



Grazer commensalism varies across the species range edge: host chiton size influences epibiont limpet incidence and spatial segregation

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ABSTRACT: Biotic interactions can determine species distributions and range limits, but little theoretical background exists regarding variation in commensalistic associations across latitudes. We estimated the geographic variation of the epibiont limpet *Scurria parasitica*'s association with its obligate host chiton species *Enoplochiton niger* across their distribution from Peru to northern Chile (12–30°S), to test the influence of host size variation on epibiont occurrence, individual spatial distribution, and body size. We analyzed the contribution of chiton body size to the pattern of abundance and distribution of occupancy of the epibiont limpet. We also examined the relationship between limpet shell size, coverage, and incidence probability function and chiton body size across latitudes. For some localities across the range edge of the host grazer's distribution (i.e. 28–30°S), incidence and densities of the epibiont limpet were higher on larger chitons. Unoccupied host chiton proportions decreased at the poleward edge of the host–epibiont species range compared with sites located to the north. Increased variation in the epibiont limpet distribution on the host chiton plates suggests that limpets' spatial segregation may have a role in lessening intra-specific interference competition with the host species at southern latitudes. Therefore, local and large-scale processes seem to contribute to modify the host–epibiont association pattern. Further studies are necessary to determine if this association shifts from commensalistic to antagonistic across the distributional range of both species.

KEY WORDS: *Enoplochiton niger* · *Scurria parasitica* · Epibiont–host interaction · Body size · Range edge · Patch occupancy · Commensalism · Intertidal ecology

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1. INTRODUCTION

Biotic interactions are involved in structuring community composition, and thus are important for the community's response to environmental change (Gilman et al. 2010, Singer et al. 2013, Chuang & Peter-

son 2016). The importance of these biotic interactions in determining species distributions and range limits, however, remains a topic of debate in ecological and biogeographic arenas (Case & Taper 2000, Sexton et al. 2009, Singer et al. 2013, Araújo & Rozenfeld 2014, Godsoe et al. 2015).

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There is now more consensus that the sign and magnitude of species interaction strengths can vary with environmental context (e.g. latitudinal gradients; Bruno et al. 2003, Harley et al. 2006, Bulleri et al. 2016). This suggests that antagonistic interactions may influence species range contraction/expansion (Cunningham et al. 2009, Pigot & Tobias 2013, Ettinger & Hillerislambers 2017, Godsoe et al. 2017a). For example, a shift in the direction of biotic interaction strength in different environmental contexts has been observed in different systems (Hacker & Gaines 1997, Singer et al. 2013), including distributional ranges (Ettinger & Hillerislambers 2017). Furthermore, as we move from benign to stressful environments, some species may shift from being competitors to facilitators (Bertness & Callaway 1994, Hacker & Gaines 1997, Bruno et al. 2003). Thus, biotic interactions can change qualitatively and quantitatively through the distributional range of one species (Chamberlain et al. 2014, Ettinger & Hillerislambers 2017). This change can strongly influence species range limits (Chamberlain et al. 2014, Louthan et al. 2015), but there is still a need to develop tools to predict the effects of biotic interactions on species range margins within different environmental contexts (e.g. Araújo & Rozenfeld, 2014, Chamberlain et al. 2014, Godsoe et al. 2017a).

Tracking species co-occurrence or coexistence patterns across latitudes can provide important clues about the role of biotic interactions on species distributions (Sexton et al. 2009, Lavergne et al. 2010, Singer et al. 2013, Godsoe et al. 2017b). However, it is difficult to separate the role of biotic interactions (e.g. competition, predation, mutualism) from environmental effects alone (Soberón 2010, Godsoe & Harmon 2012). These environmental drivers (e.g. temperature gradients) can act synergistically or antagonistically on different types of biotic interactions; e.g. exacerbating antagonistic effects but driving partial compensation by commensalisms and/or mutualisms (Singer et al. 2013). These relationships are particularly important considering that the effects of asymmetric interactions such as amensalism and commensalism on range margins are considered less frequently in the literature than competition or predation (e.g. Colwell & Rangel 2009, Lavergne et al. 2010).

Species trait variations across their distribution ranges may be a key factor influencing the impact of biotic interaction on species range limits (Sagarin et al. 2006). Different populations exhibit demographic and individual trait variations across latitudes, often captured by hypotheses such as the 'centre abun-

dance hypothesis' or 'Bergmann's rule' (Gaston & Blackburn 1996, Blackburn et al. 1999, Sagarin et al. 2006). These theories suggest that range edge populations possess traits that are more vulnerable to both demographic and environmental stochasticity (Vuetch & Waite 2003). However, these hypotheses may not capture the full variation of species interactions across their geographic distribution. How the traits of interacting species co-vary across geographic ranges can thus provide additional important information that can help forecast species range shifts (Hampe & Petit 2005, Sagarin et al. 2006, Godsoe et al. 2015, 2017b).

In this study, we examined if changes in body size of the grazer *Enoplochiton niger* (chiton) at its range margins influences the occurrence, body size, and within-host spatial distribution of its specific commensal epibiont *Scurria parasitica* (limpet). This information can shed light on the variation of the host–epibiont grazer interaction across latitudes and the potential of this interaction to influence population persistence of the host *E. niger* at its range edge. The scurrinid limpet *S. parasitica* lives exclusively on the shell or plates of several mollusk species, including the chiton *E. niger*, where the epibiont exhibits a different ecotype and presents homing behaviour, grazing on small propagules and spores of algae growing on its shell (Espoz et al. 2004, Asorey 2017). The epibiont limpet populations live and feed exclusively upon chiton plates and represent a specific commensal (i.e. no positive effects of *S. parasitica* on the chiton have been recorded). However, *S. parasitica* scrape the plates of the chiton while feeding, thus eroding them. Given that *S. parasitica* can also remove other epibiont species while feeding (e.g. barnacles, algae) which might overgrow the chiton's plates, this epibiont limpet may also have positive effects on chiton performances. However, this interaction may become antagonistic at high limpet densities, with negative consequences for chiton individual performances. No studies, however, have been conducted on the effects of the epibiont grazer on *E. niger* and the potential variation in their interactions across a latitudinal context. The chiton population varies in body size across its geographic distribution, reaching larger body lengths at its range edge than in the central populations (Ibáñez et al. 2019, 2021). If the epibiont grazer occupancy or density increases with host chiton size, its effects on chiton performance could become negative at their range edge. Concurrently, the epibiont limpet may segregate spatially on chiton plates to persist at a higher density at

their poleward ends. Given the range limit of the host chiton species has contracted in recent decades (Rivadeneira & Fernández 2005), this range contraction raises the question of how epibiont limpet incidence in the host chiton varies across the southern range edge and what role this association plays in the chiton's population persistence. There is, however, scarce information in this and other latitudes about how interactions in a grazer–grazer commensal system change through biogeographic gradients, which could shed light on how occurrences of the epibiont grazer modify the host grazer's performances and persistence at its distributional range limit.

Using this grazer–grazer system, we specifically hypothesized that (1) the probability of occurrence (i.e. limpet presence per chiton, and/or chiton area covered) of the epibiont grazer *S. parasitica* could be higher on larger *E. niger* individuals, i.e. area effect in the 'patch-occupancy' hypothesis (Fahrig 2013), corresponding to the range edge populations of the host grazer. In addition, (2) epibiont length could be positively correlated with increased chiton size. Finally, (3) The incidence of the epibiont limpet *S. parasitica* on the host grazer may depend on its individual micro-spatial distribution, with higher spatial segregation (i.e. differential use of plates) of the epibiont grazer on (a) larger than smaller chiton individuals, and/or (b) at higher limpet density on chiton plates.

2. MATERIALS AND METHODS

2.1. Study species

The chiton *Enoplochiton niger* is an important grazer in mid-to-lower intertidal levels, exerting strong effects on algae colonization and bare rock production (Aguilera et al. 2015) by eating the spores and propagules of the macroalgae (Sanhueza et al. 2008). The epibiont *Scurria parasitica* is also a scraper-grazer herbivore, foraging over the shells of species such as *Fissurella crassa*, *Scurria viridula*, and *E. niger* (Espoz et al. 2004). Given that *S. parasitica* lives exclusively on the shell or plates of other mollusks, which become eroded by its grazing, this species was considered to be parasitizing the different mollusks by early authors (Dall 1909, Marincovich 1973). No information, however, is available about the early stages of *S. parasitica* (i.e. less than 5 mm) or if individuals settle on rocky substrata first and then migrate to selected habitats like chiton shells as

observed in other limpet species (see Lewis & Bowman 1975). It seems that this species is not able to live directly on the rocky substrata (Espoz et al. 2004), as it is probably highly susceptible to being dislodged by waves like other specialist epibiont limpets (e.g. *Patelloida mufria*; Mapstone et al. 1984). It should be noted that *S. parasitica* was previously synonymized with *S. variabilis* (Espoz et al. 2004) but was reconsidered as a valid species name for recent studies (Nakano & Ozawa 2006). There is a broad spectrum of morphology and behaviour of *S. parasitica* inhabiting different microhabitats over mollusk shells, and individuals inhabiting the shell of *E. niger* are considered a specific 'variant' or 'eco-phenotype' of this species (e.g. considered previously as '*S. parasitica*-En' by Espoz et al. 2004; also see Asorey 2017). Thus, the *E. niger*–*S. parasitica* association seems to be specialized in the form of a commensalism, with the epibiont *S. parasitica* taking advantage of the host's body by scraping microalgae and algae propagules growing on the chiton's plates. There is no evidence of *S. parasitica* ecotypes living directly on the rocky substrate. Thus, the *Scurria* limpet and the chiton species conform to an obligate 'epibiont–host' grazer system which co-occurs from 10° S in Peru to 30° S in northern-central Chile (Espoz et al. 2004). The southern range limit of the host chiton *E. niger* is around 30–31° S, coincident with a well-known transition zone (subtropical–temperate) extending between 29 and 41° S, which also concentrates the polar or equatorial range edge of different intertidal species (Rivadeneira & Fernández 2005, Sorte et al. 2010). There is evidence that the range of *E. niger* has contracted from 33° 02' to 29° 41' S as suggested by historical records (i.e. 1949; Dall 1971). This range reduction corresponds to ca. 285 km of range lost and a contraction rate of 7.7 km yr⁻¹ (Rivadeneira & Fernández 2005, Sorte et al. 2010).

2.2. Geographical surveys of *E. niger*

E. niger adult specimens were collected across 7 locations from Callao, Peru (12° S), to Coquimbo, Chile (~30° S), with the latter location corresponding to the poleward range edge of this species (Fig. 1a). Thus, the surveys included 100% of *E. niger*'s range distribution, from 12° S in Peru to 30–31° S in northern Chile (Aguilera et al. 2015, Navarrete et al. 2020). We followed the methodology proposed by Ibáñez et al. (2016) for the collection of specimens. In each locality, we collected specimens of *E. niger* of different sizes for 2 h. Sampling was conducted in the

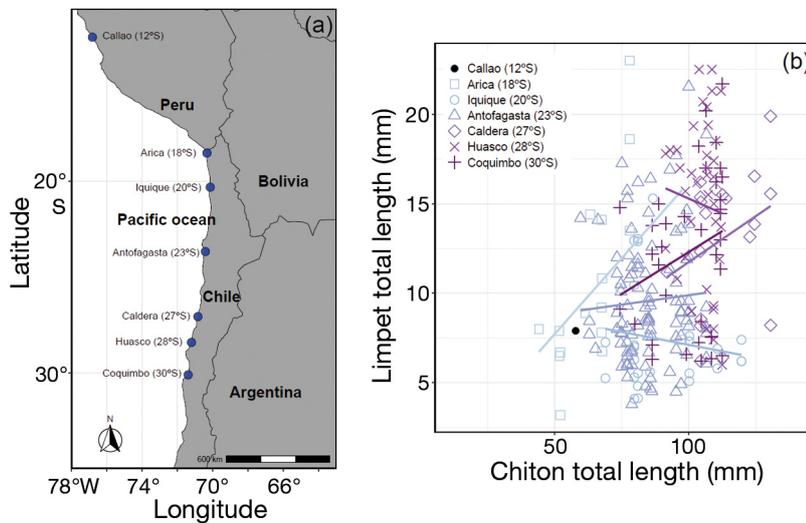


Fig. 1. Sampling sites and body size relation between the host grazer *Enoplochiton niger* and the epibiont *Scurria parasitica* along the Southeast Pacific. (a) Localities sampled along with the latitudinal range; (b) total length distribution for chiton *E. niger* and limpet *S. parasitica* split by sampling site

low to mid-intertidal level, considering rocky platforms (flattened and inclined ones), rock pools, and crevices. After collection, chitons (and their limpet epibionts) were preserved individually in 96% ethanol. All surveys were conducted from July 2011 to January 2015 during spring and summer (September to March). Once in the laboratory, each specimen of *E. niger* was measured with a manual calliper to determine the chiton total length (ChTL, mm) and width of the fourth plate (WIV, mm). With these measurements, each chiton area was estimated as a proxy of the available substrate, using the area equation of an ellipse: $\text{Chiton}_{\text{area}} = (\text{ChTL} / 2) \times (\text{WIV} / 2) \times \pi$. We measured the length (LTL, mm) and width (W, mm) of the epibiont limpet present in each chiton using the area equation of an ellipse to estimate their body area: $\text{Limpet}_{\text{area}} = (\text{LTL} / 2) \times (\text{W} / 2) \times \pi$.

To determine the abundance, occurrence, and individual spatial distribution of *S. parasitica* on *E. niger*, we counted the number of limpets found on each specific chiton plate (from plate I to plate VIII; Fig. 2). Identification of *S. parasitica* on *E. niger* plates was conducted in the field and laboratory following the particular characteristic of this ecophenotype described by Espoz et al. (2004). No other species or other *S. parasitica* ecophenotypes were recorded on chiton plates. The 'coverage proportion' (Cp) of limpets present on each chiton was calculated by dividing the sum of the area of all limpets by the chiton area.

2.3. Statistical analyses

We assessed how *E. niger* body size, conspecific abundance, and geographic distribution affect *S. parasitica* body length, using a model comparison approach (Burnham & Anderson 2002). The model comparison used limpet total length (LTL) as the response variable and chiton total length (ChTL), limpet coverage proportion (Cp), number of limpets (n Limpet), position on the host chiton plates (Plate), and geographical site (Site) where animals were collected as predictor variables. We used Akaike's information criterion for small samples (AIC_c) to select the best model and a hierarchical approach to testing the goodness-of-fit of more complex models (i.e. including more parameters). For the model with the lowest AIC_c (i.e. the model with the best fit), we

employed Cohen's f to quantify the effect size and relative contribution of main effects and pairwise interactions to the overall variation in LTL. Also, the occupancy (presence/absence) and density of the epibiont limpets on *E. niger* were evaluated using generalized linear models (GLMs) to compare with the chiton's length and site, using binomial and Poisson error distributions, respectively. All analyses were performed using the library 'AICcmodavg' for the AIC model comparisons, 'multcomp' for Tukey's pairwise comparisons, and 'ggplot2' for the figure design, all implemented in R software (R Development Core Team 2019).

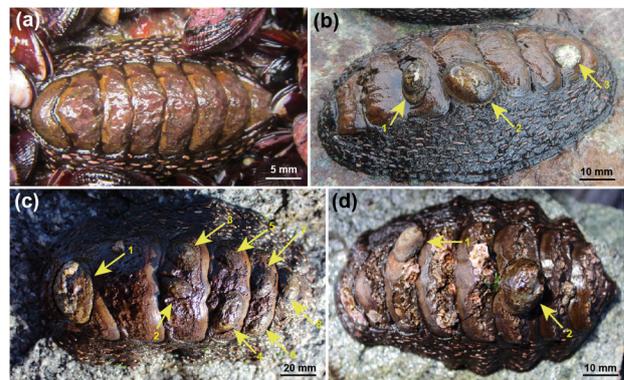


Fig. 2. (a) Small chiton without limpets from Arica (18° S), (b) medium chiton from Huasco (28° S) with 3 limpets, (c) large chiton with 8 limpets from Coquimbo (30° S), and (d) medium chiton from Antofagasta (23° S) with 2 limpets and with plates fully eroded

3. RESULTS

A total of 208 individuals of *Enoplochiton niger* were collected throughout their geographic range (Fig. 1a), with body lengths ranging from 11.7–130.5 mm ChTL (Table 1, Figs. 1b, S1A & S2A in the Supplement at www.int-res.com/articles/suppl/m674_p131_supp.pdf). The shell length of the epibiont limpet *Scurria parasitica* fluctuated from 3.2–23 mm (Table 1, Figs. 3a, S1B & S2B). There was a pattern of increased variability in the plate area covered by limpets toward southern sites (i.e. Huasco, 28° S and Coquimbo, 29° S) (Fig. 3b). Individual epibiont limpet distribution on the chiton plates was also variable across sites

(Fig. 3b). ChTL increased nearly monotonically from the northern (Arica, 18° S) to the southern edge of its geographic distribution (Coquimbo, 29° S) (Table 1, Figs. 4a & S1A). Limpet ‘occupancy’ (i.e. presence of a limpet on an individual chiton) and density were both positive and significantly related to ChTL (Figs. 3b & 5a,b), with significant variability among sites (Table 2, Fig. S1). In general, larger chitons had significantly higher limpet occupancy and density, and the proportion of unoccupied chitons increased from north to southern latitudes (Figs. 5 & S1). Post hoc pairwise comparisons of the epibiont limpet occupancy among sites revealed significant differences between the extreme northern and southern edge localities of the *E.*

Table 1. Summary statistics for length and area of the host chitons *Enoplochiton niger* and the epibiont limpet *Scurria parasitica* in the different study localities. Cp: coverage proportion of all limpets present on all chitons; (–) not applicable

Site	Location	ChitonsLength (mm)			Area (mm ²)		Limpets Length (mm)			Area (mm ²)		Cp
		(n)	Mean	SD	Mean	SD	(n)	Mean	SD	Mean	SD	
Callao	12° 47' S, 76° 80' W	19	50.15	10.55	4033.64	1529.03	1	7.90	–	138.98	–	0.0199
Arica	18° 31' S, 70° 19' W	37	54.18	14.07	4761.20	2538.49	17	8.87	4.39	475.37	580.30	0.0675
Iquique	20° 18' S, 70° 08' W	24	68.13	31.63	8919.12	6121.88	25	6.43	2.97	375.97	299.49	0.0303
Antofagasta	23° 40' S, 70° 24' W	52	63.88	27.29	7362.68	5048.51	100	8.29	3.41	800.60	534.29	0.0742
Caldera	27° 04' S, 70° 49' W	28	95.99	25.47	14 145.29	6021.17	19	11.32	3.68	667.38	392.35	0.0365
Huasco	28° 24' S, 71° 11' W	38	99.49	16.67	15 904.43	4529.07	40	12.89	4.56	855.27	589.44	0.0498
Coquimbo	30° 06' S, 71° 22' W	29	89.29	22.15	13 496.55	5131.39	36	10.76	4.23	709.96	678.51	0.0440

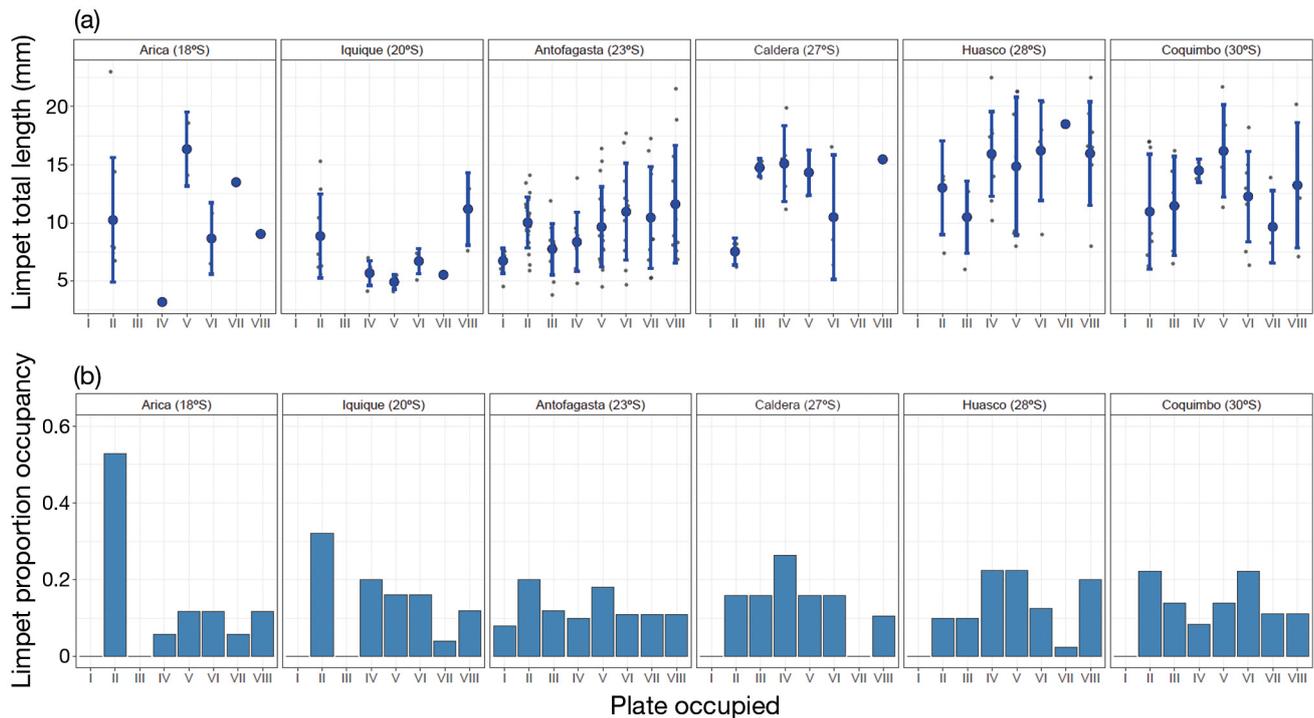


Fig. 3. Limpet *Scurria parasitica* traits, including (a) body length variation and (b) proportion of limpet occupancy on chiton *Enoplochiton niger*'s plates in the sampling sites

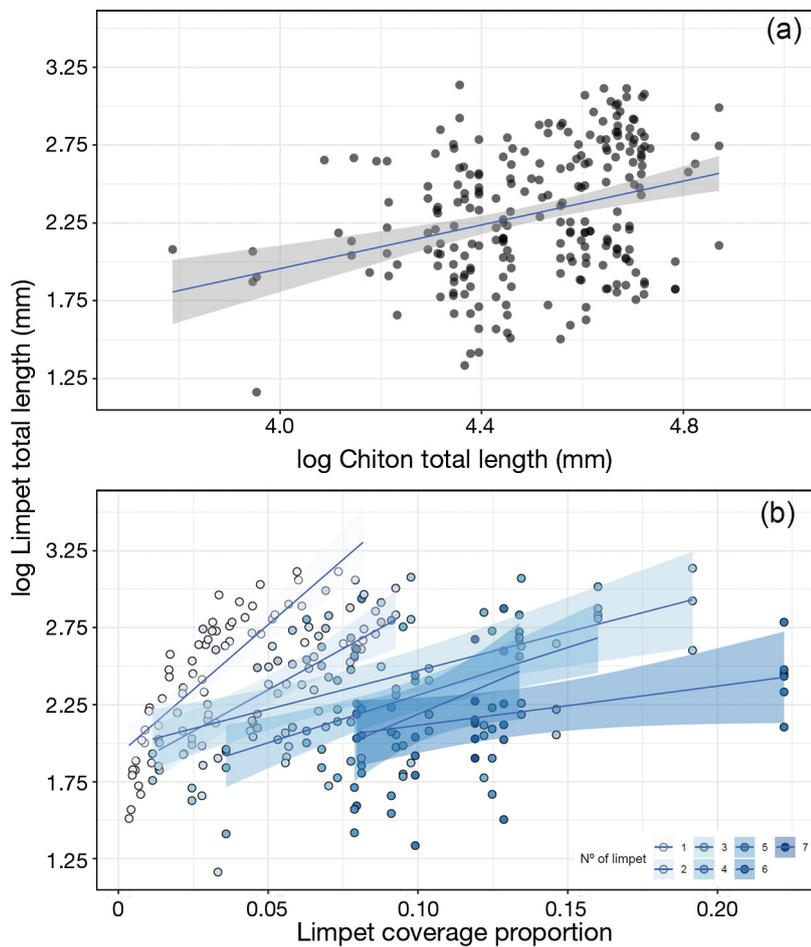


Fig. 4. (a) Best model explaining variation in limpet epibiont total length in relation to chiton host total length; and (b) limpet epibiont coverage proportion

niger geographic distribution (Fig. 5c) (i.e. Arica [18° S] vs. Huasco [28° S]: Tukey's test, z -ratio = -3.472 , $p = 0.0010$; Arica vs. Coquimbo [29° S]: z -ratio = -3.281 , $p = 0.0132$). In correspondence with occupancy patterns, densities of the epibiont limpets differed significantly between the extreme north site (Arica) and sites located in the southern range edge (Huasco: Tukey's test, z -ratio = -2.863 , $p = 0.04810$; Coquimbo: z -ratio = -3.377 , $p = 0.0095$; also Antofagasta [23°S] vs. Huasco: z -ratio = 3.221 , $p = 0.01610$). No significant relationship between LTL and ChTL was observed for the overall localities considered (Table 3) but a significant positive relationship between limpet Cp and ChTL was observed ($b = 9.848 \pm 3.65$, t -value = 2.697 , $p = 0.00751$). Thus, the best regression model based on AIC_c for the LTL (Table 3) was the one including limpet Cp ($b = 0.664 \pm 0.24$, $t = 2.707$, $p = 0.00729$), limpet density per chiton, and ChTL as co-variables ($b = -34.71 \pm 16$, $t = -2.108$, $p = 0.03612$). LTL was positively related to Cp but only at lower or intermediate

limpet densities (Table 1, Fig. 4b), while a negative relationship with limpet density was also found ($b = -0.727 \pm 0.28$, $t = -2.598$, $p = 0.00999$).

4. DISCUSSION

The present study documented strong variation in the association of the epibiont limpet *Scurria parasitica* and its host chiton *Enoplochiton niger* along a well-defined geographic context. We found that the epibiont limpet occurrences increased with increased host body size, especially in populations located at the range edge margins, in concordance with a 'patch-area occupancy' hypothesis. The proportion of unoccupied host chitons decreased in the southern latitudes, suggesting a range-effect in this grazer-grazer association. Also, epibiont limpet size was smaller at higher limpet densities, evidencing a relatively uniform distribution across chiton plates and suggesting a potential role of intra-specific competition. Although many factors still need to be understood to determine if this host–epibiont system may shift from commensalism to an antagonistic interaction at southern latitudes, our results provide an important

basis to explore the role of obligate host–epibiont association in determining either persistence or range contraction of the host chiton populations at its poleward range edge.

4.1. Occupancy and size patterns of *S. parasitica* on *E. niger*

The occupancy of *S. parasitica* observed on *E. niger* was higher and the unoccupied proportion lower at southern sites, corresponding to the host species' poleward range edge (i.e. ~ 29 – 31° S). About 48% of the chitons examined at these sites hosted between 1 and 7 *S. parasitica* individuals. In previous work, Espoz (2002) recorded higher abundances of *S. parasitica* (i.e. all ecophenotypes) between 20 and 30° S compared with northern sites. Despite chiton size appearing to be the major factor determining host occurrences, strong latitudinal clines in this association

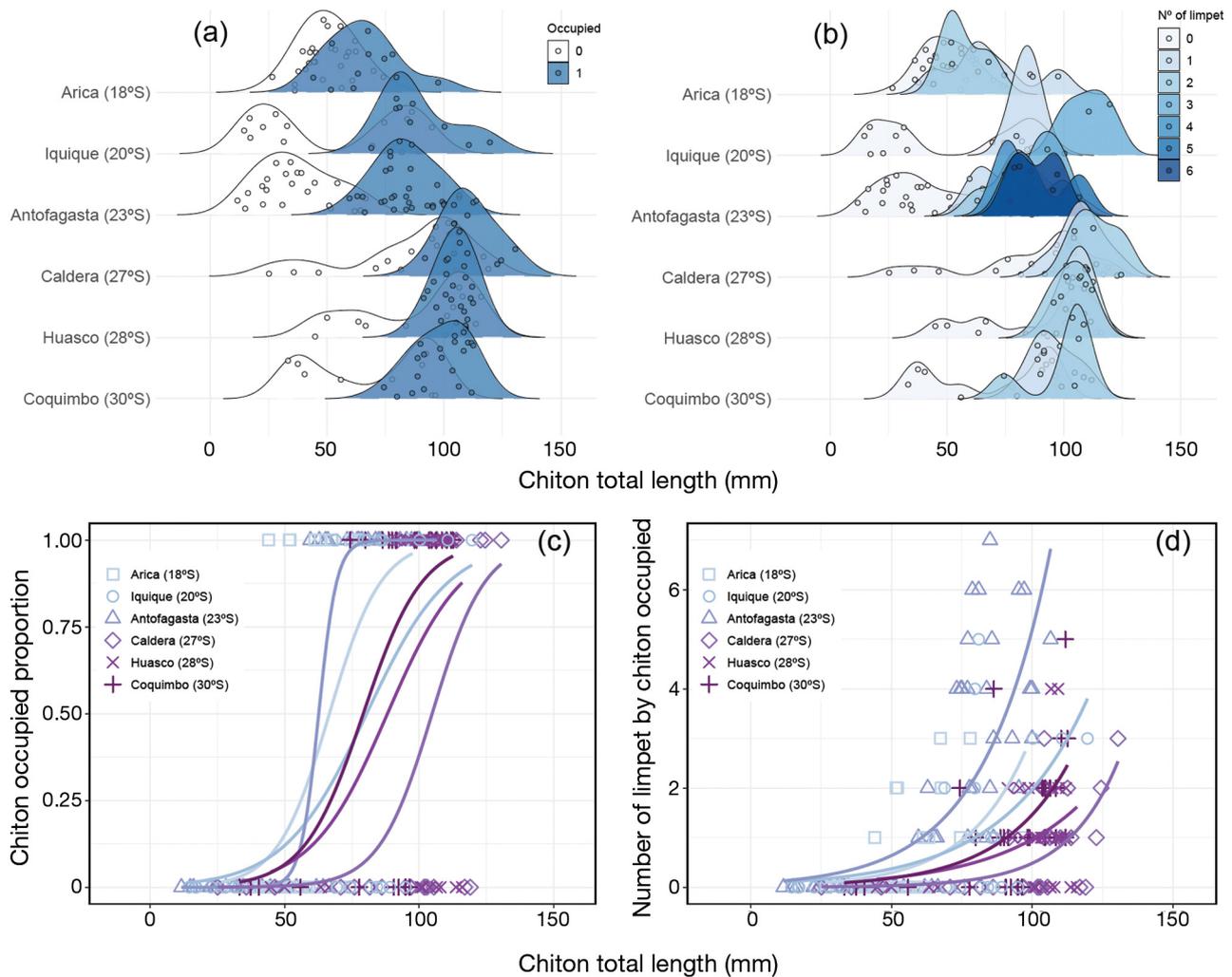


Fig. 5. Chiton total length distribution in relation to (a) limpet epibiont occupancy and (b) abundance in the 6 sampling localities. General linear model fit to (c) proportion of limpet occupancy, and (d) abundance by sampling localities

Table 2. General linear models examining limpet epibiont occupancy and the number of limpets (abundance) on host chitons, with chiton total length (ChTL; a proxy for body size) and geographical site (Site) as main factors

Variable	Factor(s)	df	χ^2	p
Occupancy	ChTL	1	82.829	<0.0001
	Site	5	39.888	<0.0001
	ChTL × Site	5	8.543	0.1287
No. of limpets	ChTL	1	72.724	<0.0001
	Site	5	108.386	<0.0001
	ChTL × Site	5	1.783	0.872

seem to be overridden by local context (e.g. predation, topography, microhabitat) (e.g. Blanchette et al. 2008). Our results also confirm that populations of the host chiton *E. niger* reached larger sizes at southern

latitudes (i.e. from Caldera to Coquimbo ~27–30°S), which seems to account for the higher occurrences of *S. parasitica* on chiton plates at those localities (our Hypothesis 1). In general, body size is expected to vary according to environmental gradients, with large sizes distributed in the higher latitudes (i.e. Bergmann’s rule; Blackburn et al. 1999, Gaston & Blackburn 1996). The host chiton *E. niger* fits well with the expected pattern of size increase at higher latitudes and inversely with temperature, as predicted for the ‘temperature size rule’ (Angilletta & Dunham 2003). In this context, the Humboldt Current System has environmental clines in temperature and productivity (Thiel et al. 2007), influencing composition, abundance, diversity, and body size of different invertebrate assemblages, including mollusks (Ibáñez et al. 2019, Carrasco et al. 2021), crustaceans

Table 3. Model comparison of the logarithm of epibiont limpet total length (LTL) versus the logarithm of host chiton total length (ChTL), epibiont coverage proportion (Cp), number of limpets (n Limpet), position on the host chiton plates (Plate), and geographical site (Site) where the animals were collected. Models include main effects and pairwise interactions; the best model is in **bold**. K : number of parameters; AIC_c : Akaike's information criterion corrected for small sample sizes; w_i : Akaike weight

Model	K	AIC_c	ΔAIC_c	w_i	LogLik
log LTL ~ log ChTL	3	243.24	108.91	0	-118.57
log LTL ~ log ChTL + Cp	5	221.15	86.82	0	-105.45
log LTL ~ log ChTL + n Limpet	5	239.73	106.38	0	-115.23
log LTL ~ log ChTL + Plate	17	235.54	101.20	0	-99.37
log LTL ~ log ChTL + Site	13	205.31	70.98	0	-88.84
log LTL ~ log ChTL + Cp + n Limpet	8	134.33	0	0.98	-58.85
log LTL ~ log ChTL + Cp + Plate	26	220.71	86.38	0	-81.01
log LTL ~ log ChTL + Cp + Site	20	182.94	48.61	0	-69.53
log LTL ~ log ChTL + n Limpet + Site	20	213.27	78.94	0	-84.69
log LTL ~ log ChTL + Plate + Site	54	236.37	102.04	0	-47.87
log LTL ~ log ChTL + Cp + n Limpet + Plate	36	153.00	18.67	0	-33.84
log LTL ~ log ChTL + n Limpet + Plate + Site	68	281.12	146.76	0	-44.63
log LTL ~ log ChTL + Cp + n Limpet + Site	28	142.71	8.38	0.01	-39.45
log LTL ~ log ChTL + Cp + n Limpet + Plate + Site	83	240.92	106.59	0	8.11

(Thiel 2002, Rivadeneira et al. 2010), and polychaetes (Hernández et al. 2005). Variation in environmental conditions such as sea surface temperature (Thiel et al. 2007) and primary productivity (as a proxy of food availability; e.g. Wieters et al. 2003) may also explain the latitudinal pattern in host size (see Blackburn et al. 1999, Angilletta & Dunham 2003, Meiri et al. 2007), which have been thoroughly examined in a concurrent study (Ibáñez et al. 2021).

Space is a limited resource for intertidal grazers (Branch 1976, Underwood 1984, Firth & Crowe 2010, Aguilera et al. 2013), particularly for species with low competitive potential (Aguilera & Navarrete 2012, Boaventura et al. 2003). Larger host size increases the 'habitat' or space available for foraging in the epibiont limpet *S. parasitica*, with potentially positive effects on reproduction and growth. A similar positive effect of the host's size (abalone *Haliotis roei* and the host limpet *Patella laticostata*) was observed for the epibiont limpet *P. nigrosulcata* (Scheibling et al. 1990). Given its morphology, the *S. parasitica* ecophenotype seems to live exclusively on mollusk shells and has a potentially high susceptibility of being dislodged by waves on open rocky substrata as observed in other epibiont limpet species (e.g. *Patelloida mufria*; Mapstone et al. 1984). This suggests that the chiton's area (i.e. size) could be an important resource for the epibiont limpet's settlement and survival; however, further field and laboratory experiments are still needed to corroborate this assumption. In addition, we also recorded higher limpet densities at southern sites, which could enhance the potential for limpet interference competition (i.e. on the chiton plates), which is common in intertidal

grazer assemblages (Branch 1976, Underwood 1984, Boaventura et al. 2003, Firth & Crowe 2010, Aguilera & Navarrete 2012, Aguilera et al. 2019). In this context, we also evidenced individual limpet segregation on the chiton plates at southern sites (Hypothesis 3b) where, despite their larger sizes, individual limpets occupied different plates in a relatively uniform distribution pattern. The consequences of the limpets' spatial distribution on the host chiton are unclear, and further field experiments designed to test competition among limpets on chiton plates (e.g. Underwood 1984), as well as analyses of chiton performance and behaviour (i.e. movement and foraging rates; see Chapman 2000), could be useful in this context.

4.2. Persistence of the range edge populations of the host *E. niger*

Previous studies documented a range contraction of southern endpoint populations of *E. niger* from 33° S (Dall 1971) to 29° S (Rivadeneira & Fernández 2005), and recent studies confirmed the range distribution of this species spanning from Callao, Perú (12° S), to Huentelauquén, Chile (31.38° S) (Aguilera et al. 2015, Ibáñez et al. 2019, Navarrete et al. 2020). It seems that direct facilitation of the limpet by large *E. niger* could guarantee habitat for colonization and food and/or reduce interspecific competition (Scheibling et al. 1990); however, the effects of high epibiont densities and size on the individual performance of the host chiton are not clear. Mapstone et al. (1984) showed that the epibiont *Patelloida mufria* can

modify the choice of habitat (e.g. pools) of their mollusk host during low tide. Therefore, increases in the densities or even size of the epibiont limpet *S. parasitica* could directly reduce the host's resistance to physiological stress and/or foraging rates at the range edge (Broitman et al. 2018). It is likely that the scars related to the 'homing' and foraging behaviour of *S. parasitica* may cause partial or complete loss of multi-channel layers present in chiton plates' tegmentum (which encompass the sensory organs called aesthetes) and/or erode the articulamentum, decreasing the ability of the chiton to adhere to the substrate (Schwabe 2010, Connors et al. 2012, Alvarez-Cerrillo et al. 2017). Since we did not evaluate plate erosion in this study, we can only speculate in this context. On the other hand, *S. parasitica* can also remove other epibiont species such as barnacles and algae while feeding, which might otherwise overgrow the chiton's plates, reducing its movement and/or growth. Thus, *S. parasitica* may also have positive effects on *E. niger* individuals at lower densities. Hence, if the host limpets cause negative effects on the host chiton's performance (e.g. due to vision damage involved in movement and orientation), this grazer–grazer system may shift from commensalism at lower latitudes to a more antagonistic interaction (i.e. parasitism) at their range edge (see Fig. S3). A shift from commensalism to mutualism has been reported previously in an annelid–crayfish symbiosis system modulated by environmental fouling pressure (Lee et al. 2009). Similar results were reported by Travis et al. (2005), who used a patch-occupancy model to show that positive interactions (commensalism and mutualisms) tend to dominate in harsher environmental conditions. Considering that the studies conducted by Nakayama et al. (2020) revealed that host utilization by the epizoic limpet *Lottia tenuisculpta* changed seasonally and differed between host species and that local contexts (i.e. habitat features at each site) can override strong latitudinal patterns (e.g. Blanchette et al. 2008), future field experimental studies should consider both latitudinal and temporal variation in the direction of the association between the focal host–epibiont grazer species. Also, assessment of the epibiont's active choice of its host, as observed in other systems (e.g. Mapstone et al. 1984, Nakayama et al. 2020), could be important to disentangle the limpet's specificity to an individual host and the epibiont's survival potential at their range edge.

Since *E. niger* is a strong interactor in this system (Aguilera et al. 2015), the extent to which geographic variation of our epibiont–host system translates into changes in the community structure (e.g. indirect

commensalism; Dethier & Duggins 1984) is of special interest. Latitudinal gradients (e.g. temperature, oxygen, productivity) and, to a lesser extent, biogeographic breaks can leave important signatures in host–epibiont grazer systems. Thus, field experiments conducted along a latitudinal gradient can be useful to examine the geographic variation in both the strength and direction of the association in a host–epibiont system.

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