

Persistence of giants: population dynamics of the limpet *Scutellastra laticostata* on rocky shores in Western Australia

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ABSTRACT: Population dynamics and life history traits of the 'giant' limpet *Scutellastra laticostata* on intertidal limestone platforms at Rottneest Island, Western Australia, were recorded by interannual (January/February) monitoring of limpet density and size structure, and relocation of marked individuals, at 3 locations over periods of 13–16 yr between 1993 and 2020. Limpet densities ranged from 4 to 9 ind. m⁻² on wave-swept seaward margins of platforms at 2 locations and on a rocky notch at the landward margin of the platform at a third. Juvenile recruits (25–55 mm shell length) were present each year, usually at low densities (<1 m⁻²), but localized pulses of recruitment occurred in some years. Annual survival rates of marked limpets varied among sites and cohorts, ranging from 0.42 yr⁻¹ at the notch to 0.79 and 0.87 yr⁻¹ on the platforms. A mass mortality of limpets on the platforms occurred in 2003, likely mediated by thermal stress during daytime low tides, coincident with high air temperatures and calm seas. Juveniles grew rapidly to adult size within 2 yr. Asymptotic size (L_{∞} , von Bertalanffy growth model) ranged from 89 to 97 mm, and maximum size from 100 to 113 mm, on platforms. Growth rate and maximum size were lower on the notch. Our empirical observations and simulation models suggest that these populations are relatively stable on a decadal time scale. The frequency and magnitude of recruitment pulses and high rate of adult survival provide considerable inertia, enabling persistence of these populations in the face of sporadic climatic extremes.

KEY WORDS: Giant limpets · Population dynamics · Growth · Survival · Rocky intertidal zone · *Scutellastra laticostata*

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1. INTRODUCTION

Limpets are a polyphyletic group of aquatic gastropods characterized by a conical, dish-shaped (patelliform) shell and large foot. They are widely distributed in marine habitats ranging from the intertidal zone to deep-sea hydrothermal vents (Chase et al. 1985). Limpets are key components of intertidal and shallow subtidal communities of temperate rocky shores, where their functional importance as mesograzers is well established (reviewed by Branch 1981, Henriques et al. 2017).

Most limpets are small, ranging in shell length from a few mm to cm, but some species reach much greater size, up to 100 mm or more. These are referred to colloquially as 'giant' limpets. In a recent review of the conservation biology of giant limpets, Espinosa & Rivera-Ingraham (2017) identified 14 species from 5 genera in the families Patellidae and Lotiidae as giant limpets based on a 100 mm length threshold. These species have a global distribution, although most occur in the South Atlantic, half of them (of the genera *Cymbula* and *Scutellastra*) along the coast of South Africa. Two species are endemic to

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islands (*Celana talcosa*, Hawaiian Islands; *Patella kermadecensis*, Kermadec Islands) and another to the western Mediterranean (*P. ferruginea*). *Lottia gigantea*, the only giant in the family Lottiidae, ranges across the west coast of the USA from Washington to the coasts of Baja California, Mexico. The largest species (*S. mexicana*) occurs along the Pacific coast of Mexico and reaches 350 mm in length. We also found published records of 6 species in the family Fissurellidae (key-hole limpets) in Peru, Chile, Argentina and USA that meet the 100 mm size criterion, but were not included in this review: *Fissurella maxima* (Oliva & Castia 1986, Durán & Oliva 1987), *F. cumingi* (Durán & Oliva 1987), *F. nigra* (McLean 1984), *F. picta* (Moreno et al. 1984), *F. crassa* (Navarrete & Castilla 1993, Serra et al. 2001) and *Megathura crenulata* (Kenner et al. 2013, Kushner et al. 2013, Reed 2020).

Most giant limpets are generalist grazers in rocky intertidal or shallow subtidal zones to about 10 m depth (Espinosa & Rivera-Ingraham 2017). Many occur on wave-exposed shores and exhibit strong attachment to the substrate. They can be territorial, exhibiting homing behaviour and aggressively defending feeding territories regularly spaced on the rock. Population density can vary greatly among species, although many occur at low density (<1 ind. m⁻²). Information on growth, survival and longevity are lacking for all but a few species, given logistical constraints of monitoring marked individuals in wave-swept areas and the absence of a reliable method of ageing by shell analysis. Large size and accessibility in intertidal or shallow subtidal habitats have long rendered giant limpets an attractive target for human collection. Increased harvesting, pollution and habitat fragmentation are major causes of population decline, and 4 species currently are considered threatened or in danger of extinction (Espinosa & Rivera-Ingraham, 2017).

Scutellastra (formerly *Patella*) *laticostata* (Blainville, 1825) is a giant patellid limpet endemic to Western Australia (Wells & Bryce 1985). It forms locally abundant populations, at densities of 8–12 ind. m⁻², in narrow bands on the outer margins of wave-swept limestone platforms (Cape Vlamingh and Radar Reef) at the western end of Rottneest Island (Scheibling & Black 1993). The lower range of *S. laticostata* extends into the shallow subtidal zone (usually <1 m depth) on adjacent rocky ledges (Scheibling et al. 1990). It is the dominant grazer in these areas and forages about a distinct home scar that enables strong attachment to the substratum (Scheibling & Black 1993). Density of a small isolated population of *S. laticostata* was lower (2 ind. m⁻²) on a vertical notch at the shore-

ward margin of a platform at Nancy Cove on the south coast (Scheibling & Black 1993). Limpets were smaller on average along the pitted edge of platforms, and on the notch at Nancy Cove, than those in sculpted concavities (terraces) on the more level, upper surface of platforms. Size distributions were right-skewed for all populations, and limpets were largest in the 'terraced zone', with maximum sizes of 100–110 mm.

In this study, we extend and expand our preliminary observations of *S. laticostata* at these sites in 3 important ways. (1) We examined population dynamics and changes in demographic structure (e.g. inter-annual variation in abundance of new recruits) at a decadal scale (13–16 yr, in line with the predicted lifespan of individuals) to assess the stability of these populations. (2) We obtained repeated annual measures of marked individuals to measure growth rate and survivorship over time and to estimate individual longevity. (3) We used estimates of the observed annual finite rate of change in abundance over the monitoring period to parameterize a simulation model that projects population change over the next 10 yr. The timespan of our study captures population responses to recruitment events and mass mortality related to heat stress, and likely a near complete turnover of individuals. Given the predicted increase in ocean warming and frequency of marine heat-waves in the region (Smale et al. 2019), our empirical data and model projections are key to determining the conservation status of this species and its ability to persist in a rapidly changing climate. Finally, to broaden the context of our study, we conducted an exhaustive literature review to compare our findings on life-history traits and population dynamics of *S. laticostata* with records for other giant limpets, and applied our simulation model to 2 other species (*Patella ferruginea* and *Megathura crenulata*) for which long-term measures of abundance were available.

2. MATERIALS AND METHODS

2.1. Study sites

Populations of *Scutellastra laticostata* at Cape Vlamingh at the western tip of Rottneest Island, and Nancy Cove on the southern coast were monitored annually in January/February between 1993 and 2006 (except 1996 and 2002). Both locations (Fig. 1) were accessible only during extreme low tides and calm sea states during these months. At Cape Vlamingh, our study sites were on 2 raised projections of a

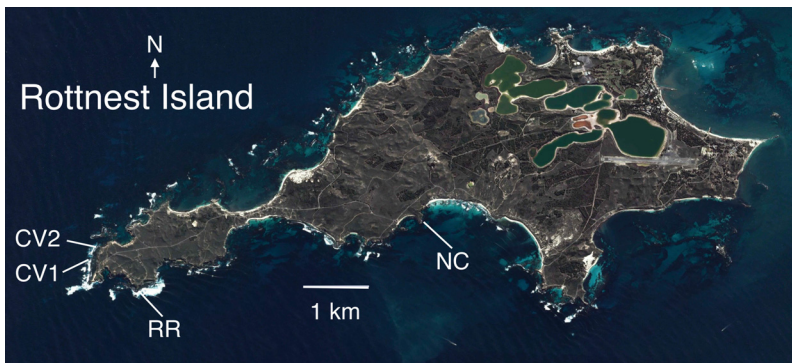


Fig. 1. Rottneest Island (32.0° S, 115.5° E), Western Australia, showing locations where populations of *Scutellastra laticostata* were sampled at Cape Vlamingh (CV1, CV2), Nancy Cove (NC) and Radar Rock (RR) (Google Earth © Google 2020, imagery date: 5/30/2016; Image © 2020 CNES / Airbus, Image © 2020 Maxar Technologies)

broad, intertidal limestone platform subject to heavy wave forces by the incoming swell (Fig. 2A). The platform rims are irregular and drop sharply into the subtidal zone, forming a vertical edge in some areas. The outer margin (low intertidal) is heavily eroded by wave action giving it an irregular, 'pitted' topography. Above the pitted zone, the rock is emersed at low tide and slopes gently to a plateau characterized by small (decimeter-scale) 'terraces'—shallow concavities with curving, ridged borders separating adjacent terraces, possibly formed by limpet grazing (Scheibling & Black 1993).

On each projection at Cape Vlamingh (CV1, CV2), we delineated sampling areas along south- and north-facing platform edges using a fixed baseline (ends marked by bolts) that extended alongshore for 7–12 m at 2–5 m from the platform edge (Fig. 2A; Table S1 in the Supplement at www.int-res.com/articles/suppl/m646p079_supp.pdf). The projection of this baseline (normal to the platform edge) to encompass the limpet population in the pitted and terraced zones defined the sampling areas (see Section 2.2). Relative tidal height measured with reference to the highest point in the terraced zone provided lower (0.8–1 m below reference) and upper (0.3–0.6 m below reference) limits to the pitted zone. Lower limits represented the vertical range of the population at some sites (CV1 South) or the limit of our sampling ability at others (CV1 North). Upper limits of the pitted zone delineated the boundary between zones.

At Nancy Cove, limpets were recorded along a 25 m baseline extending along an intertidal notch (Fig. 2C). The average width of the limpet zone, measured at 1 to 4 m intervals along this line, was 0.6 ± 0.2 SD m ($n = 16$) m in January 2003 (the vertical range did not vary throughout the study period), giving a total sam-

pling area of 15 m² (Table S1). Mean tidal range at Rottneest is <1 m at spring tides (<https://www.transport.wa.gov.au/imagery/rotnest-island-tide-and-wave.asp>). Tidal heights were provided by Prince (1992) for locations near CV1 ('Vlamingh North', -0.18 m) and Nancy Cove ('Green Island', -0.38 m).

In January 2003, following a mass mortality of *S. laticostata* in the terraced zones at Cape Vlamingh, we extended our sampling programme to include an isolated population of limpets on a large rock (Radar Rock) near the seaward edge of the platform at Radar Reef. (For a description of this platform and resident population

of *S. laticostata*, see Scheibling & Black 1993). The rock was a section of the outer edge of the platform that had been broken off and swept onto the platform by waves during a previous storm event. We set up a 6.7 m baseline across the length of the rock (Fig. 2B). Limpets initially were sampled on a relatively flat and terraced area on the upper surface (~0.75 m above the platform) encompassing a planar surface area of 12.7 m². Between 2006 and 2016, limpets also were found on a lower terraced section (4.1 m² in planar surface) along the onshore edge of the rock, extending the sampling area to 16.8 m² (Table S1).

2.2. Population sampling

At Cape Vlamingh, the positions and size (shell length, 1 mm precision) of individual *S. laticostata* were recorded within each sampling area as distance (cm) from the shell apex to each of 2 permanent benchmarks (anchor bolts) at the ends of a fixed baseline of known length (Table S1). Repeated measurements by different observers differed by <1 cm. The position of each limpet on a rectangular coordinate system was determined by triangulation (Heron's method from the lengths of 3 sides of a scalene triangle, https://en.wikipedia.org/wiki/Heron%27s_formula). For each site, we estimated the total area occupied by *S. laticostata* by plotting the positions of all individuals pooled over sample years from 1993–2003 and drawing a polygon around the outermost positions of the limpets (Fig. S1). The boundary between the pitted and terraced zone (evident by the change in topography) was mapped at about 0.5 m intervals by triangulation from the 2 benchmarks in January



Fig. 2. Study areas at (A) Cape Vlamingh, (B) Radar Rock on Radar Reef and (C) the notch at Nancy Cove. Arrows indicate individuals of *Scutellastra laticostata*. White line indicates approximate position of the baseline used to locate positions of individuals at each site. Photo credits: Robert Scheibling (A), Robert Black (B), Matilda Murley (C)

2003, and superimposed on the concatenated population data to divide the overall polygon into separate polygons for the pitted and terraced zones (Fig. S1). The area of each zone was measured (Table S1) and used to calculate limpet density in that zone from counts in the respective polygons. Density of recruits was separately recorded. Recruits were operationally defined for each sampling area and year by inspec-

tion of the size frequency distribution: individuals between 25 and 55 mm, usually separated by a gap in size from the rest of the population, were considered recruits. This is consistent with the size at reproductive maturity of *S. laticostata* of ~52 mm (Scheibling & Black 1993).

Following a mass mortality of *S. laticostata* in the terraced zone of platforms at Cape Vlamingh in January 2003, we also recorded the positions and measured the length of recently exposed home scars of dead limpets. The scars had little or no film of filamentous algae, indicating recent loss of the resident limpet, and were readily distinguished from older scars that were heavily overgrown. At CV1, we collected shells of recently dead *S. laticostata* in a large pool along the shoreward boundary of the terraced zone. The shells, which had accumulated in the deepest region of the pool (~3 m depth at low tide) within an area of ~2 m², were manually collected by snorkelling. They could be distinguished from older shells on the basis of shell wear and fouling by algal films; many still had remnants of an algal turf. Shell length was measured and tagged individuals were noted.

At Radar Rock, we recorded the position and size of limpets on the upper and lower terraced sections relative to the baseline, as described for Cape Vlamingh. We also counted and measured recently exposed home scars of *S. laticostata* that had died on the upper section of the rock in January 2003. At Nancy Cove, we recorded the position and size of individual limpets as we proceeded along the baseline from a permanent benchmark (bolt) and one end.

2.3. Individual survival and growth

To measure growth and survival of *S. laticostata*, we marked individuals with a small (6 mm diameter) numbered plastic tag affixed to the apical part of the shell with a dab of underwater epoxy putty (Emerkit®).

Although the numbered tags gradually were lost or eroded, the putty remained. During our censuses, we examined each limpet carefully for a putty mark and recorded the tag number if present. Because limpets typically move <50 cm between successive years (Scheibling & Black 1993), we could identify marked individuals, even if the tag number was lost, by comparing positions in our sampling areas between years. In January 1991, we tagged an initial set of limpets at Cape Vlamingh ($n = 206$) and Nancy Cove ($n = 34$) (Scheibling & Black 1993). In January 1997, we tagged a second set ($n = 59$) at Cape Vlamingh, including 40 smaller limpets (36–60 mm) to attain additional information on growth rate, and retagged survivors ($n = 29$) from the initial set marked in 1991. In January 2003, we tagged a third set of limpets at Cape Vlamingh ($n = 39$) as well as an additional set at Radar Rock ($n = 44$) using a different epoxy putty (Z-spar®). Because tag loss at Cape Vlamingh was high initially (Scheibling & Black 1993), we estimated survival beginning 1 or 2 yr after the year of tagging, starting from 1993 for the 1991 set and from 1998 for the 1997 set. Rarely, marked individuals missing in one year were found in the next, and the number in the previous year was adjusted so that survival curves decreased monotonically.

2.4. Simulation model

We calculated the annual finite rate of change, observed λ (yr^{-1}), of populations of *S. laticostata* as N_{t+1}/N_t , where N_t and N_{t+1} are initial and final density of limpets for pitted and terraced areas at Cape Vlamingh (CV1 North and South and CV2 North), or initial and final counts of limpets at Nancy Cove and Radar Rock. Where there were gaps in our censuses, we estimated the average λ (yr^{-1}) across the gap and added the appropriate number of estimates to the list of observed λ . For each site, we constructed a simulation model in R language (R Core Team 2019), which sampled with replacement 10 of the individual estimates of observed λ . The cumulative product (CP) of these samples is the population size after 10 years relative to a starting population of 1.0. Our simulation repeated this process 1000 times; we report the median of the CP values as an estimate of whether the simulated populations would increase (CP >1.0) or decrease (CP <1.0). We also tallied the number out of 1000 values of CP that were <0.50 and <0.10, as an indication of how likely the populations would decline to these fractions of their starting size.

2.5. Statistical analyses

We used factorial ANOVA to compare the density of the total population of *S. laticostata*, or of recruits only, between zones (pitted and terraced) and across years at 3 sites at Cape Vlamingh (CV1 North, CV1 South, CV2 North), and adjusted for missing values ($n = 5$) by restricted maximum likelihood using JMP 7.0.

We plotted the natural logarithm of the number of surviving (relocated) tagged limpets against year and used the slope of this relationship (b) to estimate the instantaneous mortality rate averaged over the respective time interval, and converted that to a finite survival rate (e^b) for each habitat (pitted and terraced zones) at Cape Vlamingh, and for Nancy Cove and Radar Rock. To compare mortality rate across habitats, locations and sets of tagged individuals (cohorts), we used analyses of covariance (ANCOVAs) to compare slopes. We used programs in Ebert (1999) based on profile likelihoods (P_LIKELIHOOD.BAS) to estimate annual survival rates (p_x), with 95% confidence intervals, for cohorts of tagged individuals in censuses. Average annual survival rate (p_x) was calculated by dividing the number of individuals at the end of an interval by the number at the start and converting this to an annual rate by taking the n^{th} root of the quotient, where n is the number of years in the interval.

To compare growth of *S. laticostata* among habitats and locations, we regressed annual changes in length of tagged limpets (2003 cohort) against initial length in that interval, for limpets in the pitted (17 individuals, 28 records) and terraced (21, 47) zones at Cape Vlamingh, at Nancy Cove (7, 12) and Radar Rock (38, 157), and used ANCOVA to compare slopes. We used an R script based on FABENS.BAS (Ebert 1999) to estimate the parameters of the von Bertalanffy growth equation and their standard errors, based on initial and final lengths for each year.

3. RESULTS

3.1. Population dynamics: recruitment and mass mortality

Density of *Scutellastra laticostata* at Cape Vlamingh approximately doubled between 1993 and 1998, increasing from 4.7 to 8.8 ind. m^{-2} (mean densities for counts pooled across both zones), and then remained relatively stable until 2002 when density decreased to 7.4 ind. m^{-2} and again stabilized over the next 4 yr (Fig. 3). Densities in the terraced zone in 3 of the 4

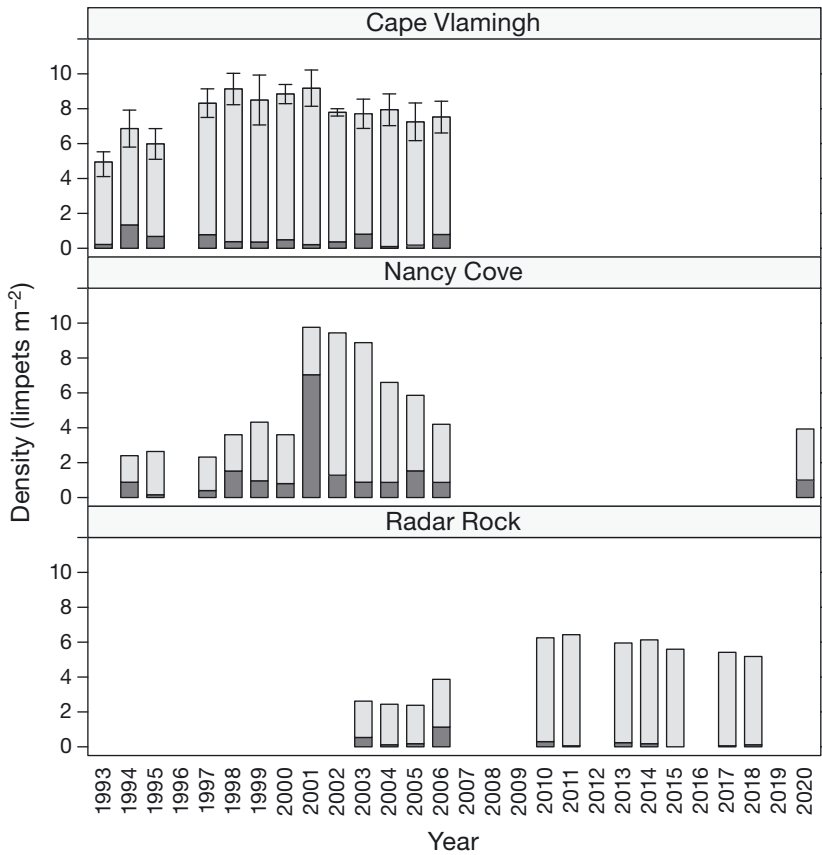
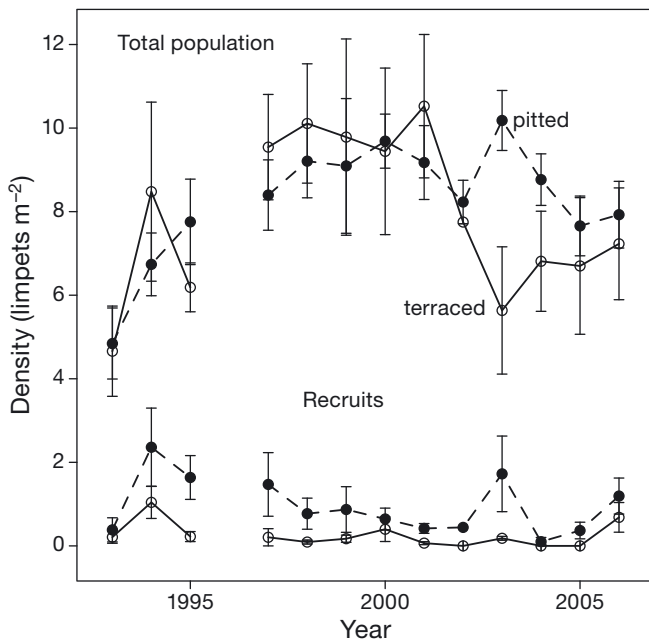


Fig. 3. Interannual variation (in January) in recruit (shell length <55 mm, dark grey) and adult (light grey) density of *Scutellastra laticostata* at all study locations: Cape Vlamingh, averaged across pitted and terraced zones for 3 sites with both zones (CV1 North and South, CV2 North; Table S1), from 1993 to 2006; Nancy Cove from 1994 to 2006 and 2020; and Radar Rock from 2003 to 2018. Gaps in records are years without sampling data. Bar height is total population density (mean \pm SE)



sites that included this habitat (CV1 North and South, CV2 North), decreased on average by ~ 2 ind. m^{-2} following the mass mortality in January 2003, while density in the pitted zone at all 4 sites (including CV South) increased by about the same amount due to a concurrent recruitment event in that zone (Fig. 4). Factorial ANOVA, based on the 3 sites with both terraced and pitted zones (CV1 North and South, CV2 North), showed that limpet density varied significantly over time ($p = 0.031$) but not between zones ($p = 0.531$), and there was no interaction between zone and year ($p = 0.159$) (Table S2B).

Recruitment rates of *S. laticostata* at Cape Vlamingh were consistently greater in the pitted (0.4–2.4 recruits m^{-2}) than in the terraced (0–1.0 recruits m^{-2}) zone (Fig. 4), although the difference in recruit density between zones was not statistically significant ($p = 0.181$) (Table S2C). Recruit density varied significantly over time ($p = 0.001$), but there was no interaction between zone and year ($p = 0.110$). High recruit densities between 1994 and 1997 and in 2003 accounted for increases in population density in the pitted zone (Fig. 4).

At Cape Vlamingh, *S. laticostata* in the terraced zone generally attained larger size (shell length, 3rd quartile: 85–90 mm) than limpets in the pitted zone (80–85 mm) (Fig. 5, Fig. S2, Table S3). Following a mortality event in January 2003, the size distribution of recently exposed home scars in the terraced zone at CV1 (North and South pooled) reflected the size distribution of adult limpets in that zone, and the bimodal size distribution of dead shells of *S. laticostata* (modes at 70–75 and 90–95 mm) collected in a tide pool landward of the platform resembled the adult modes of size distributions in the pitted and terraced zones, respectively (Fig. 6).

Fig. 4. Total population density and recruit density of *Scutellastra laticostata* in terraced (open circles, solid line) and pitted (closed circles, dashed line) zones at Cape Vlamingh in January from 1993 to 2006 (not sampled in 1996). Data are means \pm SE for 3 sites in the terraced zone (CV1 North, CV1 South; CV2 North) and 4 sites in the pitted zone (CV1, North and South; CV2, North and South)

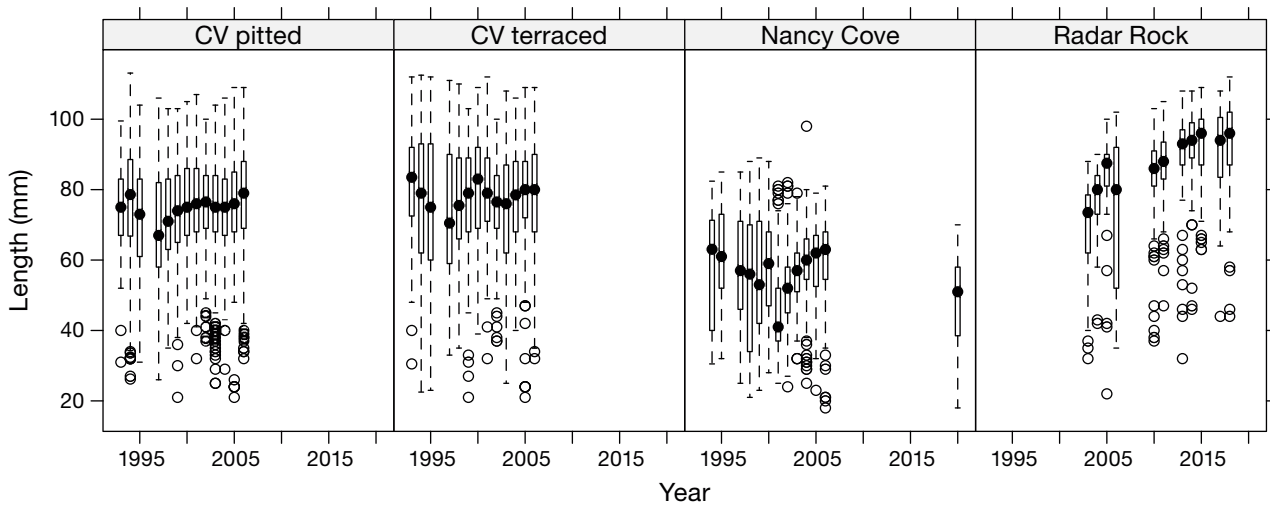


Fig. 5. Length-frequency distributions of *Scutellastra laticostata* in the pitted zone and terraced zone at Cape Vlamingh (CV, pooled across all sites, Table S1) from 1993 to 2006; Nancy Cove from 1994 to 2006 and 2020; and Radar Rock from 2003 to 2018. Gaps in records are years without sampling data. Black circle is median, box indicates 1st and 3rd quartiles, whiskers are lowest and highest values within 1.5× the interquartile range of the 1st and 3rd quartiles, respectively, and individual points are outliers

A die-off of large *S. laticostata* also occurred on the upper terraced surface of Radar Rock in January 2003, where the density of recently vacated home scars was 5.3 m⁻². The size distribution of these scars (mean ± SD: 84 ± 7 mm, n = 70) was similar to that on the platform at Cape Vlamingh. The density of surviving limpets at Radar Rock was 2.6 ind. m⁻² (Fig. 3), indicating a mortality rate of 67%. The survivors were primarily smaller individuals (mean ± SD: 68 ± 15, n = 44), including 9 recruits (<55 mm) (Fig. 3). There was no evidence of mortality among the broader population of limpets along the platform edge at Radar Reef, an area continuously swept by waves. Population density at Radar Rock remained low until 2006, when it increased with recruitment to 3.9 ind. m⁻² and then to 6.3 ind. m⁻² by 2010. Density remained relatively stable from 2010 to 2014, with a small decline to 5.2 ind. m⁻² by 2018 (Fig. 3). Limpet size progressively increased over the sampling period, reaching median sizes of 95 mm, much greater than those observed on platforms at Cape Vlamingh, where median size rarely exceeded 80 mm in the terraced zone (Fig. 5; Fig. S2)

Densities of *S. laticostata* along an intertidal notch at Nancy Cove were relatively stable between 1994 and 2000, ranging from 2 to 4 ind. m⁻², but increased sharply in 2001 to 9.8 ind. m⁻² with a large recruitment pulse (7 recruits m⁻²) (Fig. 3). The 2001 cohort presents a prominent shift in the size distribution of limpets in 2001, which gradually shifted back with the growth of these recruits between 2001 and 2006 (Fig. 5, Fig. S2). During this period, median size of

limpets progressively increased from 41 to 63 mm, regaining a median size first recorded in 1994 (Fig. 5), and population density progressively decreased to 4.9 ind. m⁻², as recruit density varied from 1 to 2 ind. m⁻² yr⁻¹ (Fig. 3). The population was resampled opportunistically 14 yr later in February 2020. Population and recruit densities (3.9 and 1 ind. m⁻², respectively) at this time were comparable to those measured over 3 yr preceding the 2001 recruitment pulse and at the end of our census period in 2006 (Fig. 3). The size distribution in 2020 was comparable to that recorded in the year following the recruitment pulse (Fig. 5, Fig. S2); however, maximum size (70 mm) of *S. laticostata* was lower than that previously recorded at Nancy Cove (79 mm, Table S3).

3.2. Individual survival and growth

Plots of the natural logarithm of the number of surviving (relocated) tagged individuals against year showed approximately linear declines in all cases, indicating a constant rate of mortality of *S. laticostata* (Fig. 7). At Cape Vlamingh, survival rate was greater for the terraced than the pitted zone for the 1991 and 1997 cohorts, although the difference was statistically significant only for the 1997 cohort (ANCOVA, Table S4A). There also were significant differences in survival rate among cohorts within sites, with the 1997 cohort at Cape Vlamingh and the 2003 cohort at Nancy Cove surviving less well than other cohorts at these sites (Table S4B). Average annual survival rates

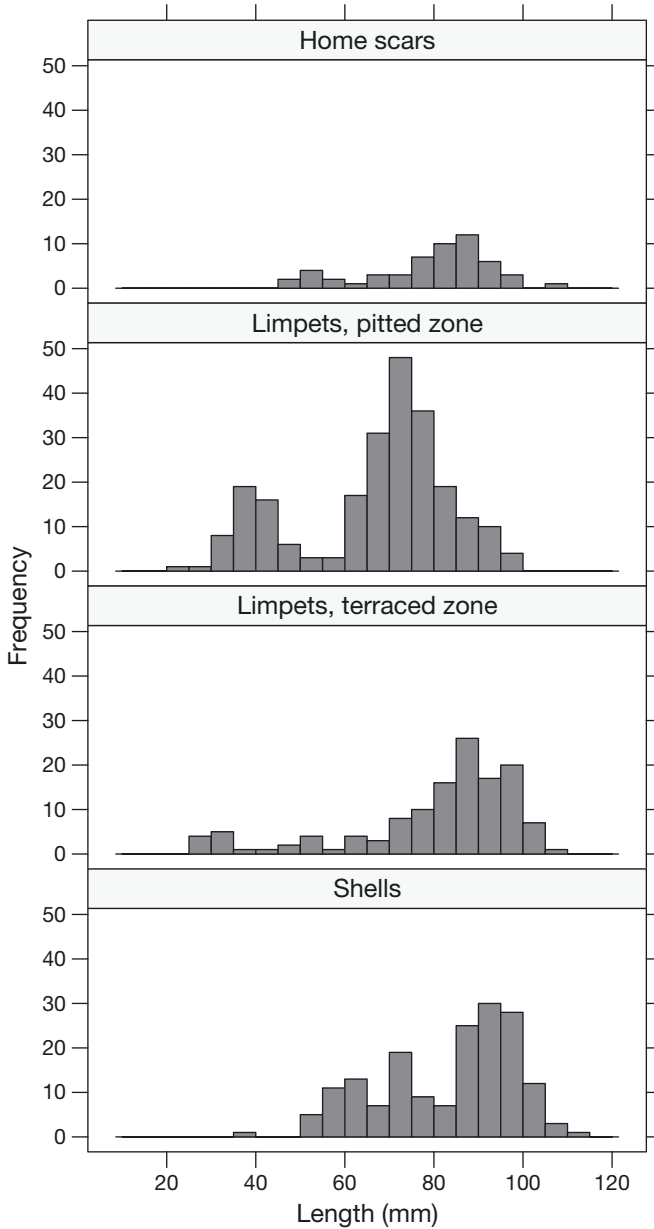


Fig. 6. Length-frequency distributions of *Scutellastra laticostata* in pitted ($n = 29$) and terraced ($n = 234$) zones, vacated limpet home scars in terraced zones ($n = 130$) and accumulated shells in a large intertidal pool landward of the platform edge ($n = 171$) at Cape Vlamingh (data pooled over CV1S and CV1N), following a mortality event in January 2003

(p_x), reflect the differences in slopes (Table S4A). Some of the upper and lower 95% confidence limits of estimates of p_x by the profile likelihood method are broad because of the small numbers of tagged individuals. Based on these estimates of annual survival rates (Table S4), 10% of individuals initially tagged in 1991 (which averaged in size between 64 mm at Nancy Cove and 86 mm at Cape Vlamingh) would be

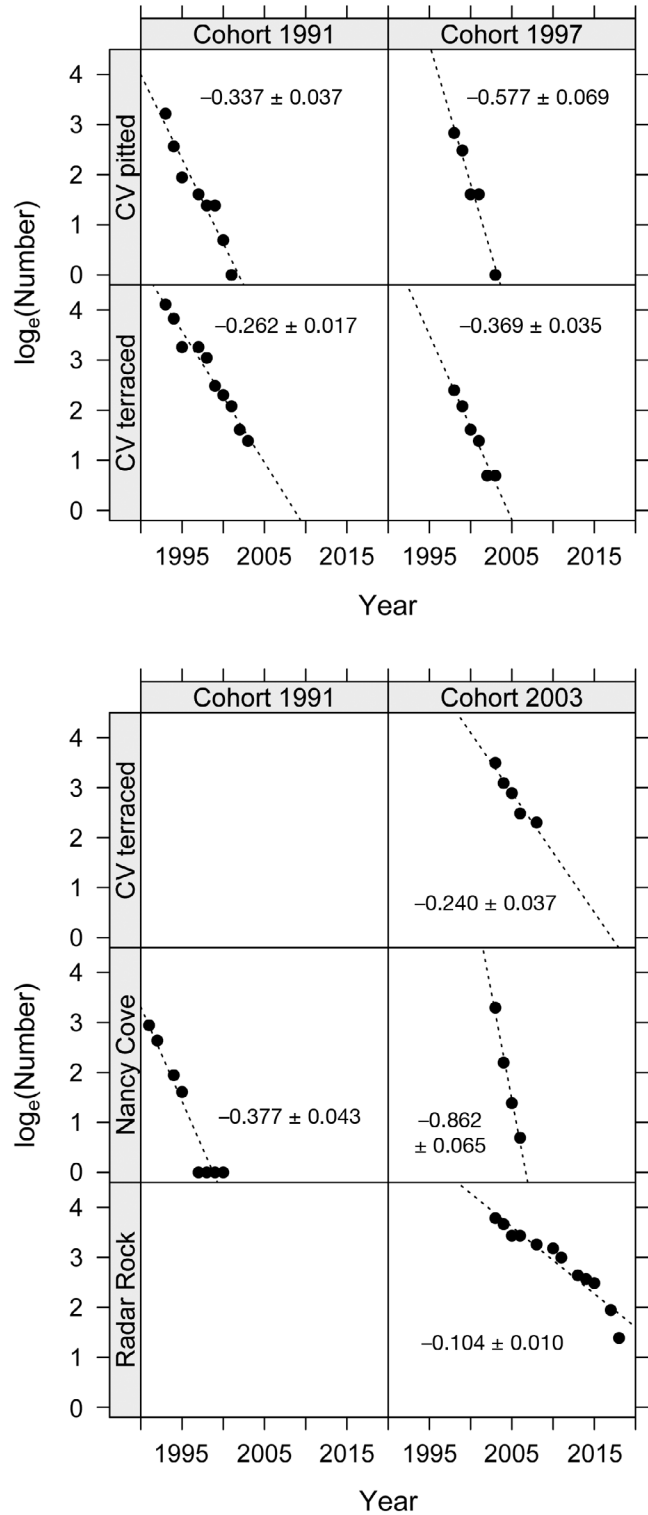


Fig. 7. Natural logarithm of numbers of marked *Scutellastra laticostata* over years of census, arranged by zone and year of marking (cohort). For 1991 and 1997 cohorts, Cape Vlamingh data are pooled numbers from pitted and terraced zones. Inset data are slope of linear regression (\pm SE), which estimates instantaneous mortality rate. See Table S4 for additional information on annual survival rates

alive after 7.0 and 7.5 yr. The greatest differences in annual survival rate occurred in the 2003 cohort, ranging from 0.42 yr^{-1} at Nancy Cove to 0.87 yr^{-1} at Radar Rock (Table S4C).

The annual growth increment of *S. laticostata* decreased as initial length increased in all habitats and sites, and linear regression provided a good fit to the data, except at Nancy Cove where there were few data over a limited size range (Fig. 8, Table S5A). ANCOVA did not detect differences in the slopes of these regressions, but revealed significant differences in elevation between habitats and sites (Table S5A,B). Adjusted for an initial length of 78 mm, Nancy Cove limpets grew slowest, but this rate was not statistically different from the other sites, likely because of the small sample size at Nancy Cove. At Cape Vlamingh, limpets in the pitted zone grew significantly less than those in the terraced zone; growth at Radar Rock was intermediate but also did not differ significantly from other sites (Table S5A,C).

3.3. Simulation model

All but 2 (CV1 South, pitted and terraced zones) of the 8 populations of *S. laticostata* that we monitored across all sites increased in abundance over the census period (Table 1). To adjust for differences in census periods among sites, we used the mean of observed finite rate of change, λ (yr^{-1}), for each population as a comparator: mean λ was <1.00 for the 2 CV1 South populations and ranged from 1.05 to 1.09 for the other 6 populations. We used year-to-year estimates of observed λ (yr^{-1}) in a simulation model which assumed that a subsequent 10 yr interval would have changes

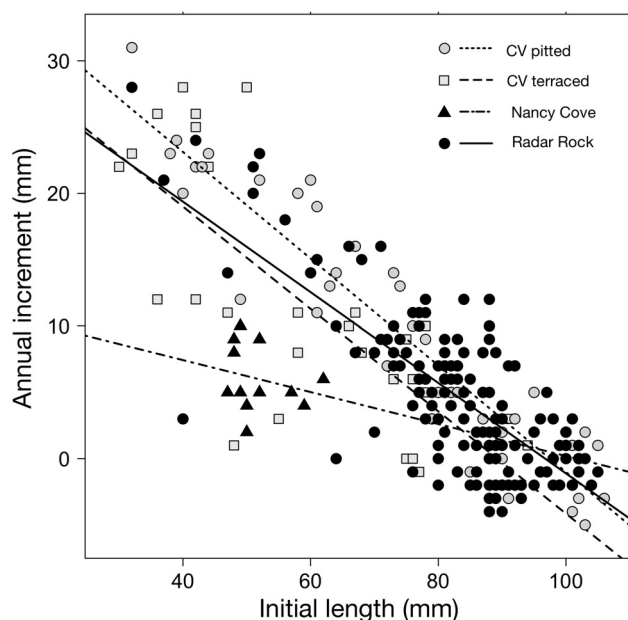


Fig. 8. Annual increment in shell length (mm) relative to initial shell length (mm) of *Scutellastra laticostata*. See Table S5 for regression equations

in abundance similar to the observations of the recent past by sampling with replacement the array of values of observed λ . Our model output shows that the median relative size of a population (with a starting value of 1.0) after 10 yr was <1.0 for the 2 CV1 South populations but ranged from 1.5 to 2.4 for the other 6 populations (Table 1). In the terraced zone at CV1 South, the proportion of 1000 simulations with declines to <0.5 of the initial population size was 0.336, but only 0.037 declined to <0.1 of the initial size. These proportions were smaller in the pitted zone at this site (0.156 and 0, respectively).

Table 1. Dynamics of populations of *Scutellastra laticostata* at sites/zones at Cape Vlamingh (CV1 South and North, CV2 North; pitted/terraced zone), Nancy Cove (NC) and Radar Rock (RR) during the monitoring period at each site. Data are starting and ending density (m^{-2} ; for all CV sites) or number (for NC and RR sites) of limpets over this period, and observed mean finite rate of change, λ (yr^{-1}). Also given are results of 1000 simulations using annual estimates of observed λ , projected over 10 yr: the median relative size of the population after 10 yr and the number of simulations with relative population size <0.5 or <0.1 .

For details, see Section 2.4

Sites (zone)	Years	Initial density (m^{-2}) or number	Final density (m^{-2}) or number	Observed mean λ (yr^{-1})	Median relative size, population after 10 yr	No. / 1000 simulations, relative size: <0.5 , <0.1
CV1 S (pitted)	1993–2006	7.14	5.90	0.99	0.89	156, 0
CV1 S (terraced)	1993–2006	6.78	4.56	0.97	0.82	336, 37
CV1 N (pitted)	1993–2006	4.91	8.76	1.05	1.56	51, 0
CV1 N (terraced)	1993–2006	3.25	8.39	1.08	1.93	86, 0
CV2 N (pitted)	1993–2006	3.12	9.55	1.09	2.39	11, 0
CV2 N (terraced)	1993–2006	3.95	8.74	1.06	1.86	0, 0
NC	1994–2006	30	63	1.06	1.59	113, 0
RR	2003–2018	44	87	1.05	1.49	0, 0

We extended the simulation model to show how an additional year of high recruitment, that would provide a larger value of observed λ (yr^{-1}), would alter the outcome for the 2 CV1 South populations. This addition is reasonable because we missed some years in our sequence of censuses, and populations at Cape Vlamingh (and Radar Rock) increased markedly during the missed years (Fig. 3). In simulations in which we added an additional value equal to the maximum observed λ for each of the 2 CV1 South populations, the median relative population size increased to 1.01 and 1.11 in the pitted and terraced zones respectively, and the proportion of 1000 simulations declining to <0.5 of the initial population decreased to 0.093 and 0.241.

4. DISCUSSION

4.1. Spatial distribution

Populations of *Scutellastra laticostata* at Rottneest Island were concentrated in narrow bands (2–4 m horizontal distance) along the seaward margins of intertidal limestone platforms at Cape Vlamingh and Radar Reef (Scheibling & Black 1993, this study). The small population on the intertidal notch at Nancy Cove, a more wave-protected area along the landward border of an intertidal platform, may be an isolated phenomenon, although *S. laticostata* occasionally is found in similar habitats at other locations (Green Island, Salmon Point) along the south coast of Rottneest Island (R. Black unpubl. data). Other giant limpets, such as *Scutellastra cochlear* (Branch 1975), *S. kermadecensis* (Schiel et al. 1986) and *P. ferruginea*, *S. mexicana* and *Cellana talcosa* (Espinosa & Rivera-Ingraham 2017) also inhabit wave-exposed intertidal or shallow subtidal environments. Density of *S. laticostata* at Rottneest Island generally ranged from 4 to 9 ind. m^{-2} , comparable to maximum densities recorded for other giant limpets in areas of high wave exposure (6–35 ind. m^{-2}) and much lower than maximum densities of species in areas of moderate or low wave action, such as *Cymbula granatina* and *S. argenvillei* (288 and 388 ind. m^{-2} , respectively) (Espinosa & Rivera-Ingraham 2017).

Individual feeding territories of *S. laticostata* on reef platforms are evident as pits or terraces that may be sculpted through prolonged grazing by limpets (Scheibling & Black 1993). At Cape Vlamingh, recruitment of juveniles was consistently greater in the pitted zone, and adults attained larger size in the terraced zone (see also Scheibling & Black 1993). Greater

density of recruits in the pitted zone could be related to protection from physical disturbance afforded by a structurally more complex substratum compared to that of the terraced zone, where strong wave shear may limit larval settlement or post-settlement survival of juveniles (see also Martins et al. 2010). Small pits and recesses also constrain the size of a limpet's feeding area, which is proportional to its body size (Scheibling & Black 1993). This may account for a larger maximum size attained by limpets in the terraced zone. *S. laticostata* exhibits a high degree of fidelity to a home scar: most individuals remain within the same pit or terrace with little or no net displacement over a year, although a few may change feeding areas as they grow, either by migrating from pitted to the terraced zone or by physically displacing smaller conspecifics in terraces (Scheibling & Black 1993). Homing behaviour is common among other territorial giant limpets, including *L. gigantea* (Stimson 1970), *S. cochlear* (Branch 1975) and *S. kermadecensis* (Schiel et al. 1986).

4.2. Individual survival and growth

Annual survival rate (p_x), based on relocation of tagged individuals of *S. laticostata*, varied between habitats at Cape Vlamingh (lower in the pitted than terraced zone) and between cohorts within sites (Cape Vlamingh, Nancy Cove), ranging from 0.42 yr^{-1} at Nancy Cove to 0.87 yr^{-1} at Radar Reef for the 2003 cohort. Wave dislodgement following periods of extreme thermal stress that weakens attachment is likely the main cause of mortality among adult limpets. We observed recently vacated home scars only during mass mortality events associated with such phenomena (see Section 4.3). Shell strength and foot tenacity of these limpets limits the range of potential predators, although the whelk *Thais orbita* occasionally drills through their shells, killing the limpets (R. Black unpubl. data). As far as we are aware, there is no incidental harvesting or collection of *S. laticostata* on these platforms, given their restricted accessibility. The particularly low survival rate of limpets on the notch at Nancy Cove may be related to their higher intertidal elevation, which could increase the frequency and magnitude of thermal stress.

There is information about survival rates for six species of giant limpets, calculated directly from mark and recapture experiments or indirectly from the combination of known rates of growth and size frequency distributions (Table S6). *S. laticostata* has 7 estimates; the other 5 species each have between 1

and 5 estimates for a total of 17. The median value of p_x for *S. laticostata* was 0.736 yr^{-1} and the median $Y_{10\%}$ (yr to reach 10% of population size) was 7.5 yr, remarkably similar to median values for the other 17 observations (0.722 yr^{-1} and 7.1 yr). Overall, estimates of p_x (excluding an outlier for *Cymbula oculus*, 0.171 yr^{-1}) ranged from 0.403 to 0.916 yr^{-1} (for *C. granatina* and *P. ferruginea*, respectively), indicating that giant limpets survive well, although we found no estimates of survival for the 6 species in the family Fissurellidae. These estimates of annual survival rate are comparable to those reported for some smaller limpets (e.g. median p_x of 0.88 yr^{-1} , range: $0.27\text{--}1.0 \text{ yr}^{-1}$, for 4 species with 15 estimates; Nakin et al. 2012).

Juveniles of *S. laticostata* grew rapidly on intertidal platforms at Cape Vlamingh and Radar Reef (including Radar Rock), generally reaching adult size ($>55 \text{ mm}$) within 2 yr of settlement (Scheibling & Black 1993, this study). Rapid growth of recruits may be an adaptation to strong wave forces that characterize these habitats. The smoothed surface of the home scar and precise fit to the shell margin enables the limpet's foot to adhere tenaciously to the substratum. In a concurrent study at these sites (with A. Metaxas, Oceanography Department, Dalhousie University), we found that foot tenacity of *S. laticostata* (vertical dislodgement force measured *in situ* with a purpose-built spring scale) increased with adult size (range: $64\text{--}110 \text{ mm}$, $n = 23$) to as high as 169 kg (A. Metaxas, R. E. Scheibling & R. Black unpubl. data), reflecting the magnitude of hydrodynamic forces potentially experienced by these limpets (Lowell 1987). Growth rate was higher in the terraced than pitted zone at these sites (Scheibling & Black 1993, this study), which may reflect spatial constraints to feeding territories within pits, as mentioned above. Stimson (1973) found that growth of *Lottia gigantea* was affected by the size of its feeding territory, and that limpets surrounded by mussels had smaller territories and lower growth rates than those in more open areas.

Growth rate and maximum size of *S. laticostata* was lower on the intertidal notch at Nancy Cove than on the platforms. Limpets on the notch occupied home scars, but there were no conspicuous feeding areas surrounding them, as in pits or terraces. Although foraging area does not appear to be spatially constrained on the notch, growth may be limited by foraging time during immersion, compared to limpets on more wave swept platforms at lower tidal elevation. Differences in the quantity or quality of algal food resources also may affect growth rate; unlike the platforms, the rocky surface of the notch was not extensively covered with encrusting or turf-forming algae.

There is information about growth for 7 species of giant limpets: estimates for K , the growth rate constant, and L_∞ , the asymptotic length, for the von Bertalanffy growth equation, either reported directly or that we could calculate from published information (Table S6). All 7 species had at least 1 study with a predicted asymptotic size $>85 \text{ mm}$. Values for 26 estimates of K (yr^{-1}), which represents how quickly asymptotic size is reached, fell into 2 groups: (1) a faster-growing group of 4 species (*S. laticostata*, *Cymbula granatina*, *C. oculus*, *Fissurella maxima*), with at least 1 value of $K > 0.4$, and (2) a slower-growing group of 3 species (*F. crassa*, *Lottia gigantea*, *Patella ferruginea*), with all values of $K < 0.4$. Using $3/K$ as an estimate of the number of years it would take a species to reach 95% of L_∞ (Taylor 1958), where estimates of K are averaged for each species within each group, there is more than a 2-fold difference in group means between the slow- and fast-growing groups (8.3 vs. 20.4 yr). *C. oculus* reaches a large size in 3.4 yr compared with 28.5 yr for *P. ferruginea*; *S. laticostata* is intermediate with a mean of 11.8 yr.

4.3. Population dynamics: recruitment and mortality

Populations of *S. laticostata* at all 3 sites were relatively stable over periods of 7–10 consecutive years: Cape Vlamingh, 1997–2006; Nancy Cove, 1994–2000; Radar Rock, 2010–2018. An abrupt increase in density (by 180%) at Nancy Cove in 2001 was associated with an unusually high recruitment pulse that was absent at Cape Vlamingh. Increases in density also occurred between 1995 and 1997 at Cape Vlamingh (47%) and between 2006 and 2010 at Radar Rock (62%), intervals when we had no records from these populations, but there must have been at least 1 episode of high recruitment to account for the observed magnitude of increase. At Radar Rock, population density increased by 72% from 2005 to 2006, with a recruitment pulse that was at least 3-fold higher than the recruitment rate recorded in the other 10 yr of observation.

Local decreases in limpet density were associated with mortality events likely due to desiccation or heat stress during periods of prolonged daytime low tides, high temperatures and calm sea conditions in mid-summer. This occurred at Cape Vlamingh in January 1991, when dislodged and moribund individuals, and shells of recently dead limpets, were found in inshore regions of the platforms (Scheibling & Black 1993). At these times, large individuals in the terraced zone

occasionally were observed raising their shell off the rock substrate, a behaviour that facilitates evaporative cooling under thermal stress (Garrity 1984, Lowell 1984). This also coincided with a mass mortality of a smaller limpet (*Patelloida alticostata*) on these platforms in January 1991 (Kohn 1993). A second mortality event of *S. laticostata* was observed at Cape Vlamingh and Radar Rock 12 yr later, in January 2003. A recruitment event in the pitted zone at Cape Vlamingh (recruitment remained negligible in the terraced zone) offset these losses such that population density did not change. In contrast, the estimated mortality on the terraced upper surface of Radar Rock (~0.75 m above the surrounding platform) was 67%. The period of thermal stress would have been prolonged on this elevated slab of rock compared to the surrounding platform from which it was displaced, and where the resident population of conspecifics apparently was unaffected. Wave action in the lowest regions of the intertidal, such as the pitted zone around the platform edge, likely limits the extent of mortality during these events. As such, the Radar Rock provides a natural experiment that supports our contention that thermal stress is a major agent of mortality in this species.

Our longitudinal sampling at Rottneest Island suggests that population dynamics of *S. laticostata* are mediated by episodic recruitment pulses and mass mortality. The high survival rate of adults provides considerable inertia, enabling persistence in the face of sporadic die-offs due to extreme climatic conditions and acting as a buffer against years of low recruitment. A decrease in recruitment rate or increase in frequency or intensity of climatic stress could tip this balance, leading to potentially catastrophic decline. However, none of the populations that we monitored changed uniformly; rather, they increased in some years and declined in others. This ability to recover after a decline is an important population attribute of *S. laticostata* that tends to maintain stability.

Our empirical measures and model estimates provide insight into how these populations are faring. Recapture rates of tagged limpets provide estimates of annual finite rate of survival (p_x). If these rates remain constant, as they did during our years of observations, it would take 9.6 and 15.9 yr for a cohort of limpets at Cape Vlamingh and Radar Rock, respectively, to be reduced to 10% of their original numbers. Our estimates of observed mean λ (based on annual estimates for each population) showed that 6 out of 8 limpet populations increased in abundance ($\lambda > 1.00$) over the census period. Adding an extra copy of the maximum observed λ in our calcu-

lations for the remaining 2 populations (CV1 South, pitted and terraced zone) resulted in observed mean $\lambda > 1.00$, suggesting the importance of an occasional year of high recruitment (which likely was missed during the gap year at this location). Using our simulation model to project how these populations might have fared over a 10 yr period following our census gave a similar pattern of results. Our recent sample at Nancy Cove, 14 yr after the census period, supported our 10 yr projection of population growth (median relative size of the population after 10 yr = 1.59) at this site. The density, demography (proportion of recruits) and size structure of the present population of *S. laticostata* are all within the range of earlier measurements (1994–2006), providing a record of persistence for this population spanning 26 yr.

We are aware of only 2 other species of giant limpet that have been censused annually over several years to decades: *P. ferruginea* in the western Mediterranean (Coppa et al. 2016, Zarrouk et al. 2016, Espinosa et al. 2018) and *Megathura crenulata* off southern California, USA (Kenner et al. 2013, Kushner et al. 2013, Reed 2020). We used time-series data on limpet density from these reports to calculate mean observed λ and applied our simulation model to project relative population size after 10 yr, and the proportion of 1000 simulations with final relative size of population <0.5 or <0.1 , for comparison with *S. laticostata* (Table 1). Our results suggest that populations of *S. laticostata* at Rottneest Island (grand mean of observed λ across all sites/zones during census period = 1.04 yr^{-1} , Table 1) fare about as well as those of *P. ferruginea* at Ceuta (1.11) in the western Mediterranean or *M. crenulata* in the California Channel Islands (1.06), but better than populations at the 2 other locations in both the western Mediterranean (0.76) and in southern California (0.62) (Table S7). However, for simulations using values of observed λ to make 10 yr projections, forecasts for the 8 populations of *S. laticostata*, with 6 populations having a final median relative population size >1.0 , 2 with a median size <1.0 and none with observed or predicted extinctions (Table 1), were better than those for the 14 populations of *P. ferruginea*, with comparable numbers of 7, 5, 1 and 1 population(s), respectively, and the 23 populations of *M. crenulata*, with 6, 8, 5 and 4, respectively (Table S7).

5. CONCLUSIONS

Our census data show that populations of *Scutellastra laticostata* exhibit stability on a decadal timescale commensurate with the expected longevity of

this species based on estimates of individual survival. Implicit in this definition of stability is that it encompasses at least 1 complete turnover of individuals (Connell & Sousa 1983). Local persistence of these populations reflects a balance between episodic recruitment and mass mortality. A decrease in recruitment rate or increase in mortality rate, due to accelerating climatic changes or human exploitation, could tip this balance, resulting in catastrophic population decline. Environmental drivers that may destabilize populations of *S. laticostata* include: (1) warming air and seawater temperatures that affect limpet survival in intertidal habitats (Harley et al. 2009, Leung et al. 2019); (2) changes in current patterns and water column productivity that affect larval supply (Waite et al. 2019); and (3) increased climate variability, including marine heat waves (Wernberg et al. 2013, Smale et al. 2019) and severe storms (Elsner et al. 2008) that may increase dislodgement.

Despite its large size and weighty foot, there are no contemporary records of harvesting or collection of *S. laticostata*. This in part may reflect the limited accessibility of isolated populations on wave-battered shores and the strong adherence of individuals to the substrate. Given our measures of life history traits of *S. laticostata*, it is unlikely that these populations could survive even under low levels of harvesting. Our empirical results and modelling approaches provide a baseline that can inform local management or conservation strategies for this species, should the need arise. More generally, our findings also are relevant to other species of giant limpet with similar life history traits and environmental challenges, particularly those that, unlike *S. laticostata*, are vulnerable to local anthropogenic impacts, such as pollution, habitat degradation and fragmentation, and commercial harvesting (Espinosa & Rivera Ingraham 2017). Transcending these local stressors is the accelerating pace of global climate change and intensifying climate variability that leave open the question of persistence of these giants.

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