



Social environment mediates habitat shifts in a range-restricted giant limpet

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ABSTRACT: The individuals of many species shift habitats at different stages in their lives. Sometimes, these habitat shifts coincide with an ontogenetic transition. These ontogenetic habitat shifts can allow species to access nutritional resources, avoid conspecific aggression or predation, or secure breeding opportunities when it is advantageous to do so. The Kermadec Islands giant limpet *Scutellastra kermadecensis* is a protandrous hermaphrodite endemic to Rangitāhua, the Kermadec Islands. These limpets have an unusual habit whereby small limpets (piggies) piggy-back on the shells of larger individuals rather than living on the rocky substrate. We investigated whether the ontogenetic habitat shift between the piggy-backing and rock-attached limpets was determined by the availability of free space on the rock or whether the ontogenetic habitat shift was a response to the properties of the surrounding limpet population. We found that the available rock space did not influence the size at which an individual transitioned from being a piggy to being rock-attached. Furthermore, larger rock-attached limpets were more likely to have piggies, they had more piggies, and the piggies were larger. Overall, our results suggest that Kermadec giant limpets are motivated to piggy-back by the properties of the social environment rather than space constraints. The piggy-backing behaviour may be a mechanism to avoid bulldozing by larger limpets, to access grazing opportunities on the shells of larger limpets, and/or to monopolise breeding opportunities with larger rock-attached females. We discuss the repercussions of this life-history strategy for this extremely range-restricted species, with reference to how these populations may be monitored and maintained.

KEY WORDS: Ontogenetic habitat transitions · Socioecology · Secondary habitat providers · Size structure · Hitchhiking · Protandry

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1. INTRODUCTION

Animals often move between habitats at different stages of their lives. When these habitat shifts coincide with a developmental transition (for example, between juvenile and mature stages, or pre- and post-metamorphosis), they are referred to as ontogenetic habitat shifts (Stamps 1983). Such habitat transitions may occur as resource requirements change with the onset of maturity and/or as individuals grow. For instance, as green turtles *Chelonia mydas* mature, they travel to deeper zones along the Pacific

coast, where adult food is abundant (López-Mendilaharsu et al. 2005). Another reason for moving between habitats may be to avoid or reduce conspecific aggression or predation. For example, juvenile fishes often live in structurally complex nursery habitats, such as mangroves, seagrasses, corals, or macroalgae, to avoid predation by larger conspecifics and heterospecifics (Nagelkerken et al. 2000, Laegdsgaard & Johnson 2001, Unsworth et al. 2009, Evans et al. 2014). In many animals, males and females may also maintain distinct habitats until it is time to reproduce. Anglerfishes (Lophiiformes) are potentially one of the

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most extreme examples, where small males transition from being free-swimming to being permanently attached to their larger female anglerfish counterparts to ensure reproductive opportunities when the female spawns (Pietsch 1976). While the mechanisms motivating ontogenetic shifts of individuals are well understood in some systems, in other systems the drivers are less clear and are likely context-dependent.

The timing of ontogenetic shifts can vary according to the environment experienced by the individual. For instance, in many marine species with bipartite life histories, individuals will often delay metamorphosis until they have acquired sufficient resources to metamorphose or until they encounter suitable settlement habitats (Marshall & Morgan 2011). In sequential hermaphrodites, the timing of a sex change can be determined by the composition of the surrounding social environment (Charnov & Bull 1989, Munday et al. 2006). For instance, in the absence of males, the largest female bluehead wrasse *Thalassoma bifasciatum* in the local population will transition into a male (Warner & Swearer 1991). The newly transitioned male will then dominate the harem of females, in turn increasing his reproductive output. The timing of such transitions in morphology, sex, or habitat can influence the acquisition and defence of resources, and thereby survival and reproductive success (Sergio et al. 2017). Ultimately, by influencing the fitness of individuals, environmentally dependent ontogenetic shifts impact the ecological and evolutionary trajectories of populations.

The Kermadec Islands giant limpet *Scutellastra kermadecensis* is endemic to Aotearoa (New Zealand), and restricted to Rangitāhua (Kermadec Islands). These islands are a small, isolated archipelago in the southwest Pacific approximately 750 km northeast of the North Island of Aotearoa. Kermadec giant limpets grow to be the dominant grazers in the low intertidal and shallow subtidal zones of Rangitāhua (Creese et al. 1990, Wood & Gardner 2007). Individuals commonly reach a shell length greater than 130 mm and populations can reach densities of up to 40 individuals m⁻² (Cole et al. 1992). Despite being locally abundant and resident in a large old Marine Protected Area (Kermadec Islands Marine Reserve), the Kermadec giant limpet is extremely range-restricted, occupying only these few isolated islands and outcrops, and therefore there has been much interest in its population ecology and extinction risk (Fleming 1973, Schiel et al. 1986, Creese et al. 1990, Cole et al. 1992, Wood and Gardner 2007).

Like other patellid limpets, Kermadec giant limpets are broadcast spawners with external fertilisation and pelagic larvae (Lindberg & Marinovich 1988, Wood & Gardner 2007). The embryos and larvae disperse in the ocean before settling to the substrate and metamorphosing. The adults are largely sedentary, or faithfully homing, which is evident from the home scars they leave on the rocky substrate (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m666p089_supp.pdf; Creese et al. 1990, Wood & Gardner 2007). Kermadec giant limpets are protandrous hermaphrodites, with the unusual habit that smaller individuals, typically male, often piggy-back on the shells of larger, typically female, individuals (Creese et al. 1990). The reasons for the piggy-backing behaviour are unknown, but it may be that male limpets piggy-back on larger females to ensure mating opportunities, to avoid competition and being bulldozed by larger limpets, and/or to graze algae that grows on the back of larger older limpets—a resource that would otherwise remain ungrazed. Creese et al. (1990) showed that when Kermadec giant limpets reach a size of 55–67 mm, they shift microhabitats from predominantly piggy-backing to being mostly attached to the rock surface. As Kermadec giant limpets of various sizes can be found piggy-backing or rock-attached, it is unlikely that the timing of this ontogenetic habitat shift is predetermined; rather, the habitat shift appears to be dependent on environmental factors such as space, food, or the social environment.

While often overlooked, the importance of the social environment in determining individual behaviour, life-history outcomes, and population demography of gastropods has been highlighted in numerous studies (e.g. Branch 1975a,b, Schroeder 2011, Le Cam et al. 2014, Martins et al. 2017). Hence, we investigated whether the social environment (the number and size of surrounding limpets) influences the shell length—our proxy for age or life stage—at which piggy-backing limpets transition to becoming rock-attached. We hypothesized that if access to algal resources was the strongest driver of piggy-backing behaviour, the number of piggy-backing limpets would increase as rock availability decreased. Alternatively, if smaller limpets are piggy-backing to avoid competition, to avoid bulldozing, or to secure breeding opportunities with larger, rock-attached females, we hypothesized that the number of piggies (i.e. piggy-backing limpets) would increase as the number and size of rock-attached limpets increased. Furthermore, we expected that piggies would delay the transition to being rock-

attached with increasing host size, but would transition to being rock-attached sooner as the number and size of piggy-backing limpets increased, reflecting a situation where limpet shell habitat becomes limiting. Deducing the consequences of population density and size structure in this species is critically important for understanding demographic change in these relict populations of an extremely range-restricted endemic species.

2. MATERIALS AND METHODS

2.1. Study design and population survey

The study was conducted during November 2015 at 3 locations, separated by 100s of meters around islands and islets of the largest island in the Rangitāhua archipelago, Raoul Island (Fig. 1). Nested within each location were sites separated by 10s of meters (Boat Cove: 8 sites; North Meyer Island: 7 sites; South Meyer Island: 6 sites), and nested within each site were three 0.25 m² quadrats (separated by 1–2 m) placed on the substrate in the low intertidal zone inhabited by Kermadec giant limpets. For each quadrat, a photograph with the camera parallel to the quadrat was taken (Fig. S1). From these photos, we collected information at 3 scales: quadrat level, subquadrat level (3 randomly placed 0.0225 m² quadrats within each quadrat), and individual (limpet) level. Individual limpets were classified as either limpets attached to the shells of other limpets (re-

ferred to as ‘piggies’) or limpets directly attached to the rock surface (referred to as ‘rock-attached’). We then further distinguished between rock-attached limpets with piggies attached to their shells (‘hosts’) and rock-attached limpets without limpets attached to their shells (‘non-hosts’).

2.2. Habitat and social environment analysis

Quadrat-level data were used to describe the social environment surrounding the subquadrats. To quantify the available rock space, we used the image analysis software ImageJ (Schneider et al. 2012) to randomly place 125 points within the borders of each quadrat (Fig. S1). Points that landed on or outside the quadrat, as well as points that landed on undefined space inside the quadrat (blurriness and/or water), were excluded. The proportion of available rock space was calculated by counting the points that did not land on limpets or home scars (Fig. S1). Then, for each quadrat, we counted the total number of rock-attached limpets (both hosts and non-hosts) including home scars and the number of piggies on the hosts. We then randomly placed three 0.0225 m² subquadrats within each quadrat using ImageJ and counted and measured the shell length of each rock-attached (host and non-host) and piggy limpet. For the individual-level data, we measured the size of 10 randomly selected hosts in each quadrat, and then we counted the number of piggies and measured the size of all piggies. Although we were able to count all

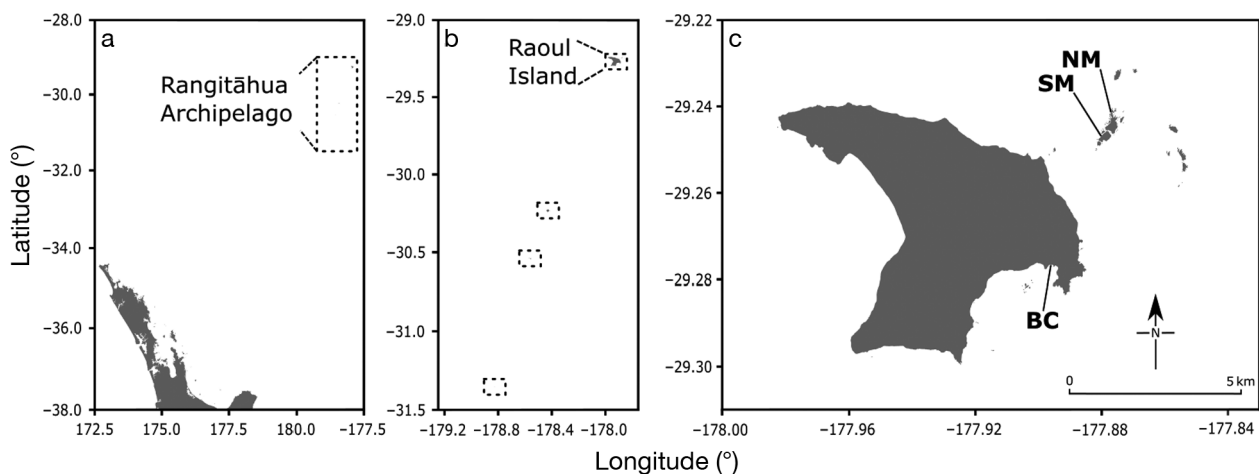


Fig. 1. (a) The location of Rangitāhua, the Kermadec archipelago, relative to the North Island of Aotearoa (New Zealand), indicated by the dashed rectangle. (b) The location of Raoul Island relative to the other islands in the Rangitāhua archipelago. (c) The sampling locations distributed around Raoul Island: the western side of North Meyer (NM) and South Meyer (SM) Islets, as well as Boat Cove (BC) on the eastern side of Raoul Island

limpets at the subquadrat and individual levels, we only measured limpets where the shell was oriented parallel, or close to parallel, to the camera and where the individual was clearly visible (i.e. not obscured by blurriness and/or water).

2.3. Statistical analysis

To determine whether the relationship between shell length and the probability of a piggy transitioning into a rock-attached limpet varied according to the social environment (i.e. size and number of rock-attached limpets, as well as piggy size and number), we used binomial generalised linear mixed models (GLMM) with a logit link. In this analysis, the response variable was binary, where 1 indicated the individual was a piggy and 0 indicated the individual was a rock-attached limpet (i.e. host or non-host). The fixed effects were shell length, rock-attached limpet number and size, piggy number and size, available rock space, and the interactions between shell length and rock-attached limpet number and size, piggy number and size, and available rock space. The random effects were location, site nested within location, quadrat nested within site, and subquadrat nested within quadrat (which was treated as an observation-level random effect; Elston et al. 2001).

To determine whether the relationships between shell length and the probability of a rock-attached limpet becoming a host varied depending on the social environment, we used a binomial GLMM in which the response variable was binary, with 1 indicating the individual was a host and 0 indicating the individual was a non-host. The same fixed and random factors were used in this model as in the model for piggy-backing behaviour.

To examine the relationship between host size and piggy number, we used a Poisson GLMM with a log link. The response variable was the number of piggies, the fixed effect was host size, and the random effects were location, site nested within location, and quadrat nested within site.

Lastly, to examine the relationship between piggy size and host size, a linear mixed model (LMM) was used with piggy size as the response. The fixed and random effects in the LMM for piggy size were the same as in the Poisson GLMM for piggy number.

For both the subquadrat-level data and the individual-level data, we used backward model selection using nested log-likelihood ratio tests to determine the significance of each term (Tables S1, S2, S4 and S5 in the Supplement). If none of the random effects were significant, we retained the observation-level random effect (i.e. subquadrat) to account for any possible overdispersion (Elston et al. 2001). To test for overdispersion, we used a χ^2 test using the sum of the squared Pearson residuals divided by the residual degrees of freedom as the test statistic, and degrees of freedom equal to the residual degrees of freedom (residual degrees of freedom = 548). All analyses were implemented in the lme4 package (Bates et al. 2015) for R version 4.0.2 (R Core Team 2020) using RStudio (RStudio Team 2020). To determine the robustness of our parameter estimates we assessed each model fit for all available optimisers and compared the equivalence of the parameter estimates. Lastly, to explore the influence of collinearity among our predictor variables on the variance of our parameter estimates, we confirmed that the generalised variance inflation factor for each parameter in our best-supported models was less than 3 (Zuur et al. 2010).

3. RESULTS

At the individual level, piggy number had a positive relationship with host size, and this trend was consistent across all locations (Fig. 2a, Table S5). Most hosts had only one piggy (58%); however, there were hosts with large numbers of piggies and, in particular, one relatively small rock-attached individual (48.5 mm shell length [SL]) that hosted 7

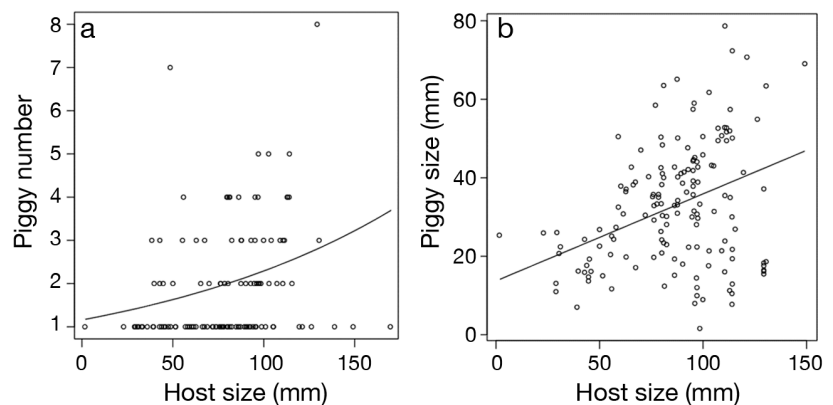


Fig. 2. Relationship between host size and (a) total number of piggies and (b) piggy size for Kermadec giant limpets at Raoul Island, Rangitāhua. Lines are predicted values from the linear mixed models

piggies (Fig. 2a). When piggies were present, there was also a positive relationship between piggy size and host size (Fig. 2b, Table S5). Overall, bigger hosts were more likely to have piggies, had more piggies (Fig. 2a), and those piggies were larger (Fig. 2b).

At the sub-quadrat level, the relationship between shell length and the probability of a limpet being a piggy versus rock-attached varied depending on the rock-attached limpet number, rock-attached limpet mean size, and piggy mean size, but not rock space availability or piggy number (Table S2). The shell length at which a piggy transitioned to being rock-attached was smaller when mean piggy size was larger (Fig. 3a). However, when mean piggy size was large (>55 mm SL), there was an equal probability of

a limpet being a piggy or rock-attached at all shell lengths. When the rock-attached limpet number was higher, the shell length at which piggies transitioned into a rock-attached limpet was smaller than when the rock-attached limpet number was lower (Fig. 3b). When mean rock-attached limpet size was large, the shell length at which piggies transitioned into rock-attached limpets was also larger. Importantly, there appeared to be a minimum size (indicated by the largest SL where a zero predicted probability of an individual being rock attached was identified) before piggies transitioned to becoming rock-attached limpets (approximately 32 mm SL; lower left of Fig. 3c).

The shell length at which rock-attached individuals became hosts varied depending on piggy number, host size, and piggy size (Table S2). When piggy number was higher, the shell length at which rock-attached limpets became a host was smaller. However, there was a minimum shell length for a rock-attached limpet to become a host (approximately 47 mm SL; Fig. 4a). When piggies were smaller, the shell length at which a rock-attached limpet became a host was smaller (Fig. 4b). Lastly, when neighboring rock-attached limpet mean size was larger, the shell length at which rock-attached limpets became hosts was also generally larger, although, in the presence of very large rock-attached limpets (approximately 100 mm SL), small rock-attached limpets also had a high probability of being hosts (upper left of Fig. 4c). More typically, rock-attached limpets became hosts at approximately 66 mm SL (Fig. 4c). Overall, the probability of a piggy transitioning into a rock-attached limpet did vary significantly among subquadrats, but not locations, sites, or quadrats (Table S2). Furthermore, the probability of a rock-attached limpet transitioning into a host did not vary across any spatial scale sampled (Table S2).

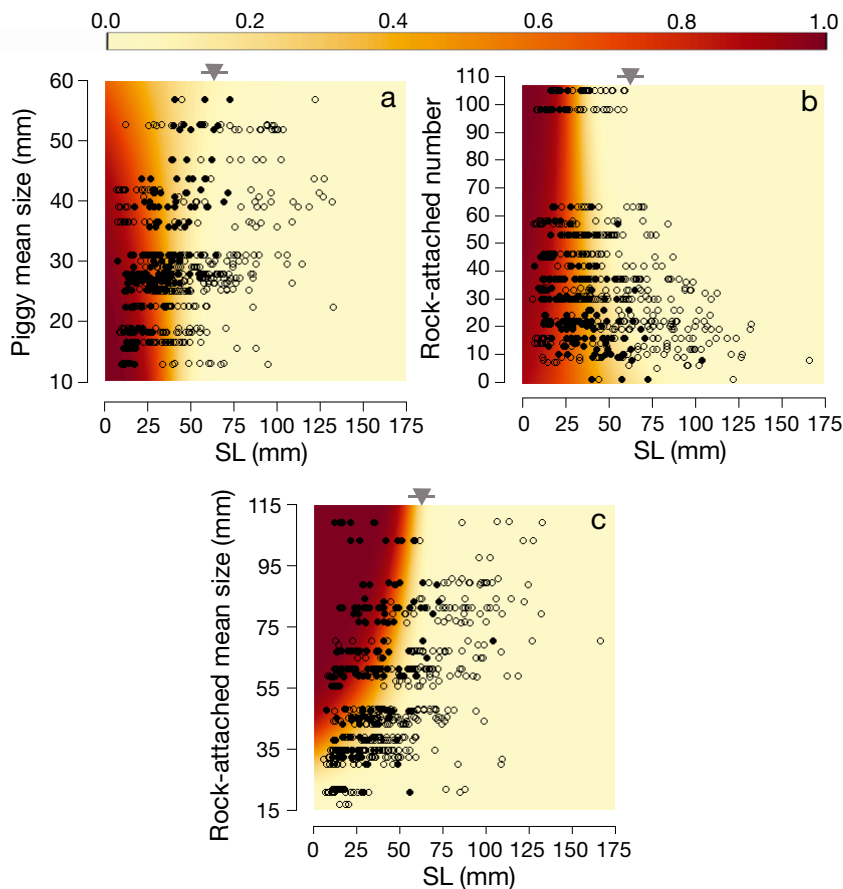


Fig. 3. The probability of a Kermadec giant limpet piggy-backing (red) or being rock-attached (pale yellow) for the interaction between shell length (SL) and (a) the mean size of piggies in the surrounding environment (piggy mean size); (b) the number of rock-attached limpets in the surrounding environment (rock-attached number); and (c) the mean size of rock-attached limpets in the surrounding environment (rock-attached mean size). Symbols indicate the observed values for piggies (filled circles) and rock-attached limpets (open circles). The grey triangle and bar above each panel indicates the sizes (55–67 mm) at which Creese et al. (1990) observed a habitat shift from piggy-backing to rock-attached

4. DISCUSSION

The social environment played an important role in the size at which Kermadec giant limpets transitioned habitats, and available rock space did

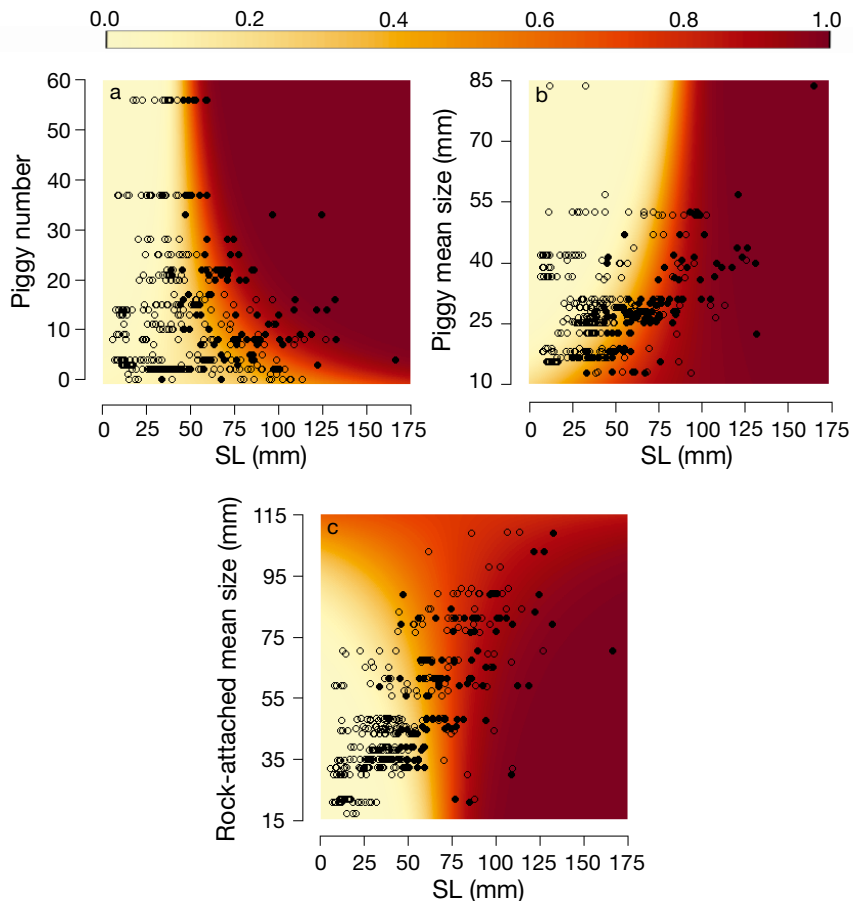


Fig. 4. The probability of a Kermadec giant limpet hosting a piggy (red) or being a non-host rock-attached limpet (pale yellow) for the interaction between shell length (SL) and (a) the number of piggies in the surrounding environment (piggy number); (b) the mean size of piggies in the surrounding environment (piggy mean size); and (c) the mean size of rock-attached limpets in the surrounding environment (rock-attached mean size). Symbols indicate the observed values for non-hosting rock-attached limpets (filled circles) and host limpets (open circles)

not influence piggy-backing behaviour (Table S3 in the Supplement). Piggies on larger hosts were larger and more densely packed, suggesting that piggies preferentially sought out these larger hosts or they persisted as piggies for longer when attached to larger hosts. Furthermore, if large hosts were absent and piggy densities were high, rock-attached limpets became hosts at a smaller size, suggesting that these ontogenetic shifts are socioecologically plastic. While it is clear from our results that small Kermadec giant limpets preferentially occupy the back of the shell of host limpets, and that the social environment influences the timing of habitat transitions, there are several possible explanations for these behaviours. For instance, it could be that piggies are utilizing hosts to access grazing opportunities that would otherwise go ungrazed, to avoid bulldozing by larger conspecifics,

and/or to secure breeding opportunities with larger, rock-attached females. Although we cannot distinguish among these hypotheses with the data in hand, below we discuss each in turn with regard to our results and the supporting literature.

The Kermadec giant limpet is numerically and spatially dominant in the intertidal zone of Rangitāhua (Schiel et al. 1986, Creese et al. 1990, Cole et al. 1992, Wood & Gardner 2007). In several of our subquadrats/quadrats, more of the area was made up of Kermadec giant limpet backs than limpet-free rocky substrate. Shell-forming invertebrates such as limpets are known to be important secondary habitat for conspecifics and other organisms (Branch 1975a,b, Thyrring et al. 2013, Martins et al. 2014), including algae, which can then be consumed by grazers (van Tamelen 1987, Wernberg 2010). For instance, the large shell of the turban snail *Turbo torquatus* is readily colonised by foliose algae, which in turn attracts and supports other grazers such as patellid limpets (Wernberg 2010). In the case of Rangitāhua, an abundance of intertidal algae occupies the rocky intertidal, including the backs of the limpets (Fig. S1). Piggy-backing Kermadec giant limpets may simply reside on the back of larger limpets to graze the available resource. Our results indicating that larger limpets have larger and more piggies support this idea. However, our finding that rock availability, and thereby the availability of algal resources attached to the rock surface, was less important than aspects of the social environment suggests that piggy-backing behaviour is not purely resource-driven.

Given that Kermadec giant limpets are the most abundant macrograzer in the intertidal zone of Rangitāhua (Schiel et al. 1986, Creese et al. 1990, Cole et al. 1992, Wood & Gardner 2007), a large proportion of the biotic interactions for individual Kermadec giant limpets would be with conspecifics. Mobile macrograzers such as limpets are known to negatively impact newly settled larvae and recruits of benthic marine invertebrates through bulldozing (Dayton 1971, Ellrich et al. 2020). For example, ses-

sile species such as barnacles are often bulldozed by mobile grazers such as periwinkles and limpets (Underwood et al. 1983, Bertness 1984). Barnacles can avoid this bulldozing effect by growing rapidly and achieving a size refuge (Denley & Underwood 1979, Bertness 1984). Mobile species that are also susceptible to bulldozing have behavioural responses to avoid these disturbances (Dayton 1971, Tegner et al. 1995, Day & Branch 2002). For instance, recruits of the South African abalone *Haliotis midae* avoid being bulldozed by hiding beneath larger urchins and moving with their host urchin, thereby remaining concealed and protected from bulldozing as well as predators (Tegner et al. 1995, Day & Branch 2002). The shells of larger Kermadec giant limpets offer a substrate where smaller individuals can avoid antagonistic interactions with the largest individuals in the population, and thereby provide a potential refuge from competition, physical bulldozing, and death. Moreover, we observed cases where small limpets were piggy-backing on piggies, suggesting that size-structured bulldozing among piggies might also occur on the backs of host Kermadec giant limpets.

Resource partitioning and antagonistic interactions are 2 mechanisms that could underlie piggy-backing behaviours; a third mechanism is the aggregation of males and females to maximise their reproductive output (Pietsch 1976, Chen et al. 2018). Broadcast-spawning marine organisms commonly form mating aggregations to maximise fertilisation success by reducing sperm limitation (Stanwell-Smith & Clarke 1998, Yund 2000), with males in closer proximity to broadcast-spawning females typically having greater reproductive success (Picken & Allan 1983, Collin et al. 2006, Marshall & Bolton 2007, Henry et al. 2010, Suda et al. 2015, Chen et al. 2018). Creese et al. (1990) used histology to reveal that Kermadec giant limpets are protandrous; small limpets are typically males, transitioning to become females at a larger size and presumably older age. Importantly, none of the limpets that Creese et al. (1990) could confidently identify as female were piggies. Thus, it could be that small male limpets preferentially piggy-back on larger, rock-attached females to ensure they are near eggs when they are released, allowing greater fertilisation success.

In accordance with studies demonstrating that limpets will transition to becoming female at a smaller size when females are rare or when male density is high (*Patella ferruginea*, Rivera-Ingraham et al. 2011; and *Crepidula coquimbensi*, Brante et al. 2012), we found that limpets transitioned to being rock-attached, and potentially transitioning to becoming

females, at a smaller size in denser piggy populations. These developmental and habitat transitions may allow individuals to gain reproductive opportunities as a female sooner when there is an abundance of smaller males to sire offspring and to avoid male-male competition for fertilisations (discussed in Munday et al. 2006). However, although quadrats with larger, rock-attached limpets had lower overall numbers of piggies, there were greater numbers of larger piggies on each host. These results appear to support another socially mediated behaviour: individuals delay the transition to becoming rock-attached, and presumably to becoming female, when they have access to large, presumably female, hosts (e.g. also observed in *Crepidula* spp. by Coe 1938 and Brante et al. 2016). To support the hypothesis that the timing of habitat transitions may be driven by reproductive opportunities, we would need to establish that there is a strong association between the timing of sex change and the timing of the habitat transition in Kermadec giant limpets.

Ontogenetic habitat shifts are often associated with a transition from a life stage focused on growth and survival to a stage focused on reproduction and survival (Stearns 1989). By avoiding bulldozing and grazing the algae on the shells of host limpets, piggy-backing may allow greater survival and growth of small male limpets while keeping them in the immediate proximity of females should they release their eggs. The positive relationship between female size and fecundity in animals is pervasive (Nobili & Accordi 1997, Chaparro et al. 1999, Chaparro & Flores 2002, Espinosa et al. 2006, Kasamatsu & Abe 2015), and previous studies suggest that larger females have a disproportionately large fecundity advantage over smaller females (Espinosa et al. 2006, Barneche et al. 2018). Thus, piggy-backing in Kermadec giant limpets could be a strategy that maximises growth and survival, and ensures reproductive opportunities for males, while simultaneously maximising population growth by allowing the largest individuals to be female, and ensuring females have a reliable supply of sperm to fertilise their eggs when they are spawned.

Here, our focus has been on density-dependent population processes. Of course, populations in small isolated locations are dependent on the retention of locally produced offspring, as there is little or no metapopulation connectivity (Liggins et al. 2014). Some of the variation we observed in the size structure of these limpet populations may be due to the sporadic recruitment of limpets and the number of recruitment seasons that have contributed to the

population. A previous genetic study of the Kermadec giant limpet suggests that populations separated by as little as 400 m can be genetically differentiated, and recruiting limpets are predominantly from the local population (Wood & Gardner 2007). The socioecological plasticity we observed in the timing of habitat transitions could be a mechanism to ensure population persistence despite the inherent stochasticity in the recruitment dynamics of Kermadec giant limpet subpopulations.

The Kermadec giant limpet populations at Rangitāhua are the last relict populations of the world's second-largest limpet (Fleming 1973). Although at risk of extinction due to their restricted range, these limpets are common in the lower intertidal zone of these islands, suggesting that their life-history strategies and behaviours ensure a relatively large population size and local retention of offspring. For instance, most hosts had only a single piggy; if piggies are not close kin of their host, these behaviours may ultimately help to maintain genetic diversity within a small population. Furthermore, if the transition to becoming rock-attached at a smaller size when piggies are densely packed is associated with a sex change at a smaller size (or younger age), these behaviours would be indicative of a mechanism to ensure population-level reproductive output is maintained (Wright 1989, Warner et al. 1996, Rivera-Ingraham et al. 2011). Nevertheless, while these limpets appear well suited to life on small remote islands, and although these islands are one of the least human-modified ecosystems on our planet (Edgar et al. 2005), they are not immune to global climatic changes. External environmental factors (e.g. illegal fishing or natural disasters) that affect population composition, and therefore the social environment, can influence the timing of sex change (Martins et al. 2017) and potentially ontogenetic shifts in limpets. Given that Kermadec giant limpets are protandrous and have a skewed gender ratio, such changes could be detrimental to the population-level reproductive success (Martins et al. 2017) and, ultimately, the persistence of the species. Our work has shown that changes to the recruitment dynamics of these limpets or to the survival of larger, typically female limpets will trigger a cascade of interactions affecting this already vulnerable species.

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