind/m² at Cape Vlamingh. The number of tropical (12) and temperate (12) species identified at Radar Reef was equal and there were 8 WA endemic species. Tropical species (83.8 ± 17.0 ind/m²) dominated density, almost all of which were the mytilid *Septifer bilocularis*. The 8 WA endemic species had a density of 36.3 ± 7.2 ind/m², and were primarily the small (1cm) gastropod *Euplica bidentata*. Temperate species contributed only 10.7 ± 1.6 ind/m². A similar diversity pattern occurred at Cape Vlamingh: tropical (18) and temperate (16) species had the greatest species richness, with only 10 WA endemic species. However, mollusc density at Cape Vlamingh was dominated by WA endemic species (89.7 ± 11.9 ind/m²), primarily *E. bidentata*. Tropical species were 35.1 ± 7.3 ind/m², again dominated by *S. bilocularis*. Temperate species (10.5 ± 1.4 ind/m²) were only a small proportion of total mollusc density.

Fifty-four species of molluscs were found in 2007 at Rottneest Island: 27 at Radar Reef and 43 at Cape Vlamingh (Figures 2A, 3A; Table 1). Of the 50 identified species on these two platforms, 21 were temperate, 17 tropical and 12 WA endemics. The numbers of temperate (12) and WA endemic species (8) at Radar Reef was the same in 2007 as in 1982, but only 7 tropical species were found in 2007 (12 in 1982). Species composition at Cape Vlamingh in 2007 was very similar to 1982: 17 temperate, 16 tropical and 10 WA endemic. Density of molluscs at Radar Reef and Cape Vlamingh were similar in 1982 but diverged in 2007: increasing to 197.5 ± 37.1 ind/m² at Radar Reef and decreasing at Cape Vlamingh (51.9 ± 7.1 ind/m²). Tropical species (67%), primarily *S. bilocularis*, again dominated density at Radar Reef followed by WA endemics (24%), primarily *E. bidentata*. As in 1982, the situation was reversed at Cape Vlamingh, where *E. bidentata* had a density of 39.2 ± 6.7 ind/m² and *S. bilocularis* was only 2.6 ± 1.9 ind/m². Total density at Cape Vlamingh was dominated by WA endemic species (82%), primarily *E. bidentata*. Temperate species were 11% of total density at Cape Vlamingh and tropical were 7% of the total mollusc density.

A catastrophic decline was recorded in 2021 for diversity (27 species down to 11; 59% decline) for molluscs at Radar Reef compared to 2007 (Figures 2A, 3A; Table 1) where all distribution patterns (tropical, temperate and WA endemic) declined sharply at Radar Reef, particularly tropical species, with only a single species being recorded in 2021. Similarly, the number of species declined from 43 to 17 at Cape Vlamingh (60% decline). Species richness in all three distributional patterns was reduced, again led by tropical species which declined from 16 to 2. Total mollusc density declined catastrophically between 2007 and 2021 at both platforms: a decline of 98.4% at Radar Reef and of 85.6% at Cape Vlamingh.

TABLE 1 Distribution patterns of mollusc species identified on intertidal platforms at Rottnest Island and the Perth coastline, Western Australia.

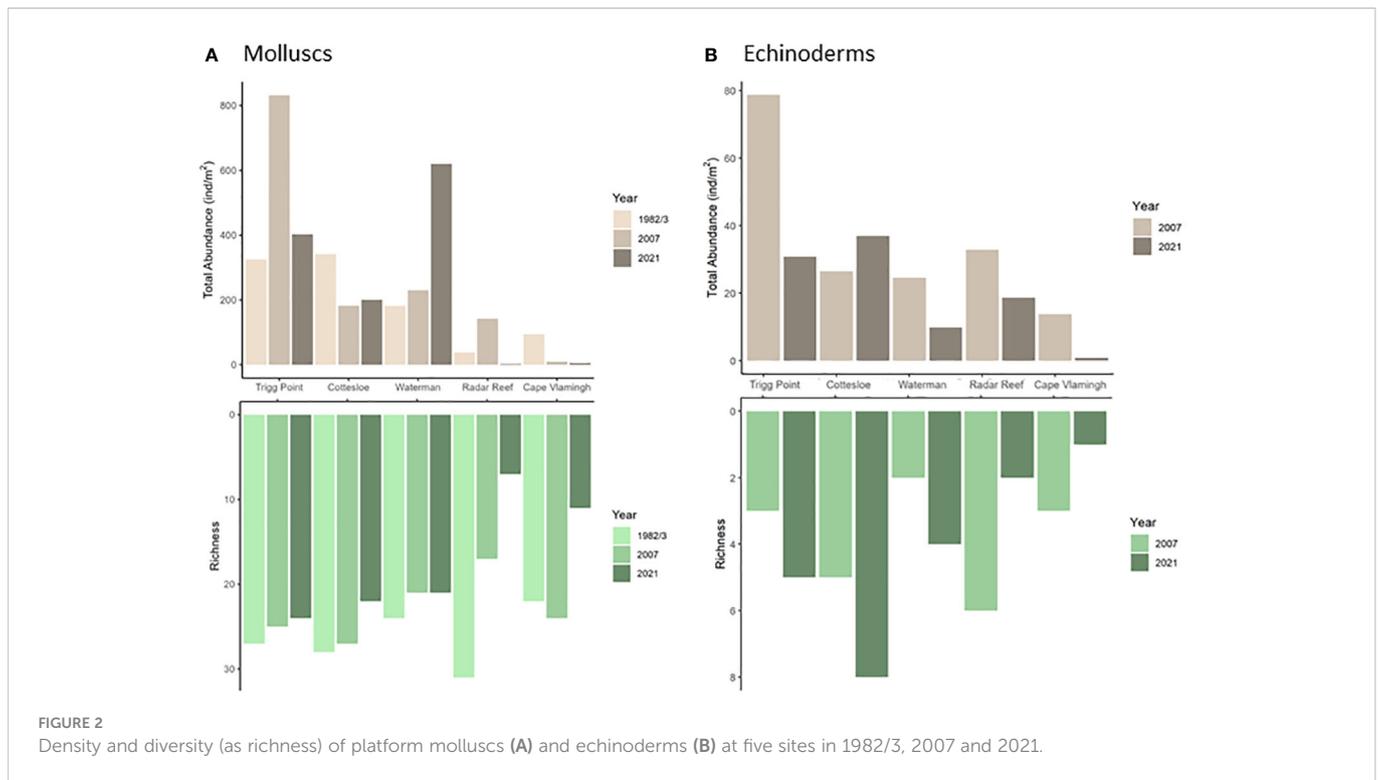
			No. species			Density \pm SE (ind/m ²)		
			1982/83	2007	2021	1982/83	2007	2021
ROTTNEST ISLAND	Radar Reef	Temperate	12	12	6	10.7 \pm 1.6	10.0 \pm 2.4	2.3 \pm 0.5
		Tropical	12	7	1	83.8 \pm 17.0	133 \pm 35	0.1 \pm 0.0
		<i>Septifer bilocularis</i>	-	-	-	82.0 \pm 17.0	132.5 \pm 34.6	0
		WA endemic	8	8	4	36.3 \pm 7.2	55.0 \pm 53.9	0.8 \pm 0.3
		<i>Euplica bidentata</i>	-	-	-	31.0 \pm 7.2	48.2 \pm 12.3	0.5 \pm 0.0
		Total	32	27	11	130.8 \pm 17.9	197.5 \pm 37.1	3.2 \pm 0.6
	Cape Vlamingh	Temperate	16	17	9	10.5 \pm 1.4	5.8 \pm 1.2	2.4 \pm 1.2
		Tropical	18	16	2	35.1 \pm 7.3	3.5 \pm 1.9	2.8 \pm 2.6
		<i>Septifer bilocularis</i>	-	-	-	26.3 \pm 7.3	2.6 \pm 1.9	2.6 \pm 0.0
		WA endemic	10	10	6	89.7 \pm 11.8	42.6 \pm 6.7	2.2 \pm 0.5
		<i>Euplica bidentata</i>	-	-	-	86.3 \pm 11.6	39.2 \pm 6.7	0.8 \pm 0.0
		Total	44	43	17	135.0 \pm 14.8	51.9 \pm 7.1	7.4 \pm 2.8
COASTAL	Cottesloe	Temperate	26	22	21	346 \pm 4.9	67.3 \pm 2.5	134 \pm 7.7
		<i>Prothalotia pulcherrima</i>	-	-	-	186.5 \pm 3.3	0.8 \pm 0.4	52.8 \pm 2.9
		Tropical	5	5	4	1225 \pm 73	5.5 \pm 0.6	4.4 \pm 1.1
		<i>Brachidontes sculptus</i>	-	-	-	1218.5 \pm 73.2	3.2 \pm 0.6	0.4 \pm 0.0
		>WA endemic	5	4	5	4.0 \pm 2.0	4.8 \pm 0.4	22.4 \pm 1.6
		Total	36	31	30	1574.0 \pm 49.8	77.6 \pm 10.1	160.8 \pm 5.0
	Trigg Point	Temperate	26	23	22	314 \pm 30.5	262.1 \pm 9.8	245.3 \pm 11.1
		<i>Prothalotia pulcherrima</i>	-	-	-	111.7 \pm 3.9	1.1 \pm 0.2	128.3 \pm 6.4
		Tropical	5	4	3	1511 \pm 371	754.4 \pm 18.9	2162 \pm 234
		<i>Brachidontes sculptus</i>	-	-	-	1510 \pm 371	754 \pm 49	2159.8 \pm 234.3
		WA endemic	3	4	3	12.5 \pm 4.0	11 \pm 0.3	9.0 \pm 3.9
		Total	34	31	28	1838.6 \pm 208.0	1028.0 \pm 388.0	2416.9 \pm 141.8
	Waterman	Temperate	20	18	19	188 \pm 7.9	165 \pm 3.2	458 \pm 20.9
		<i>Prothalotia pulcherrima</i>	-	-	-	39.5 \pm 2.9	1.4 \pm 0.0	306.2 \pm 16.8
		Tropical	4	4	4	0.9 \pm 0.1	2.8 \pm 0.1	1.3 \pm 0.1
		<i>Brachidontes sculptus</i>	-	-	-	0.2 \pm 0.1	1.3 \pm 0.4	0
		WA endemic	4	4	4	34.8 \pm 1.8	13.8 \pm 0.8	34.5 \pm 2.0
		Total	28	26	27	224 \pm 9.4	182 \pm 11.6	494 \pm 21.5

The decline in mollusc populations between 2007 and 2021 was not uniform across the platforms. The “limpet zone” at the seaward margins of the platforms receives incoming wave action which dissipates as it travels inshore across the platform. Large species: the giant limpet (*Scutellastra laticostata*), chitons (WA endemic *Liolophura hirtosa* and temperate *Onithochiton quercinus*) and abalone (temperate *Haliotis roei*) occur near the seaward margin. Total mollusc density on the general platform surface declined markedly in 2021 at Radar Reef (-99%) (Figures 2A, 3A; Table 2), but the declines in the seaward limpet zone were much lower (-54%). A similar pattern occurred to a lesser extent at Cape Vlamingh; the overall decline between 2007 and 2021 was 85.6% of

density (Table 2). Density on the general platform surface declined by 99% but increased slightly (14%) in the wave swept limpet zone.

Coastal platforms

Species diversity on the coastal platforms was remarkably consistent in the three years surveyed: the total numbers of species at Cottesloe ranged from 30 to 36; 28-34 at Trigg Point and 26-28 at Waterman. Temperate species dominated in all years on all three platforms, ranging from 69% of mollusc species at Waterman in 2007 to 79% at Trigg Point in 2021 (mean 72.4 \pm 1.1%) (Table 1). The percentages of WA endemic species (mean 13.6 \pm 0.9%) were similar to tropical species (mean 14.2 \pm 0.6).



In contrast to the relative stability of species richness, total mollusc density varied considerably on the coastal platforms (Table 1). Trigg Point had the greatest total mollusc density in all years. Cottesloe was second in 1983, but had lower total mollusc density than Waterman in 2007 and 2021.

Total mollusc density declined sharply (-95.1%) at Cottesloe from 1574.0 ± 49.8 ind/m² in 1983 to only 77.6 ± 10.1 ind/m² in 2007. This was largely due to reductions in the small (≤ 1 cm) tropical mussel *Brachidontes sculptus*. Total mollusc density at Cottesloe recovered slightly to 160.8 ± 5.0 ind/m² in 2021, primarily due to the increase in *P. pulcherrima* to 52.8 ± 2.9 ind/m². The pattern was somewhat different at Trigg Point. *B. sculptus* formed continuous carpets on the rock surface in some areas of the *Sargassum* zone; individual quadrats had densities of *B. sculptus* of up to 10,000 ind/m². Total mollusc density on the overall platform in 1983 was 1838.6 ind/m² but declined to 1028 ind/m² in 2007, driven primarily by a decline in *B. sculptus*. Total mollusc density at Trigg Point in 2021 was 2416.9 ± 141.8 ind/m², 32% higher than in 1983, with the increased density of *B. sculptus*. In contrast to Cottesloe and Trigg Point, *B. sculptus* did not form dense aggregations at Waterman; the highest density measured at Waterman was 1.3 ± 0.4 ind/m² in 2007. Total mollusc density at Waterman was driven by *P. pulcherrima*, which declined from 39.5 ± 2.9 ind/m² in 1983 to 1.4 ± 0.0 ind/m² in 2007, but increased to 306.2 ± 16.8 ind/m² in 2021.

Comparison of molluscs at Rottneest Island with coastal platforms

Differences in mollusc communities between coastal platforms and Rottneest Island sites, and between sampling years are illustrated by an unambiguous separation within the ordination space of the nMDS plot (Figure 4). Coastal sites were dominated by predominantly temperate species in all years, whereas offshore sites

were influenced mostly by endemic and tropical species in 1982 and 2007, but not in 2021.

Assemblages at coastal sites were significantly different from those at Rottneest Island (ANOSIM, $R = 0.26$; $p = 0.04$), hence changes in mollusc communities over the decades in both coastal and Rottneest Island habitats were statistically analysed independently of each other. Regardless, changes in assemblages from 1982/3, 2007 and 2021 were not significantly different for either coastal (ANOSIM, $R = -0.07$; $p = 0.45$) or Rottneest Island sites (ANOSIM, $R = 0.50$; $p = 0.13$).

The increase in annual mean sea surface temperatures was congruent with the progression of sampling years within the ordination space.

Echinoderms

Nine species of echinoderms with a total density of 39.2 ± 5.7 ind/m² (Figure 2B; Table 3) were recorded at Radar Reef in 2007. The tropical urchin *Echinometra mathaei* dominated, accounting for 80% of total echinoderm density. Two additional tropical species, the ophiuroid *Ophiocomella sexradia* and the echinoid *Tripneustes gratilla*, contributed a further 17% of echinoderm density; 3 temperate species represented only 3% of density. Only 4 species of echinoderms were recorded in 2021. Total echinoderm density declined by 52% to 18.7 ± 2.8 ind/m² in 2021. *Echinometra mathaei* was 99% of the remaining echinoderm density and biomass at Radar Reef in 2021.

Four species of echinoderms were recorded at Cape Vlamingh in 2007 with a total density of 7.4 ± 1.4 ind/m² (Table 3); *E. mathaei* contributed over 97% of total density. Only *E. mathaei* was recorded in 2021; its density had declined by 88%.

Diversity of echinoderms was also low on coastal platforms in 2007 (Figures 2B, 3B; Table 3); 6 species each at Trigg Point and Waterman and 9 at Cottesloe were recorded in 2007. Waterman (24.6

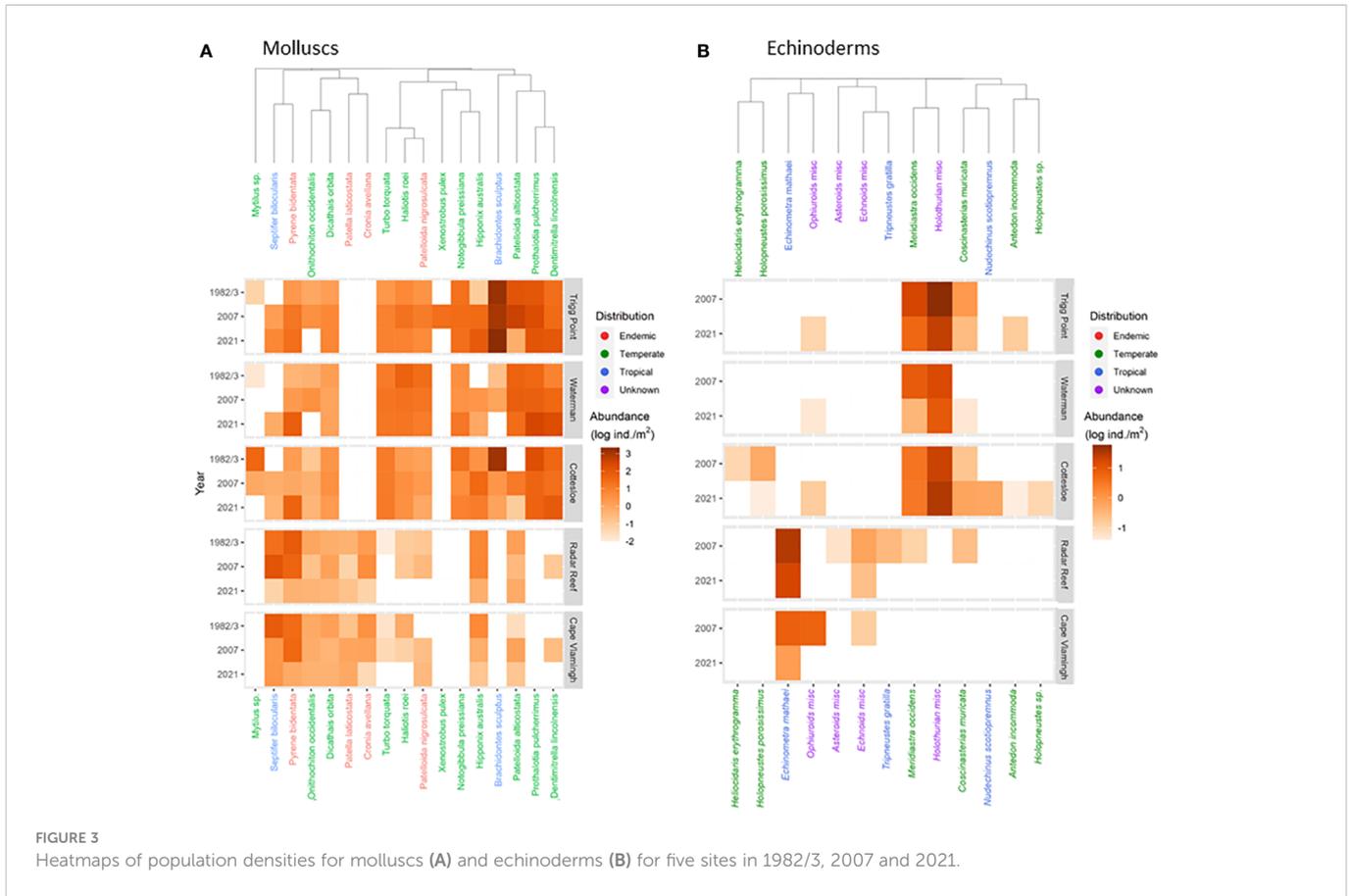


FIGURE 3 Heatmaps of population densities for molluscs (A) and echinoderms (B) for five sites in 1982/3, 2007 and 2021.

± 5.5 ind/m²) and Cottesloe (26.7 ± 7.3 ind/m²) had much lower total echinoderm density than Trigg Point (78.7 ± 19.7 ind/m²). Diversity and density of echinoderms on coastal platforms increased in 2021, relative to the 2007 sampling (Table 3). The increased diversity at Trigg Point and Waterman (7 species versus 6) was negligible, but the increases in density (+56% at Trigg Point to 449% at Waterman) were substantial, partly because of reduced sand coverage of the coastal platform in 2021. Three species of small (≤2cm) sea cucumbers (WA endemic *Psolidiella maculosa*, tropical *Psolidium spinuliferus* and temperate *Apsolidium handrecki*) living attached to the underlying limestone rock on the coastal platform together constituted 83% of total density of echinoderms.

Echinoderm community assemblages differed between coastal and Rottneest Island sites, but not between sampling years, as

demonstrated by a distinct separation within the nMDS ordination plot (Figure S1).

Discussion

Intertidal limestone platform reefs at the western end of Rottneest Island have long been known to have a relatively large component of tropical species compared to similar platforms along the Perth coast (Hodgkin and Marsh, 1957; Hodgkin et al., 1959; Black and Johnson, 1984; Wells, 1985; Veron and Marsh, 1988; Jones and Morgan, 1993). Description of the southward flowing Leeuwin Current (Cresswell and Golding, 1980) provided a mechanism for the distribution of tropical species to the west end of Rottneest Island, where Radar Reef

TABLE 2 Density of molluscs on intertidal platforms at Rottneest Island, Western Australia in 1982, 2007 and 2021.

		Mean Density (ind/m ² ± 1SE)			Change 2007-2021
		1982	2007	2021	
Radar Reef	Platform	138 ± 28.3	204 ± 49.6	2.6 ± 0.6	-99%
	Limpet zone	11.5 ± 2.5	26.0 ± 2.0	12.0 ± 0.8	-54%
	Overall	131 ± 17.9	198 ± 37.1	3.2 ± 0.6	-98%
Cape Vlamingh	Platform	146 ± 15.6	54.3 ± 7.9	0.8 ± 0.2	-99%
	Limpet zone	61.4 ± 40.2	41.0 ± 16.2	46.8 ± 6.9	14%
	Overall	135.0 ± 14.8	51.9 ± 7.1	7.4 ± 2.8	-86%

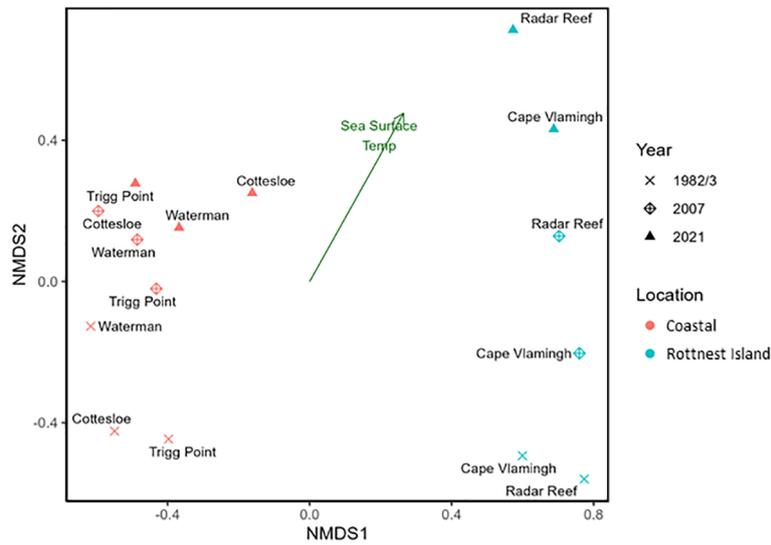


FIGURE 4 nMDS plot of mollusc assemblages in 1982/3, 2007 and 2021 for Perth coastal platforms and Rottnest Island sites.

and Cape Vlamingh are located. The current reaches the west end of Rottnest Island but has limited influence along the continental coastline in the Perth region. Wells (1985) and this paper demonstrated that in 1982/3 tropical species were a significant component of mollusc diversity and density at both Cape Vlamingh and Radar Reef at Rottnest Island. In contrast, diversity of molluscs on coastal platforms was dominated by temperate species and density by the tropical mussel on the coastal platforms, tropical species were limited in species richness. A similar pattern was found in 2007 (Wells et al., 2007). While there were differences in species composition and densities, essentially the same patterns were found at Rottnest Island and coastal sites in 2007.

A follow-up survey in 2021 unexpectedly showed a catastrophic decline in both molluscs and echinoderms at the west end of Rottnest Island in species diversity and density. Compared to the 2007 data, mollusc diversity at Radar Reef in 2021 decreased by 59% and density by 98%. Corresponding figures for Cape Vlamingh were 60% and 86% decline in diversity. Echinoderm diversity decreased by 56% and density by 52% at Radar Reef. Three of the four echinoderm species recorded at Cape Vlamingh in 2007 were not found in 2021. Virtually

the total density of echinoderms in 2007 was due to the tropical urchin *Echinometra mathaei* which had decreased by 88% at Cape Vlamingh in 2021.

What caused the catastrophic declines of molluscs and echinoderms at Radar Reef and Cape Vlamingh between 2007 and 2021? There are several unlikely possibilities. The platforms are at the western end of the island, furthest away from Perth, the Western Australian capital. While the island is a key short-term holiday hotspot, it is a Class A reserve, the highest level of protection in WA. Visitors congregate in Thompson Bay and Geordie Bay in eastern side of Rottnest Island. There are no public access routes to the two platforms. Radar Reef and Cape Vlamingh are in sanctuary zones and removal of benthic marine species is totally prohibited. There have been no reports of eutrophication and there are no artificial structures on the platforms. The only pollutant recorded at the western end of Rottnest Island was low levels of tributyltin (TBT) (Burt and Ebell, 1995), an antifoulant added to vessel paints that came into widespread use worldwide in the early 1970s. The first detection of imposex, a reproductive abnormality caused by TBT, in Western Australia was at Rottnest Island in 1991 (Kohn and Almasi, 1993),

TABLE 3 Diversity and density of echinoderm species identified on intertidal platforms at Rottnest Island and the Perth coastline, Western Australia.

			No. species		Density (ind/m ² ± 1 SE)	
			2007	2021	2007	2021
ROTTNEST	Radar Reef	<i>Echinometra mathaei</i>			31.4 ± 4.7	18.5 ± 2.8
		Total echinoderms	9	4	39.2 ± 5.7	18.7 ± 2.8
	Cape Vlamingh	<i>Echinometra mathaei</i>			7.2 ± 1.4	0.9 ± 0.2
		Total echinoderms	4	1	7.4 ± 1.4	0.9 ± 0.2
COASTAL		Cottesloe	9	14	26.7 ± 7.3	146.5 ± 15.1
		Trigg Point	6	7	78.7 ± 19.7	122.5 ± 11.4
		Waterman	6	7	24.6 ± 5.5	38.8 ± 4.0

primarily from specimens collected at the western end of the island. Restrictions on the use of TBT were imposed, and imposex is now virtually absent in snail populations at Rottneest Island, including both Cape Vlamingh and Radar Reef (Wells et al., 2017; Wells and Gagnon, 2020). It is unlikely the above causes impacted diversity and densities of molluscs and echinoderms at the two study sites on Rottneest Island.

Marine heat waves are another possible cause of the declines recorded at Radar Reef and Cape Vlamingh. Over the five months from late December 2010 to late May 2011 SST off Rottneest Island were up to 4°C higher than the long-term monthly average of 21.5–21.9°C, with the increased temperatures extending down to >50m (Thomson et al., 2011). The 2011 marine heatwave during a La Niña event caused extensive coral bleaching at Rottneest Island (Thomson et al., 2011; Moore et al., 2012). Nearly 30% of the Rottneest Island corals were bleached five years later (2016) during a record El Niño event (Le Nohaïc et al., 2017). In another effect of the 2011 marine heatwave, two tropical species of fish increased in abundance (Pearce et al., 2016).

Most of the adverse effects of the 2011 marine heatwave in WA occurred in subtidal environments. The known exception was a small commercial fishery of the temperate abalone *Haliotis roei* which was wiped out during the 2011 marine heatwave on intertidal platforms at Kalbarri (27.7°S) near the northern limit of its range. There has been virtually no natural recovery of the Kalbarri population (Caputi et al., 2019; Strain et al., 2020), paralleling the situation at Rottneest Island. The catastrophic mortality recorded here was apparently restricted to Radar Reef and Cape Vlamingh. Rifai et al. (2020) used haphazardly scattered quadrats to survey invertebrates on four intertidal platforms at Rottneest Island in the summer of 2018; three in Strickland Bay on the south coast of the island 2.7–4km east of Radar Reef and one at North Point 8km to the northeast of Radar Reef. Forty species were recorded, including 23 species of molluscs. *Echinometra mathaei*, the population of which crashed at Radar Reef and Cape Vlamingh, was abundant at all four sites surveyed by Rifai et al. (2020) in 2018, ranging from 26.5% of total invertebrates at Strickland West to 71.2% at Strickland Far East. *Pyrene bidentata*, another species that crashed at the west end was recorded in small numbers at two sites but was abundant at Strickland West (22.3% of total invertebrates) and North Point (32.3%). Similarly, Wells et al. (2021) found the heterobranch gastropod *Bursatella hirsuta* to be abundant on the platform at Little Armstrong Bay, adjacent to North Point, with an estimated population of >600,000 individuals over the ~300m long platform (Wells et al., 2021). The Western Australian Museum conducted a detailed survey of Roe Reef, 1 km offshore of the northeastern end of Rottneest Island in 2013 and 2014, recording 287 marine species, including 40 species of molluscs and 16 echinoderms (Richards et al., 2016). The ranges of 28 mollusc species from Roe Reef could be determined: 19 were temperate, 4 tropical and 5 endemic to WA. These results suggest the catastrophic mortality reported here was restricted to Radar Reef and Cape Vlamingh at the western tip of the island, where the influence of the Leeuwin Current is greatest.

The presence of viable populations of invertebrates on adjacent platform reefs at Rottneest Island suggests there would be ample planktonic larvae available to repopulate the platforms at Radar Reef and Cape Vlamingh. In addition, there are numerous islands and subtidal reefs in the area which could be sources of local species

for replenishment (Kendrick and Rule, 2014). Further north, the Houtman Abrolhos Islands provide a source of tropical species that can be brought south to Rottneest Island by the Leeuwin Current (Wells, 1997).

In contrast to the catastrophic declines in mollusc and echinoderm populations at the western end of Rottneest Island, viable populations of both groups remained on the Perth coastal platforms. Echinoderms increased modestly in species richness between 2007 and 2021 but substantially in density. Wells et al. (in prep.) combined the data in this paper into a temporal study of mollusc populations on all three coastal platform reefs (Cottesloe, Trigg Point and Waterman) and also reformatted data collected annually from 1984 to 1986 conducted (Wells and Keesing, 1986; Wells et al., 1986). The full dataset was conducted annually in summer from 1983 to 1987, and in 2007 and 2021. Total mollusc densities varied considerably between years at Cottesloe and Trigg Point, primarily because of changes in the populations of the short-lived mussel *Brachidontes sculptus* (as *B. ustulatus*) and the small gastropod *Prothalotia pulcherrima*, which has a one year life cycle (Wells and Keesing, 1987; Wells et al., in prep.). Mollusc density at the Waterman platform, which lacked the mussel populations, was relatively stable between 1983 and 2021. Despite the reduced sampling effort, the total number of species recorded on the three platforms in 2007 (52) and 2021 (44) was consistent with the results in the 1980s. The 44 species recorded in 2021 was a single species less than the 45 recorded in 1987. The 52 species identified in 2007 was within the 1980s range of 45–58. The eight most commonly recorded species in the 1980s were also common in 2021.

Increasing SST typically cause temperate biota to be replaced by tropical species (Yamano et al., 2011; Gervais et al., 2021), a phenomenon reported for subtidal environments off the west coast of Western Australia (Wernberg et al., 2011; Baird et al., 2012; Wernberg et al., 2013; Hyndes et al., 2016; Wernberg et al., 2016); however the responses of intertidal invertebrates to rising sea surface temperatures did not translate into population replenishments on the intertidal platform reefs at Rottneest Island. All three marine biogeographic components of molluscs and echinoderms (tropical, temperate and WA endemic species) suffered extensive population declines; temperate species were not replaced by tropical ones. The reason(s) for the catastrophic decline in tropical, temperate and WA endemic mollusc and echinoderm species and their failure to repopulate the intertidal rock platforms at Cape Vlamingh and Radar Reef are unknown, but the data presented here provide a sound basis for exploring the possible causes and monitoring for recovery.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

FW and JK contributed to conception and design of the study. FW, JK, MG, TI, and CB participated in field surveys. FW and JK

were primarily responsible for species identifications. FS performed the statistical analysis. FW wrote the first draft of the manuscript. All authors contributed to the article and approved the submitted version.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2023.1075228/full#supplementary-material>

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